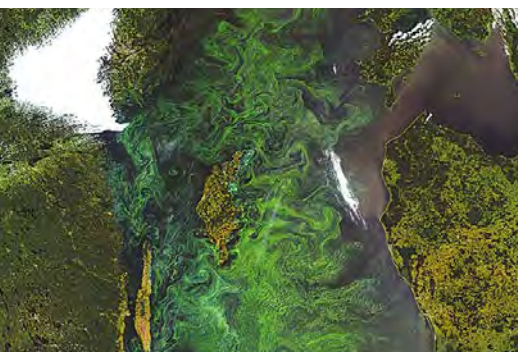




Ocean deoxygenation: Everyone's problem

Causes, impacts, consequences and solutions

Edited by D. Laffoley and J.M. Baxter



IUCN GLOBAL MARINE AND POLAR PROGRAMME



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Foreword

Reports of the impact of warming water on coral reefs from as long ago as 1983 have been recently and rapidly surpassed by much more in-depth knowledge that all parts of the ocean are being transformed by anthropogenic effects driven by ever-increasing greenhouse gas emissions. When IUCN and its members realized the enormity of these issues, we developed a new set of publications to raise global awareness, covering issues like ocean acidification, ocean warming, ocean carbon flows, and ocean plastics. Taken in isolation any one of these areas clearly has negative consequences for the ocean. All these shifts taken together, however, result in a rapid and serious decline in ocean health.



With the build-up of carbon dioxide in the atmosphere, more carbon dioxide is being dissolved in the ocean which is altering the acidity and having large effects on marine ecosystems. In response IUCN has been developing both global, and regional policy work to prepare managers and policy makers to address the issue. Ocean acidification alters the balance of the ocean system. Some species may be more resilient than others, but many are projected to be affected. Some will be unable to tolerate the new conditions, some will cope but at a cost of expending more energy on survival, whilst others will find the new conditions more restricting and may change their distribution or abundance as a result. There are still many unknowns.

Another effect of the build-up of greenhouse gases in the atmosphere is that the planet as a whole is heating up. About 93% of this excess heat from the enhanced greenhouse effect over the past few decades is now stored in the ocean. Such is the scale of heating that it is already affecting all parts of the ocean from inshore to the high sea, from the poles to the tropics and from the surface down to the depths. All forms of marine life are being affected from plankton to whales. Some of this has been known for a long time, for example coral bleaching causing the decline of reefs around the planet, but increasingly we are also starting to see shifts in many other ecosystems. This is leading to changes in community composition, changes in abundance, shifts in distribution and changes in predator/prey relationships. Again this is leading to a complex picture of change, and impacts and effects on one species may be very different to the next.

The ocean is also a key part of the carbon cycle. Until IUCN produced our report on coastal carbon sinks in 2009 there was little awareness of the critical role that coastal ecosystems play in trapping and sequestering carbon. Up until then the story was mostly about forests and soils rather than what happens at the coast and in the sea. Much more awareness still needs to be raised and action needs to be taken to respect the role marine ecosystems and species have in maintaining the carbon cycles.

Pollution flowing into the ocean is also increasing and can be a driver for change. Whilst the public is now largely aware of this as an issue of global concern few realize the magnitude of what we have done. Plastic particles are now so widespread in the ocean that they have been accumulating in sea ice, resulting in a shift in seasonal melting patterns. With less sun reflection from ice cover at sea, the absorption of heat accelerates at the poles and speeds up climate change in the ocean. This positive feedback has consequences for many polar species but also for the planet as a whole. The link between plastic pollution and climate shifts is not yet well understood, so developing more work and a deeper understanding of this issue and preventative measures will be a priority in the future.

On top of these problems is then the topic of this current report. Having sufficient available oxygen in the air or water is of paramount importance to most living organisms. As this report describes in some detail, oxygen levels are currently dropping across the ocean. Several drivers are responsible for this decline, but the root causes are nutrient run-off from land now coupled with the significant warming of sea water, resulting from build-up of greenhouse gases. As the following pages show in great detail one of the major consequence of this is habitat compression and reduction in suitable habitat for many species. This leads to migration of species, increased vulnerability of species of conservation or commercial concern, reductions in abundance, and accordingly an overall reduction in ocean resilience.

Solutions to ocean deoxygenation and development of adaptation strategies depend on sound knowledge. Progress is now starting to be made in understanding the causes, consequences and future patterns of ocean oxygen decline. Widespread awareness also is key. Natural and social science advances are critical to increasing the recognition of ocean deoxygenation as an important consequence of human alterations to our global environment and the impacts it will have on human welfare.

The sense of urgency to improve the ocean health has never been greater. With this new report our aim is to complement the recent IPCC Special Topic report by providing a ‘deep dive’ into the issues surrounding ocean deoxygenation. We hope by providing sound science to better inform policy and decision makers, this will help them in turn develop and adopt adaptation and mitigation strategies in the face of such new realities. Without a doubt more concerted global action is required now to reverse the direction of ocean degradation.

Ocean deoxygenation is perhaps the ultimate wakeup call on how ignoring the ocean jeopardizes the interests of us all, but particularly future generations. Ocean deoxygenation will not be easy to reverse, but the costs of doing so clearly must outweigh the costs of any inaction for all our sakes.



Minna Epps
Director



Carl Gustaf Lundin
Principal Scientist

IUCN Global Marine and Polar Programme

Preface

At any given moment, up to 97% of the world's water resides in the ocean. Whether you live by the sea or far from it, eat seafood or not, the future of all of us depends on a healthy ocean. Saving our ocean and the life below the surface is a matter of our survival.

Our ocean has not been getting the attention it deserves, until now, in spite of the vital functions it bestows. The ocean generates more than half the oxygen we breathe. By absorbing over a quarter of the excess carbon dioxide generated from the burning of fossil fuels and by absorbing most of the excess heat and the ocean has, until now, shielded us from the worst impacts of climate change.

Now, imagine sucking the oxygen out of the ocean. We have global evidence of deoxygenation and it's scary. Over the past 50 years, global dissolved oxygen in the ocean has decreased by ~2% and scientific data indicate that this trend is set to continue. The number of reported sites affected by low oxygen conditions has dramatically increased during the last few decades. Increased river export of nitrogen and phosphorus has resulted in eutrophication in coastal areas worldwide. Take the Baltic Sea for example; oxygen depletion near the sea bed has resulted in extensive dead zones.

Whilst we have known about dead zones in the ocean for many decades, ocean warming is now expected to further amplify deoxygenation across great swathes of the ocean. Deoxygenation affects many aspects of the ecosystem services provided by the ocean and coastal waters. The ocean is the primary source of protein for more than 1 billion people around the world. Ocean deoxygenation will have socio-economic implications, as it will affect fisheries and, the abundance and distribution of certain species, thereby changing ecosystem dynamics. Ocean deoxygenation is putting life at risk. Failing to protect our ocean will jeopardize humankind, as our security, economy and our very own survival depends on it.

We must start to address the challenge of reversing the decline in oxygen in the ocean. Stakes are high and stocks are low – we need to recognize the challenge and work together to get the ocean oxygen budget back in balance. This is why Sweden supports cutting-edge ocean research on the scale of our impacts, to strengthen proposed adaptations and solutions to declining ocean oxygen. The urgency, complexity and geographical extent of ocean deoxygenation requires that the best science from across the globe be used if we are going to slow and reverse ocean oxygen decline. To date this has been a topic that mainly concerned a few scientists, but should now concern and occupy all of us.

With this report its time to put ocean deoxygenation among our top priorities to address climate change and restore ocean health. Our welfare and that of future generations depend on it. The societal cost of inaction is too great to ignore. International and regional collaboration in science, policy development and implementation are critical to getting the ocean oxygen budget right.



Ms. Isabella Lövin
Minister for Environment and Climate, and Deputy Prime Minister of Sweden

Preface

Just over fifty years ago, thanks to our intrepid astronauts, humanity looked back at Earth from the moon and saw the first colour photos of our planet from afar - blue, beautiful, finite, and seemingly hanging in the dark void of space. Since then, our collective fascination and innovation have taken our discoveries well beyond the moon, to explore distant planets, the outer reaches of our solar system, and beyond.

In so doing, in my view we have taken for granted a basic element of our existence. For too long we have neglected the blue heart of our own planet; the heart that maintains the balance of conditions for the fostering and support of the universe's rarest of commodities - life.

Realization of the need for the marriage of policy and action to properly safeguard life on Earth is, surprisingly, only just getting underway. Until very recently, the focus has always been on what happens on land, rather than what is affecting the source of life on this planet - the ocean. This has been short-sighted of us, for science now shows how the ocean buffers us from the extremes of climate change, helps shape and drive our weather, and provides food, inspiration and a myriad of socio-economic benefits to sustain us all.

And it is only in the last decade that we have realized how humanity's actions are having such a profound impact on the ocean's well-being. This ranges from how our carbon emissions are driving the ocean to hotter and more acidic conditions, through to how our everyday actions can dramatically influence and change marine life and the food chain of which we are all part. I am in particular referring to issues such as overfishing, chemical pollution from the products we use in agriculture, industry, and cosmetics, and of course plastic pollution.

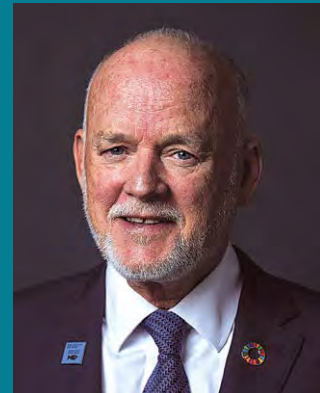
But perhaps the key question we should all be asking is: have we yet realized the true scale of the impact that we're having on the ocean as our planetary life support system? I for one think not.

To assist in improving our perception of that scale of impact, I am particularly pleased to welcome this new study on ocean deoxygenation, which is, as far as I'm aware, the first global in-depth study on this critical subject. I believe it provides a new perspective on the scale of our impacts, thereby logically leading us, with a greater sense of urgency, to much higher levels of ambition for the restoration of respect and balance to our relationship with the ocean and the planet.

We were taught at school that hotter liquids contain less gas, and the ocean and the oxygen within it are no exception to this rule. This report clearly shows that with the heating of the ocean, the quantity of life-giving oxygen within it is dropping.

Of all reports, this one needs to be heeded urgently. Regardless of nationalities, ideologies, wealth or situation, the message of this report is everyone's business, everyone's challenge to overcome.

By cataloguing the progressive impacts and changes already underway in the ocean, I believe the report demonstrates that the next ten years will be more important for humanity than the last hundred, indeed thousands of years have been for our survival. Please read it, then play your rightful part in the communal decision-making processes necessary for the future well-being of all life on planet Earth.



A handwritten signature in white ink, appearing to read 'Peter Thomson', written in a cursive style.

Ambassador Peter Thomson
United Nations Secretary General's Special Envoy for the Ocean

Executive summary

Breathing water is hard work as a given volume of water holds far less oxygen than the equivalent volume of air. This makes the physiological performance and behavioural repertoire of marine organisms heavily dependent on their ability and capacity to extract oxygen from the ambient sea water. Ocean deoxygenation generally affects marine organisms as soon as conditions depart from full aeration, with downstream consequences on their activities and capacity to face natural contingencies. The importance of maintaining adequate levels of oxygen in the ocean is perhaps best summarized by the motto of the American Lung Association: “if you can’t breathe nothing else matters”.

Whilst the focus of actions on trying to clean-up the ocean is on the impacts from pressures such as fishing, pollution, habitat destruction, invasive species and plastic, there is no environmental variable of such ecological importance to marine ecosystems that has changed so drastically in such a short period of time as a result of human activities as dissolved oxygen. Hypoxia - a condition that deprives an organism of adequate oxygen supply at the tissue level - is one of the most acute symptoms of the reduction in dissolved oxygen. The present-day losses of oxygen in the ocean - ocean deoxygenation - is starting to progressively alter the balance of life, favouring hypoxia- tolerant species at the expense of hypoxia sensitive ones.

Working with 67 scientific experts from 51 institutes in 17 countries, what is presented here is the largest peer-reviewed study conducted so far on ocean deoxygenation. Expressed in the words of the world’s leading scientists on this topic it shows the inescapable fact human activities are now driving life sustaining oxygen from our ocean-dominated planet. Society needs to wake up - and fast - to the sheer enormity of detrimental changes we are now causing to the Earth’s regulatory systems, and the now near-monumental efforts that will be needed by governments and society

to overcome and reverse such effects. This report is probably an underestimation of what is happening now. Science is incomplete and awareness of ocean deoxygenation is just happening, but what is already known is very concerning.

The loss of oxygen in the ocean can broadly be put down to two overlying causes – eutrophication as a result of nutrient run-off from land and deposition of nitrogen from the burning of fossil fuels, and the heating of ocean waters as a result of climate change, primarily causing a change in ventilation with the overlying atmosphere so that they hold less soluble oxygen, and compounded by reduced ocean mixing and changes in currents and wind patterns. Ocean deoxygenation is but the latest consequence of our activities on the ocean to be recognized. Ocean warming, ocean deoxygenation, and ocean acidification are major ‘stressors’ on marine systems and typically co-occur because they share a common cause.

Increasing carbon dioxide emissions into the atmosphere simultaneously warm, deoxygenate, and acidify marine systems, whilst nutrient pollution also contributes to increases in the severity of deoxygenation and acidification. As a result, marine systems are

currently under intense and increasing pressure from the cumulative effects of these multiple stressors, and with current sustained trajectories expected for greenhouse gas emissions the changes in the ocean will only continue and intensify. Awareness of these phenomena, on top of existing issues such as overfishing, pollution and habitat destruction, has begun to trigger significant concern on the impacts on marine biodiversity and the functionality of the ocean as a whole, and how this may influence factors such as weather, crop success and water supplies, and then affect people everywhere.

In the last 65 years we have come to realize that over-enrichment of waters with nutrients or organic matter (eutrophication) is a problem that threatens and degrades coastal ecosystems, alters fisheries, and impacts human health in many areas around the world. Over 900 areas of the ocean around the world have already been identified as experiencing the effects of eutrophication. Of these, over 700 have problems with hypoxia, but through improved nutrient and organic loading management on adjacent land about 70 (10%) of them are now classified as recovering. The global extent of eutrophication-driven hypoxia and its threats to ecosystem services are well documented, but much remains unknown as to the long-term human health, social, and economic consequences.

What is particularly new with this report is the additional focus on the more recently recognized effect of lowered oxygen resulting from ocean warming, which is now affecting enormous areas of the ocean. The atmospheric warming resulting from greenhouse gas emissions being taken up in ocean water is now driving vast changes in the physical and biological make-up of the sea. The two causes also interact, with warming-induced oxygen loss tipping coastal areas into eutrophication-driven hypoxia and may contribute to the dramatic increase in regards of coastal hypoxia. The combination of eutrophication-driven hypoxia, which can be relatively easily and quickly reversed if the necessary measures are put in place, and hypoxia due to climate change driven warming, that can't easily be reversed - if at all - is causing the emergence of ocean deoxygenation as a new issue of global significance.

At regional to local scales the overall concerns about ocean deoxygenation are further exacerbated by outbreaks of Harmful Algal Blooms. The development of hypoxic or anoxic waters is regularly listed as one

of the consequences of algal blooms. Such events of low oxygen associated with harmful algal blooms are characterized by high initial oxygen concentrations, exceptional rates of respiration following bloom senescence and short timescales. The coastal environments subject to high biomass harmful algal blooms and associated events of low oxygen are typified by elevated inorganic nutrients because of either natural or cultural eutrophication.

In the short term, marine organisms respond to ocean deoxygenation through changes in their physiology and behaviour. Alteration in feeding behaviour and distribution pattern are classically observed, potentially leading to reduced growth and to more difficulties completing their life cycle. Vertical habitat compression is also predicted for organisms in the upper ocean. In the medium term, epigenetic processes (non-genetic influences on gene expression) may possibly provide marine populations with a rapid way to acclimate to the rapidly changing oxygenation state. However, this developing field of biological sciences is too recent for a full evaluation of the contribution of epigenetic responses to marine organisms' adaptation to ocean deoxygenation to be made. Changes in the phenology (timing of life stage-specific events) of marine species, related to ocean deoxygenation have not yet been observed. However, deoxygenation generally co-occurs with other environmental disturbances (ocean warming and acidification) which are also liable to affect marine species' life cycles. The lack of understanding of their interactions and synergies currently restricts our ability to assess marine populations' capacity to phenologically respond to ocean deoxygenation.

The overall consequences of perturbations to the equilibrium state of the ocean-atmosphere system over the past few decades are that the ocean has now become a source of oxygen for the atmosphere even though its oxygen inventory is only about 0.6% of that of the atmosphere. Different analyses conclude that the global ocean oxygen content has decreased by 1-2 % since the middle of the 20th century. There is good evidence that ocean temperature increases explain about 50% of oxygen loss in the upper 1000 m of the ocean, but there is less confidence of the knock-on effect on respiration – another factor to explain lowered oxygen. Less than 15% of the oxygen decline can be attributed to warming-induced changes in respiration of particulate and dissolved organic matter.

Most of the oxygen loss has been caused by changes in ocean circulation and associated ventilation - gas exchange - from the ocean into the atmosphere with oxygen from the ocean surface. As the ocean warms from the surface, stratification is expected to increase, with a tendency for a slowing down of the ocean circulation. A slowed down circulation is expected to account for up to 50% of the observed deoxygenation in the upper 1000 m, and for up to 98% in the deep ocean (> 1000 m depth). Spatial patterns and individual mechanisms are not yet well understood. The current state-of-the-art models available predict deoxygenation rates only half that of the most recent data-based global estimates. Human activities have altered not only the oxygen content of the coastal and open ocean, but also a variety of other physical, chemical and biological conditions that can have negative effects on physiological and ecological processes.

Further climate-driven warming of bottom waters may also result in enhanced destabilization of methane gas hydrates, leading to enhanced release of methane from sediments, and subsequent aerobic respiration of methane to carbon dioxide. There is, however, little observational evidence for a warming-induced acceleration of methane release taking place already. As the ocean continues to warm, it will lose yet more oxygen due to the direct effect of temperature on gas solubility, as warmer waters hold less soluble gas. Additionally, reductions in vertical mixing associated with enhanced upper-ocean buoyancy stratification will also occur leading to respiration-driven oxygen depletion at depth. The ocean as a whole is expected to lose about 3–4% of its oxygen inventory by the year 2100 under a “business-as-usual” scenario (RCP8.5) with most of this loss concentrated in the upper 1000 m where species richness and abundance is highest.

The future intensification and expansion of low oxygen zones (LOZ) can have further ecosystem consequences as oxygen dependent cycling of elements by microbes alter the supply of nutrients or in extreme cases, lead to increased production of toxic hydrogen sulphide gas. Low oxygen conditions and increased temperature jointly limit the viable habitat for marine macro-organisms. Continued ocean warming accompanied by deoxygenation will drive habitat contraction and fragmentation in regions where oxygen levels decline below metabolic requirements. Expansion of suboxic zones will likely disrupt the cycling of nitrogen in the

ocean; denitrification may increase, yielding greater rates of fixed nitrogen loss from the ocean. Perturbations to the nitrogen cycle may include substantial changes to nitrous oxide production, though this is currently highly uncertain.

It is predicted that there will be distinct regional differences in the intensity of oxygen loss as well as variations in ecological and biogeochemical impacts. There is consensus across models that oxygen loss at mid and high latitudes will be strong and driven by both reduced solubility and increased respiration effects. Projections are more ambiguous in the tropics, where models suggest that there will be compensation between oxygen decline due to reduced solubility and oxygen increase caused by reductions in cumulative respiration. Thus, oxygen concentrations in the core of present-day oxygen minimum zones may increase; however, the total volume of waters classified as “suboxic” and “hypoxic” is still likely to grow substantially.

While the biogeochemical and physical changes associated with ocean warming, deoxygenation and acidification occur all over the world’s ocean, the imprint of these global stressors has a strong regional and local nature. Perhaps the most familiar areas subject to low oxygen are the Baltic Sea and Black Sea. These are the world’s largest semi-enclosed low oxygen marine ecosystems. While the deep basin of the Black Sea is naturally anoxic, the low oxygen conditions currently observed in the Baltic Sea have been caused by human activities and are the result of enhanced nutrient inputs from land, exacerbated by global warming. The impacts of deoxygenation are not though limited to enclosed seas. The eastern boundary upwelling systems (EBUS) are some of the ocean’s most productive biomes, supporting one fifth of the world’s wild marine fish harvest. These ecosystems are defined by ocean currents that bring nutrient rich but oxygen-poor water to coasts that line the eastern edges of the world’s ocean basins. As naturally oxygen-poor systems, EBUS are especially vulnerable to any changes in global ocean deoxygenation and so what happens to the oxygen content of EBUS ultimately will ripple out and affect many hundreds of millions of dependent people.

Oxygen limited waters, hypoxic and even anoxic conditions are now found in many coastal areas in the Atlantic Ocean including in connected seas like the Mediterranean, the Gulf of Mexico, and as previously

mentioned the Black Sea, and Baltic Sea. Alongside this, large ocean basins such as the equatorial and southern Atlantic are being affected by decreasing oxygen levels, although studies show that such conditions were present in deep waters long before anthropogenic activities started to have an influence on the marine environment. In addition to many coastal waters of the Atlantic, oxygen limited waters are also found at mid-water depths in most of the Atlantic Ocean basins, usually at 300 to 1000m. The oxygen concentrations in these areas have decreased during the last 60 years, partly due to ocean warming, partly as a result of decreased mixing and ventilation.

Elsewhere the low-oxygen zones of the Indian Ocean are expected to continue to expand and intensify. There does, however, remain a critical lack of information from potential hotspots for deoxygenation, including the mouths of the Indus, Ganges-Brahmaputra, and Irrawaddy rivers. Thus, pictorial representations of the current extent of ocean deoxygenation almost certainly underplay the effects being experienced in the world ocean. Capacity building and networking are needed to expand/improve monitoring of deoxygenation and other impacts of global change in the ocean.

It is currently difficult to predict - if at all – whether marine species will be able to adapt successfully to the changes now being observed in dissolved ocean oxygen. In the long term, adaptation through natural selection may occur in species with very short generation times. This is, however, far more difficult to envisage in most commercial fish species which are characterized by long generation times, especially given the fast-changing ocean conditions.

This report should accordingly be of interest and concern to everyone. It is intended to spur additional interest in the underlying research needed, especially as we are about to enter the United Nations Decade of Ocean Science for Sustainable Development (2021-2030). The focus of this decade is to support efforts to reverse the cycle of decline in ocean health, so awareness of ocean deoxygenation is very timely. The Decade of Ocean Science is also intended to align ocean stakeholders worldwide behind a common framework that will ensure ocean science can fully support countries in creating improved conditions for sustainable exploitation of the ocean.

The scientific community is already concerned about and acting on ocean deoxygenation. The Intergovernmental Oceanographic Commission of UNESCO (IOC-UNESCO) established the Global Ocean Oxygen Network (GO₂NE), which is committed to providing a global and multidisciplinary view of deoxygenation, with a focus on understanding its multiple aspects and impacts. It is this network which has largely contributed to the production of this report. At a recent Ocean Deoxygenation Conference the 300 attending scientists from 33 countries published the “Kiel Declaration”. This Declaration, with the subtitle ‘the ocean is losing its breath’, calls on all nations, societal actors, scientists and the United Nations to raise global awareness about ocean deoxygenation, take immediate and decisive action to limit pollution and in particular excessive nutrient input to the ocean, and to limit global warming by decisive climate change mitigation actions. This Declaration now needs to be heard loud and clear by policy advisers, decisions makers ocean users and the general public.

This report on ocean deoxygenation is perhaps the ultimate wake-up call needed to dramatically raise our ambitions to tackle and immediately curb our emissions of carbon dioxide and other powerful greenhouse gases such as methane. This is needed before human actions irreparably impact and change the conditions favourable for life on earth, and that drive and underpin the natural values we all hold close in our daily lives.

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Glossary

Acidification: Ongoing decrease in the pH of the ocean caused by the uptake of carbon dioxide from the atmosphere.

Adaptation: An adjustment of natural or social systems which moderates harm or exploits opportunities for benefit.

Adaptive capacity: The ability of a natural or social system to adjust to accommodate environmental hazards or policy change and to expand the range of variability with which it can cope. In natural systems, adaptive capacity is determined by factors such as genetic diversity of species, the geographical range of a population, species or biome, and the biodiversity of particular ecosystems. In social systems, adaptive capacity is determined by a group's social, human, material, and natural capital and power differentials play an outsized role.

Adenosine triphosphate – ATP: The chemical energy 'currency' of the cell that powers all metabolic processes.

Anoxic Marine Zone – AMZ: Areas of the ocean totally depleted of oxygen.

Anammox: An abbreviation for anaerobic ammonium oxidation. A microbially mediated process through which ammonium is oxidized by nitrite to form N_2 . Anammox is responsible for a substantial part of the loss of fixed nitrogen in the ocean (~up to 50%, Kuenen, 2008).

Anoxia: Waters with totally depleted oxygen levels (i.e. below the detection limit of sensors).

Anthropogenic fertilization: Otherwise known as ocean fertilization or ocean nourishment, it involves the introduction of nutrients that would otherwise be limiting into the upper ocean to increase productivity and help remove carbon dioxide from the atmosphere.

Axenic: A culture of a single species in the absence of all others.

Bathypelagic: The water column that extends from a depth of 1000 to 4000m below the ocean surface.

Benthos: The community of organisms that live on, in or near the sea bed.

Billfishes: Group of predatory fish characterized by prominent bills or rostra and large size, include sailfish, marlin and swordfish.

Biogeochemical pathway: The process by which a chemical substance moves through biotic and

abiotic (lithosphere, atmosphere and hydrosphere) compartments of Earth.

Bioherms: An ancient reef or mound like structure built by a variety of marine invertebrates such as corals, echinoderms, molluscs and calcareous algae.

Biomass: Collective term for all plant and animal material.

Canonical threshold: An invariant of singularities in algebraic geometry.

Catch per unit effort – CPUE: An indirect measure of the abundance of a target species in fisheries.

Chemosynthesis: The biological conversion of one or more carbon-containing molecules and nutrients into organic matter using the oxidation of inorganic compounds or methane as a source of energy rather than sunlight.

Chemosynthetic symbionts: The partnership between invertebrate animals and chemosynthetic bacteria. The bacteria are the primary producers providing most of the organic carbon needed for the animal host's nutrition.

Coastal ocean: The coastal ocean here encompasses the river-estuary-ocean continuum, strongly influenced by their watershed while the 'open ocean' refers to waters where such influences are secondary.

Continental margin: The shallow water area found in proximity to the land consisting of the continental rise, the continental slope and the continental shelf.

Dead zones: A name commonly used when referring to hypoxic ecosystems because of early observations by fishers that traps came up empty or filled with dead fish and crabs, although typically some life remains in these areas.

Demersal: Found in deep water or on the sea bed.

Denitrification: The process of the reduction of nitrates to nitrites, nitrous oxide or nitrogen by microbes under anaerobic conditions.

Denitrifying bacteria: A diverse group of bacteria capable of performing denitrification as part of the nitrogen cycle.

Deoxygenation: The reduction in oxygen content of the ocean due to anthropogenic effects.

Diapause: A period of suspended development in response to regularly and recurring periods of adverse environmental conditions.

Diazotrophs: Bacteria and archaea that fix atmospheric nitrogen gas into a more useable form such as ammonia.

Dissolved organic matter – DOM: The fraction of total organic carbon that ranges in size from 0.22 to 0.7 μm .

Dissolved oxygen – DO: The oxygen that is dissolved in water.

Eastern boundary upwelling systems – EBUS: Regions located in equatorial and coastal regions of the eastern Pacific and Atlantic oceans where nutrient rich waters from the deep ocean are brought to the surface, often associated with highly productive areas.

Ecosystem services: The range of benefits the natural environment provides to humans and which can be translated into human well-being via social systems.

Ectotherms: Organisms in which internal physiological sources of heat are of relatively small or negligible importance in controlling body temperature, i.e. cold-blooded.

Emission scenarios: Possible pathways that society might take in the emission of greenhouse gases in the future used to make projections of possible future climate change.

Epigenetic processes: The external modification to DNA that turn genes 'on' or 'off'. These do not change the DNA sequence but simply affect how cells 'read' genes.

Epithelium: One of the four basic types of animal tissue along with connective tissue, muscle tissue and nervous tissue. Epithelial tissue lines the outer surfaces of organs and blood vessels as well as the inner surfaces of cavities in many internal organs.

Equilibrium state: In a chemical reaction it is the state in which both reactants and products are present in concentrations which have no further tendency to change, so that there is no observable change in the properties of a system.

Euphotic zone: The surface layer of the ocean that receives sufficient light for photosynthesis to occur, extending to 200 m depth.

Eutrophication: When a body of water becomes overly enriched with minerals and nutrients which induce excessive growth of algae that can result in oxygen depletion and ultimately hypoxia or anoxia.

Euxinic zone: Basin where the anaerobic decomposition of organic matter occurs through sulphate reduction with the production and accumulation of dissolved sulphide.

Exposure: The nature and degree to which a system experiences environmental or socio-political stress; characteristics of stress include their magnitude, frequency, duration and areal extent of the hazard.

Fixed nitrogen: Nitrogen that is directly available for primary production (bioavailable nitrogen).

Global oxygen inventory: A record of the levels of consumption and production of oxygen in the global oxygen cycle.

Hypoxia: This is a relative term with no strict definition or associated value. A definition of hypoxia based on oxygen concentration (e.g. $\mu\text{mol kg}^{-1}$) rather than oxygen partial pressure (i.e. PO_2 kPa) is not useful because solubility changes with temperature, influencing the PO_2 and the driving force for diffusion across biological membranes.

Hypoxic zone: Areas of the ocean where oxygen levels are so low (i.e. $< 2 \text{ mg O}_2 \text{ L}^{-1}$) that most marine life is unable to survive.

Indian Ocean Dipole - IOD: Also known as the Indian Niño, is an irregular oscillation of sea-surface temperatures in which the western Indian Ocean becomes alternately warmer and then colder than the eastern part of the ocean.

Low Oxygen Zone – LOZ: A region where the oxygen concentration reaches a certain threshold below which living organisms and biogeochemical processes may be impacted. Although this threshold differs between organisms, a threshold value of $61 \mu\text{mol O}_2 \text{ kg}^{-1}$ is used for the coastal zone while a value of $20 \mu\text{mol O}_2 \text{ kg}^{-1}$ is typically used for the open ocean.

Macroalgae: Collective term for seaweeds that are generally visible to the naked eye.

Macro-organisms: Collective term for organisms that are generally visible to the naked eye.

Meiofauna: Collective term that defines organisms by their size, larger than microfauna but smaller than macrofauna. Typically organisms that can pass through a 1mm sieve but are caught by a $45 \mu\text{m}$ sieve.

Mesopelagic: Otherwise known as the twilight zone – that part of the water column that lies between 200 m and 1000 m depth.

Mesopelagic fauna: The animals that are found in the water column between 200 m and 1000 m depth.

Mesopelagic micronekton: Relatively small but actively swimming organisms consisting mainly of decapod crustaceans, small cephalopods and small fish.

- Metabolic demands:** The amount of energy used by organisms to perform basic functions under differing conditions.
- Metabolic rate:** The rate of aerobic energy usage, estimated from oxygen consumption and expressed in mass-specific units - $\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$.
- Metazoans:** All animals having a body composed of cells differentiated into tissues and organs and usually a digestive cavity lined with specialized cells.
- Methane gas hydrates:** A solid compound in which a large amount of methane gas molecules are caged within a crystalline structure of water under low temperature and high pressure forming a solid similar to ice.
- Mitochondria:** The organelles that convert oxygen and nutrients into ATP which is used to power the cell's metabolic activities.
- Net primary production – NPP:** The amount of organic material available to support consumers (i.e. herbivores and carnivores).
- North Atlantic Oscillation – NAO:** The primary source of climate variability on interannual to decadal time scales over the North Atlantic region.
- Nitrogen fixation:** The process by which microbes can convert unreactive diatomic nitrogen into a usable reactive form.
- Oceanic stratification:** Water masses with different properties – salinity, oxygenation, density, temperature – form layers that act as barriers to water mixing.
- Orographic effects:** A change in atmospheric conditions caused by a change in elevation, primarily due to mountains.
- Oxycines:** A sharp gradient in oxygen concentration.
- Oxygen Minimum Zones – OMZ:** Regions of the open ocean located between 100-1000 m where the oxygen concentrations are particularly low. Usually, a threshold of $20 \mu\text{mol O}_2 \text{ kg}^{-1}$ is used.
- Oxygen partial pressure – PO_2 :** Expressed in units of kilopascals (kPa), this represents the portion of the pressure exerted by gas in sea water that is attributed to oxygen. At air saturation the PO_2 is 21% of the total, or -21kPa.
- Oxitaxis:** The movement or orientation towards to supply of oxygen.
- Pressure and Release (PAR) Model:** A theoretical framework rooted in political ecology that presents a group's level of risk as a product of the level of natural hazards experienced combined with the level of the group's vulnerability to those hazards. Vulnerability is considered to result from a social progression of root causes that lead to dynamic pressures, which result in unsafe conditions.
- Pacific Decadal Oscillation – PDO:** Results in an intensification of westerlies over the central North Pacific, which leads to a cooling over much of the subpolar central and western Pacific and a warming in the eastern North Pacific.
- Palaeoecology:** The study of interactions between organisms and / or interactions between organisms and their environments across geologic timescales.
- Pelagic:** The zone of the water column of the open ocean that is neither close to the bottom nor near to the shore.
- Photorespiration:** The process of light-dependent uptake of molecular oxygen concomitant with release of carbon dioxide from organic compounds.
- Photosynthesis:** The chemical process by which plants convert light energy, carbon dioxide and water into chemical energy.
- Phytoplankton:** The photosynthetic members of the plankton.
- Phytoplankton blooms:** A rapid increase or accumulation in the population of microscopic algae typically resulting in discoloration of the water and often involving toxic or otherwise harmful species.
- Powerful greenhouse gas:** Methane and nitrous oxide are two heat-trapping gases 30 and 300 times more potent than carbon dioxide.
- Primary production:** The synthesis of organic compounds from atmospheric or aqueous carbon dioxide.
- Protozoans:** Single-celled eukaryotes (organisms whose cells have nuclei) that commonly show characteristics usually associated with animals, notably mobility and heterotrophy.
- Reactive oxygen species - ROS:** A type of unstable molecule that contains oxygenated that easily reacts with other molecules with a cell.
- Redox potential:** A measure of the ease with which a molecule will accept electrons (called reduced); the more positive the redox potential, the more readily a molecule is reduced.
- Remineralization:** The breakdown or transformation of organic matter into its simplest inorganic forms, thus liberating energy and recycling matter to be reused as nutrients.
- Resilience:** The capacity to absorb disturbance and maintain essential function.
- Respiration:** The production of energy, typically with the intake of oxygen and the release of carbon dioxide from the oxidation of complex organic substances.
- Saturation level:** The gas concentration that a water mass would attain if it were to equilibrate with the atmosphere at its *in-situ* temperature and salinity. At equilibrium sea water is 100% saturated. If the percentage of saturation is greater (respectively lower)

than 100, the sea water is super- (respectively under-) saturated. If the ocean surface is over- (respectively under-) saturated in oxygen, the oxygen will undergo a net transport from the ocean (respectively the atmosphere) to the atmosphere (respectively the ocean) until its aqueous concentration reaches its equilibrium level defined by the saturation level.

Sea Surface Temperature – SST: The water temperature close to the ocean's surface.

Seicheing: A periodic oscillation of the surface of an enclosed or semi-enclosed body of water caused by such phenomena as atmospheric pressure changes, winds, tidal currents, etc.

Sensitivity: The degree to which a system is modified or affected by perturbations. In social terms, this reflects the degree to which a group of people depends on or benefits from an ecosystem service and will, thus, be affected by its increased or reduced availability.

Solubility: Oxygen solubility is the amount oxygen (e.g. volume or concentration) that dissolves in one litre of sea water when the sea water is equilibrated with 1 atm of O₂.

Sorption: A physical and chemical process by which one substance becomes attached to another.

STOX: The STOX microsensor is a specialized oxygen sensor that allows you to measure ultra low oxygen concentrations in the laboratory or *in situ*. The STOX sensor has been used to demonstrate that oxygen concentration in the oxygen minimum zone of Peru contains less than 2nM oxygen.

Stratification: The formation of layers of water based on salinity or temperature differences.

Suboxic: Areas of the ocean where oxygen levels are extremely low i.e. <0.3 mg O₂ L⁻¹.

Sulphidic basin: Where the anaerobic decomposition of organic matter occurs through sulphate reduction with the production of dissolved sulphide trophic cascades.

Terminal Electron Acceptors - TEA: A compound that receives or accepts an electron during cellular respiration or photosynthesis.

Units of oxygen concentration: Most often oxygen concentrations are reported in μmol O₂ kg⁻¹ because these units are independent of temperature, salinity and pressure, but volumetric concentration units like ml O₂ L⁻¹, μmol O₂ L⁻¹ or mg O₂ L⁻¹ can also be used. When addressing the physiological state of animals, the oxygen level is expressed in partial pressure units (kPa or μatm) or saturation values because the partial pressure is the thermodynamic driving force for molecular transfer through tissue.

Upwelling: An oceanographic phenomenon that involves wind-driven motion of dense, cooler and usually nutrient-rich water towards the ocean surface replacing the warmer, usually nutrient depleted surface water.

Varved sediment [core]: A varve is an annual layer of sediment or sedimentary rock.

Vulnerability: The level of susceptibility to a hazard; determined by the exposure and sensitivity to the hazard, and adaptive capacity.

Well-being: Reflects the level of personal and social functioning and consists of five primary qualities: (1) basic material for a good life, (2) health (mental and physical), (3) good social relations, (4) security, and (5) freedom of choice and action. Well-being is the ultimate value people derive from ecosystem services.

Zooplankton: Floating and drifting animal life.

Editors' introduction

History shows that there is not a steady and progressive change in our knowledge about the ocean. Over the past few decades as editors and scientists we have been involved in some notable step changes in knowledge. Back in 2004 we became involved in what was then called surface ocean acidification - latterly now called simply ocean acidification - as the true depth of changes it is having to the ocean have become apparent. This was at a time before the words were even a search term in Google, and it has led us to help champion the issue ever since, working alongside many scientists from around the world.



In 2009 we were then involved in a landmark report on coastal and marine carbon sinks - latterly known as blue carbon. This was instrumental in and has helped ignite an interest in safeguarding some of the most threatened ecosystems such as mangroves, saltmarshes and seagrass meadows and more recently acknowledgement of the importance of seabed sediments and various biogenic habitats as long-term carbon stores. It has helped drive a recognition in the climate change world that actions without the ocean will simply not solve the climate fix we find ourselves in.

In 2016 we worked again with leading scientists this time to bring attention to the threats posed by ocean warming. Up to that point ocean warming was an issue which had been acknowledged but not really recognized as a key threat to the quality and persistence of life on earth. In what has now become one of the most downloaded reports in recent history of IUCN, we set out the scientists' views on what warming (or as might now more correctly called - ocean heating) are having on ocean health and well-being, and how this could ripple out to affect all of life on earth. Unfortunately, and alarmingly, in the few years since that publication was launched, some of the predictions made by the scientists started to materialize. Ocean warming is becoming an all to present concern and impact for many societies around the world. For example, coral bleaching and kelp forest die-offs are becoming a too frequent and regular norm, storms are becoming stronger and more intense, and species are moving, affecting coastal communities as well as other species that depend on them.

In light of the ocean warming report we were approached by the co-chairs of the IOC's ocean deoxygenation network (GO2NE) to see if we would also help raise awareness of this topic at a global scale. For us, in realizing the enormity of what is now taking place in the ocean, this became not just an overriding imperative but a personal mission to make this happen. We are delighted therefore to bring this latest volume to fruition. It represents the most comprehensive review to date on ocean deoxygenation. To build up the report, leading scientists from around the world were invited to join with colleagues to contribute

individual chapters. Each has been subject to peer review and tells in the scientist’s own words the scale and nature of the changes being driven by ocean deoxygenation, often in association with other stressors, such as ocean warming. It has been a great privilege to work with them and we hope that in the following pages we have done justice to their efforts. We also thank them for their persistence with us to make this peer reviewed report happen. The report as a whole represents today’s state of science on ocean deoxygenation. Whilst clear gaps in science, capabilities and understanding remain we already know enough to be very concerned. A keen eye will see that there is a degree of duplication across chapters in this report. This is because the report has been designed, through experience, so that each chapter can be read in isolation or as part of an overall story. This thus enables readers in the following 588 pages to easily dip into specific aspects of ocean deoxygenation that have a particular relevance to them whilst still retaining an overview.

The gap between a world that supports all life, and a changed world which will provide less benefits and support fewer people has significantly narrowed just within the last few years. Professor Bob Watson, when summing up the findings of the recent intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) report documenting the likely extinction of a million species, many within decades, said ‘boy are we in trouble’. Factor in ocean acidification, ocean heating, and now ocean deoxygenation, and perhaps that quote should be reset as ‘boy are we in deep, deep trouble’.

We hope that this report, and the accompanying slimmer Summary for Policy Makers, will raise informed concern and hopefully an acute awareness that humanity needs to deploy far greater ambition, leadership and action than it has done to date. This is if we are to resolve the critical declines we now see in ocean health - an ocean that supports each and every one of us. Ultimately, our intention is that it may help in some ways to bring the global community closer together much more, in a determination to live in greater harmony with nature than we have achieved to date, for all our benefits.



Dan Laffoley



John M Baxter

*"The global ocean oxygen content has decreased
by 1-2% since the middle of the 20th century."*

Chapter 1 authors

What is ocean deoxygenation?

1

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Summary

- The equilibrium state of the ocean-atmosphere system has been perturbed these last few decades with the ocean becoming a source of oxygen for the atmosphere even though its oxygen inventory is only ~0.6% of that of the atmosphere. Different analyses conclude that the global ocean oxygen content has decreased by 1-2% since the middle of the 20th century. Global warming is expected to have contributed to this decrease, directly because the solubility of oxygen in warmer waters decreases, and indirectly through changes in the physical and biogeochemical dynamics.
- Since the middle of the 20th century, the increased river export of nitrogen and phosphorus has resulted in eutrophication in coastal areas world-wide. Eutrophication implies huge oxygen consumption, and when combined with a low ventilation, often due to vertical stratification, this leads to the occurrence of oxygen deficiencies near the sea bed. The number of reported sites affected by low oxygen conditions (>500) has dramatically increased in the last few decades. Climate warming is expected to exacerbate the decrease of oxygen by reducing the ventilation and extending the stratification period.
- The volume of anoxic zones has expanded since 1960 altering biogeochemical pathways by allowing processes that consume fixed nitrogen and release phosphate and iron, and possibly nitrous oxide (N₂O). The relatively small inventory of essential elements, like nitrogen and phosphorus, makes such alterations capable of perturbing the chemical composition equilibrium of the ocean. Positive feedback loops (e.g. remobilization of phosphorus and iron from sediment particles) may speed up the run away from this equilibrium in ways that we hardly know or understand.
- Deoxygenation affects many aspects of the ecosystem services provided by the ocean and coastal waters. For example, deoxygenation effects on fisheries include low oxygen affecting populations through reduced recruitment and population abundance, and also through altered spatial distributions of the harvested species causing changes in the dynamics of the fishing vessels. This can lead to changes in the profitability of the fisheries and can affect the interpretation of the monitoring data leading to misinformed management advice.
- Model simulations for the end of this century project a decrease of oxygen in the high and low emission scenarios, while the projections of river exports to the coastal ocean indicate that eutrophication will likely continue in many regions of the world. Warming is expected to further amplify the deoxygenation issue in coastal areas influenced by eutrophication by strengthening and extending the stratification.

Effects of low oxygen conditions	Potential Consequences
Reduction of the habitat available for pelagic, mesopelagic, and benthic organisms.	<ul style="list-style-type: none"> • Reduced growth and reproduction of aerobically-respiring organisms in regions with very low oxygen levels. • In extreme cases and for non-mobile species, low-O₂ induced mortality. • Cascading effects and alteration of the foodweb structure including the diversion of organic matter flow to low oxygen tolerant species like microbes. • In extreme cases, oxygen can become completely depleted and the waters become anoxic and even euxinic, in which only anaerobically respiring microbes can survive.
Reduction in the abundance and recruitment of fish populations.	<ul style="list-style-type: none"> • Alterations in the spatial distribution of harvested species. • Accumulation of species in well-oxygenated waters; these species may become more vulnerable to fishers targeting these high oxygen refuge areas. • Changes in the dynamics of the fishing vessels and in the profitability of the fisheries. • Affect the interpretation of the monitoring data leading to misinformed management advice.
Expansion of the volume of anoxic zones since 1960.	<ul style="list-style-type: none"> • Alteration of biogeochemical pathways of essential elements like nitrogen, phosphorus and iron. • Modification of the fixed nitrogen budget, with enhanced nitrogen fixation and denitrification but the balance of the two is not yet known. • Release of phosphate and iron from sediment particles and possibly nitrous oxide (N₂O). • Positive feedback loops may speed up the run away from equilibrium.
Challenges in model development and observation quality.	<ul style="list-style-type: none"> • Model development needs new observations and dedicated experiments (e. g. definition of critical thresholds for biogeochemistry and living species). • Model uncertainty. • Requirement for specific sensors for measuring ultra low oxygen conditions (at nM scale).

1.1 Introduction

During the Earth's history, the ocean has evolved through various oxidation states. The ocean was largely anoxic 3.85 billion years ago, mildly oxygenated in its upper layer up to 0.54 billion years ago and, finally, quite well oxygenated in its present state (Holland, 2006). Evidence is mounting that oxygen is declining in the modern ocean. Estimates are for a 1-2% decrease (i.e. 2.4-4.8 Pmol or 77-145 billion tons) of the global oxygen inventory since the middle of the last century (e.g. Bopp et al., 2013; Schmidtko et al., 2017). This results in modifications of the equilibrium state of the ocean-atmosphere coupled system with the ocean recently becoming a source of oxygen for the atmosphere. Regions with historically very low oxygen concentrations are expanding and new regions are now exhibiting low oxygen conditions. Schmidtko et al. (2017) estimate that the volume of anoxic waters worldwide has quadrupled since 1960.

While the importance of the different mechanisms responsible for the loss of the ocean oxygen content is uncertain, global warming is expected to contribute to

this decrease, directly because the solubility of oxygen in warmer waters decreases, and indirectly through changes in ocean dynamics that reduce ocean ventilation. Today's processes are reminiscent of those thought to have promoted the occurrence of oceanic anoxic events (OAEs) that occurred episodically during the past several hundred million years and that led to major extinction events (Holland, 2006; Watson, 2016). While a full-scale OAE would take thousands of years to develop, the small oxygen inventory of the ocean (i.e. the oxygen inventory of the ocean is only ~0.6% of that of the atmosphere) makes it particularly sensitive to perturbations of its equilibrium oxidative state. The consequences of such perturbations on the biogeochemistry and ecosystem state are not well known.

The deoxygenation process is also affecting the estuary-coastal ocean continuum (referred as the coastal ocean throughout the following). The global increase of the nutrients exported by rivers from the land to the ocean and the resulting development of eutrophication in many hundreds of sites around the world has promoted algal productivity and the resulting over-consumption of oxygen in the bottom layer that is effectively isolated

through stratification from being replenished with the oxygen in the surface waters. Climate warming is expected to worsen the situation by further reducing the ventilation of bottom waters.

Deoxygenation in the global and coastal ocean will reduce the habitat available for pelagic, mesopelagic, and benthic organisms. In some regions, the oxygen level is so low that aerobically-respiring organisms can exhibit reduced growth and reproduction and, in extreme cases and for non-mobile species, experience low- O_2 induced mortality. The effects on individuals exposed to low oxygen can cascade and result in altered foodweb structure, including the diversion of organic matter flow to low oxygen tolerant species like microbes. In the case of anoxia and the eventual occurrence of sulphidic conditions, only anaerobically respiring microbes can survive. While the impact of low oxygen conditions on individual organisms can be investigated in laboratory experiments, the impact at the scale of the ecosystem, as well as on the goods and services delivered to humans, rely on field data and modelling and are more uncertain.

The transition towards anoxic conditions also affects important microbial and chemical processes governing the biogeochemical cycling of essential elements like nitrogen (N), phosphorus (P) and iron (Fe). Anoxic conditions halt nitrification and aerobic respiration and activate denitrification and the anaerobic ammonium oxidation (anammox) leading to a net loss of fixed nitrogen. On the other hand, nitrogen fixation is expected to be stimulated in waters with an excess of phosphorus over nitrogen; whether this can compensate for the loss of fixed nitrogen due to denitrification and anammox is uncertain.

The chemical composition of the ocean can be considered as fairly stable for the past several hundred millions of years (Watson et al., 2017), but the relatively small inventory of essential chemical elements (e.g. fixed N and P) makes them sensitive to relatively small perturbations. Perturbations of biogeochemical cycling of the order of those caused by deoxygenation have the potential to have significant effects on the biogeochemistry and resulting chemical composition on relatively short time scales of several thousands of years. Positive feedback loops like the remobilization of phosphorus and iron from sediment particles in low oxygen conditions can further accelerate the process by then stimulating primary production. In the geological

past, perturbations of the phosphorus cycle drove the system away from equilibrium and promoted the occurrence of OAEs (Watson et al., 2017).

Model projections of the oxygen content of the ocean for the end of the 21st century show a decrease of oxygen under all current emission scenarios. Projections of river nutrients exports to the coastal ocean indicate that eutrophication will likely continue in many regions of the world and will be further amplified by warming acting to strengthen and extend stratification (Seitzinger et al., 2010).

1.2 Description of deoxygenation

The dynamics of oxygen in the ocean are governed by physical and biogeochemical processes. The ocean gains oxygen in the upper layer due to photosynthesis by autotrophic organisms and oxygen from the atmosphere dissolving in the under-saturated waters. Conversely, the ocean loses oxygen throughout the whole water column: at the surface, due to the outgassing of oxygen to the atmosphere in over-saturated waters, and from the surface to depths due to the respiration of aerobic organisms and oxidation of reduced chemical species. Evidence suggests that the global ocean oxygen inventory has been perturbed since the middle of the last century (Figure 1.1). We can assume that the oxygen produced by photosynthesis (i.e. net primary production) in the upper layer is roughly consumed by respiration within the water column, except for a small production of $0.002 \text{ Pmol } O_2 \text{ yr}^{-1}$ that corresponds to burial (Wallmann, 2000). An oxygen loss ranging from $0.048 \text{ Pmol } O_2 \text{ yr}^{-1}$ (Manning & Keeling, 2006) to $0.096 \text{ Pmol } O_2 \text{ yr}^{-1}$ (Schmidtko et al., 2017) results from a modification of the balance in the atmosphere-ocean fluxes with a decreasing influx from the atmosphere to the ocean and an increasing outflux from the ocean (e.g. Bopp et al., 2002; Frölicher et al., 2009). The lack of observations with sufficient resolution of sampling in space and time limits the rigour of our oxygen budget for the coastal zone.

1.2.1 Ventilation mechanisms

The surface mixed layer is well oxygenated in most of the ocean by photosynthesis and dissolution of atmospheric oxygen. But below the sunlit surface layer, there is no photosynthesis, so that the renewal of the oxygen consumed requires the existence of a physical mechanism that transports well-oxygenated waters

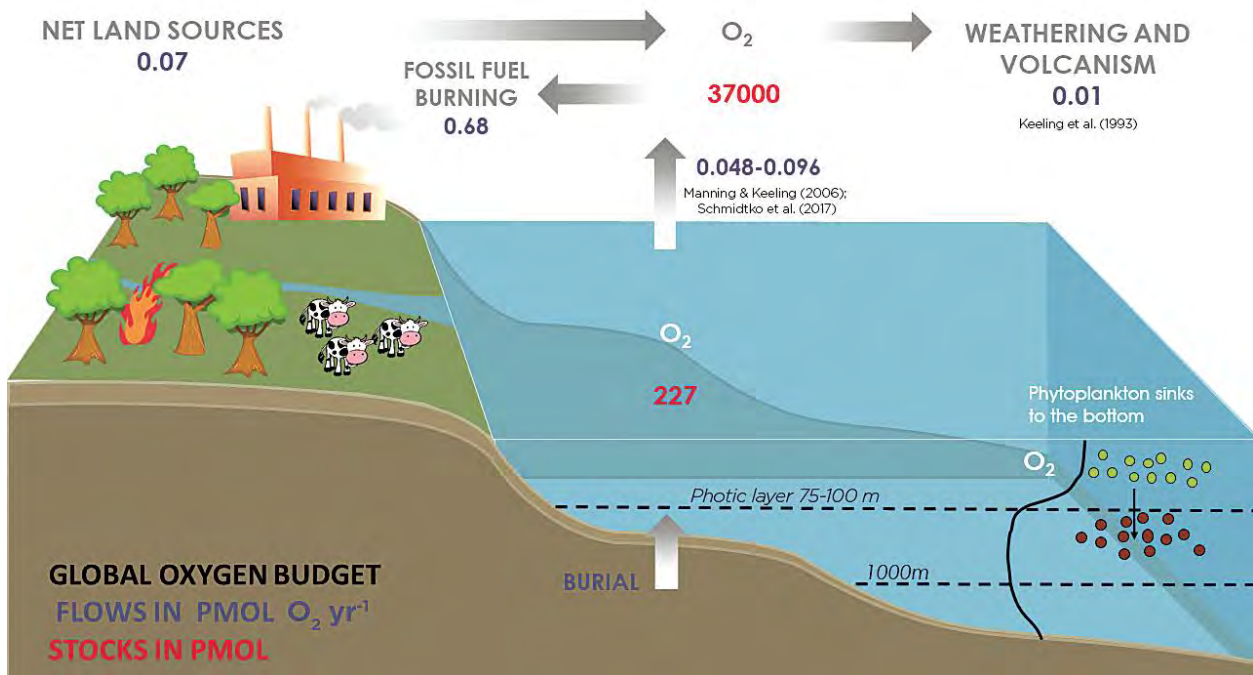


Figure 1.1 Tentative oxygen budget for the Ocean-Atmosphere system for the period 1960-2014. The stocks are in Pmol (for the Ocean from Schmidtke et al. (2017); for the atmosphere from Keeling et al. (1993)) while the fluxes are in Pmol O₂ yr⁻¹.

Globally the amount of oxygen produced by photosynthesis (estimated as the Net Primary Production, NPP from Bopp et al. (2013)) is compensated by the amount required for the degradation except for a small burial that results in a net production of oxygen of 0.002 Pmol O₂ yr⁻¹. The net air-sea oxygen flux is directed to the atmosphere and its range has been estimated from (lower value) Manning and Keeling (2006) (for 1993-2003) and (higher value) from Schmidtke et al. (2017) (for the last 50 years).

For the atmosphere, the oxygen consumed by the combustion of fuels and industry, land-use change as well as the net oxygen produced by the biosphere has been computed using the averaged estimates (over 1960-2014) from the global carbon project (Le Quéré et al., 2015) using the O₂:C ratios from Keeling and Manning (2014).

to the low oxygen waters. This mechanism, called ocean ventilation, is responsible for the oxygenation of deep and intermediate ocean waters and modifies the spatial distribution of oxygen within the ocean. The intensity of ocean ventilation strongly varies vertically and horizontally and over time. In the coastal ocean, ventilation of bottom waters results from advection from offshore, and mixing processes from surface cooling and wind mixing and in some areas tidal action and flushing events from the rivers.

In the global ocean the main ventilation mechanisms and pathways are as follows:

- Waters of a given density, an isopycnal, within the permanent thermocline (i.e. layer of significant temperature gradient) of the subtropical gyres are ventilated at the latitude where that isopycnal intersects the base of the surface mixed layer during the winter. At the end of each winter, waters near the base of the mixed layer subduct into the ocean interior, and then begin to slowly diffuse

equatorward. This ventilation process is particularly intense at the high latitude end of the subtropical gyres, where subtropical mode water (STMW) is formed (Figure 1.2). This process ventilates subtropical gyres to depths of about 500 to 900 m.

- In the Southern Ocean, a surface convergence zone between about 50°S and 60°S causes local water to sink and the formation of Antarctic Intermediate Water (AAIW) which ventilates water depths between about 700 and 1200 m. The Southern Ocean is also home to the formation of the densest waters of the world ocean, Antarctic Bottom Waters (AABW), formed in areas of intense sea ice freezing and brine rejection around the continent of Antarctica. These waters sink all the way to the bottom of the three major ocean basins and propagate northward (Figure 1.2).
- In the northern hemisphere, ventilation processes vary quite a lot between the major ocean basins. In the North Atlantic, to the north of the Denmark-Faroe-Shetland ridge, deep convection in the Greenland-Iceland-Norwegian Sea (GINSEA) is

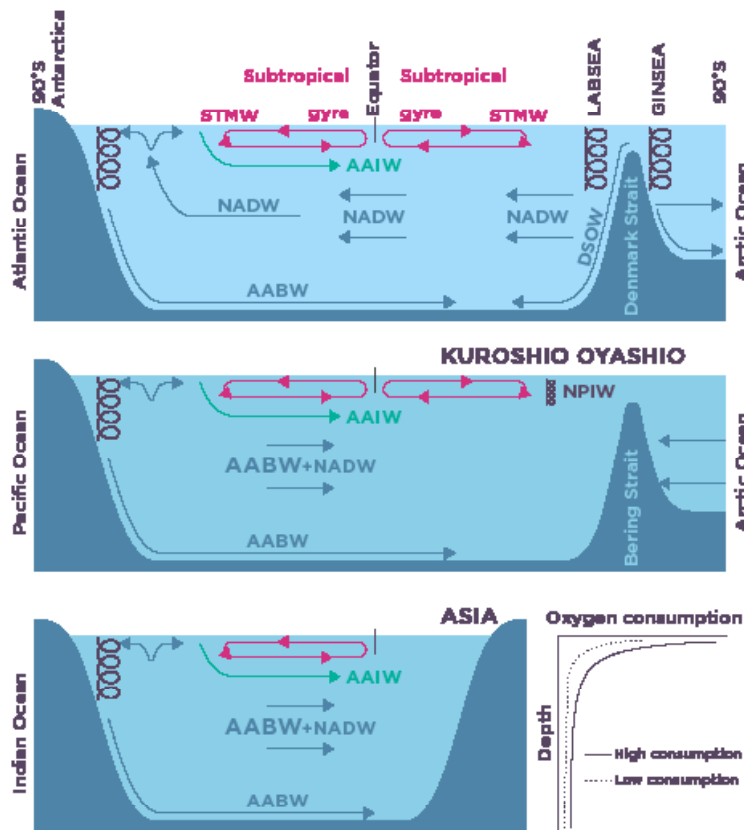


Figure 1.2 Meridionally averaged view of ventilation in the global ocean. STMW: Subtropical Mode Water, AABW: Antarctic Bottom Waters, AAIW: Antarctic Intermediate Waters, DSOW: Denmark Strait Overflow Water, NADW: North Atlantic Deep Water, NPIW: North Pacific Intermediate Waters, LABSEA: Labrador Sea, GINSEA: Greenland-Iceland-Norwegian Sea.

the source of Denmark Strait Overflow Water (DSOW) that spills over the Denmark Strait sill (625 m deep) and then descends to the bottom of the North Atlantic. Some of this dense water also flows northward and propagates towards the Arctic Ocean. The Labrador Sea, and to a lesser extent the Irminger Sea, is another important site of deep-water formation in the North Atlantic, with convection events reaching up to 2000 m depth. This leads to the formation of North Atlantic Deep Water (NADW) which then propagates southward. The ultimate fate of NADW is to either i) upwell into a surface divergence zone of the Antarctic Circumpolar Current; ii) ventilate the Indian Ocean; or iii) ventilate the Pacific Ocean (Figure 1.2).

- During the very long journey from its formation region in the northern North Atlantic, NADW remains isolated from the atmosphere and its oxygen content becomes progressively lower as it gets further away from its source region. In the Indian and Pacific Oceans, a mixture of NADW and predominantly AABW (Johnson, 2008) propagates northwards. No deep-water formation takes place in the Pacific and Indian Oceans, so that they are

less well ventilated than the North Atlantic (Figure 1.2) and have lower oxygen content. The formation of North Pacific Intermediate Water (NPIW) in the mixed water region of the Oyashio (i.e. cold current flowing south-westward from Kamchatka to Japan) and Kuroshio (i.e. warm current flowing northward from Taiwan to Japan) ventilates the upper 300 to 700 metres of the North Pacific subpolar gyre (Talley, 1993).

Projections from Earth System Models that simulate global warming from rising CO₂ levels indicate that ventilation processes will likely become more sluggish in the next decades (Bopp et al., 2013). An analysis of oxygen data from the global ocean tentatively suggests that such reduced ventilation may already be underway (Schmidtko et al., 2017). But large interdecadal variability is present, causing us to remain prudent in this conclusion. For instance, records preserved in the sediments underlying Oxygen Minimum Zones (OMZs) show that the rate of ventilation changes on multiple time scales. Climatic phenomena like El Niño, the Pacific Decadal Oscillation (PDO) and Ice Ages all change the rate at which the deep ocean gets replenished with

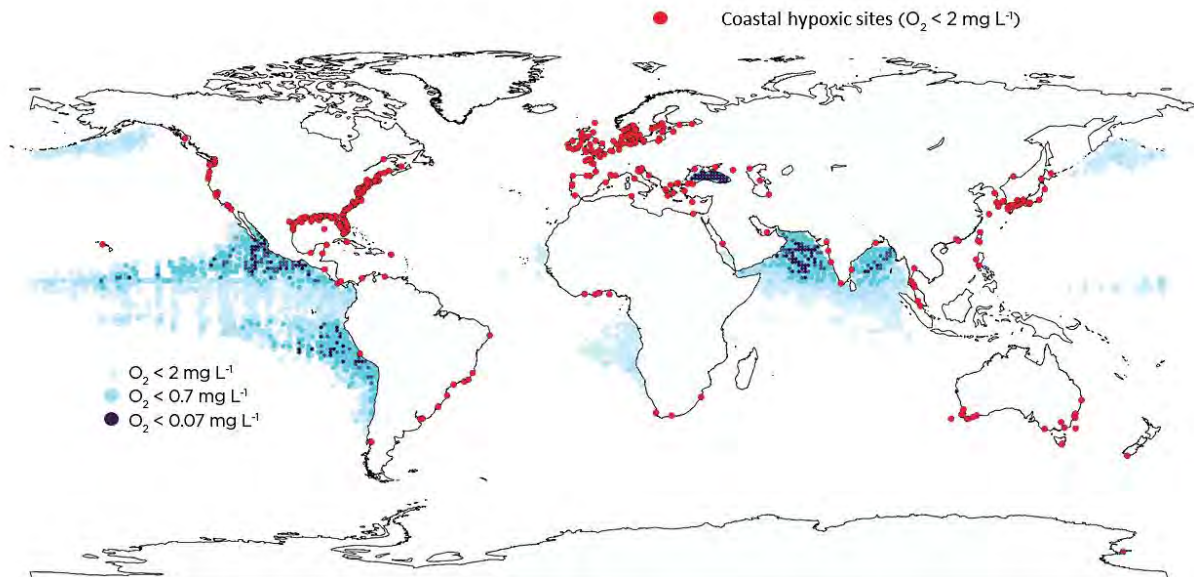


Figure 1.3 Global distribution of deoxygenation in the coastal and global ocean (from Breitburg et al., 2018). In the coastal area, more than 500 sites have been inventoried with low oxygen conditions while in the open ocean the extent of low oxygen waters amounts to several millions km³.

oxygen. In the north Pacific Ocean, Deutsch et al. (2014) have found that the variability over the last 150 years of the extent of the anoxic zone responds to the variability of the trade winds intensity that impacts on the thermocline depth and hence on the level of respiration (i.e. a shallower thermocline is expected to be associated to higher respiration rates). For most of the 20th century up to 1990, they found that the thermocline depth increased in answer to the weakening of the intensity of the tropical trade winds and this reduced the respiration demand and anoxia extent. The long-term variability of the extent of OMZ and, in particular of their anoxic part, results from the interplay of wind-driven and stratification-driven effects but the relative influence of these effects is not yet known (Deutsch et al., 2014).

During the last glacial termination (from 20 000 to 10 000 BP), the upper ocean generally became less oxygenated while the deep ocean became more oxygenated. All these changes are driven by a subtle balance between decreased oxygen solubility due to warming, increased ventilation of the abyssal ocean, shift of organic matter respiration rates from the deep to the upper ocean, and possibly a global reduction of respiration due to nutrient inventory (Jaccard & Gallbraith, 2012).

1.2.2 Formation of a Low Oxygen Zone (LOZ)

The oxygen concentration realized in waters below the surface layer results from the equilibrium between its consumption via oxygenated respiration and its renewal

by ocean circulation. Oxygen consumption processes (animal respiration, bacterial degradation of organic matter) remove oxygen from the water column. In the global ocean, the rate of oxygen consumption is greatest near the ocean surface and decreases exponentially with depth (Figure 1.2). Most of the respiration of the exported production occurs in intermediary waters, between 100-1000 m, and the fraction of organic matter that reaches waters below 2000 m is rather small. Any modification of this organic matter flux is expected to impact on the vertical distribution of oxygen and oxygen content of the deeper waters. In the coastal ocean, a significant part of the surface primary production reaches the bottom layer where it is degraded with possibly high oxygen consumption rates in the sediment.

Some regions of the global and coastal ocean below the surface are permanently poorly ventilated (e.g. intermediate waters of some regions of the tropical ocean) or periodically ventilated (e.g. bottom waters in coastal systems). In these regions, the oxygen concentration reaches such low values that it alters the ecosystem and biogeochemical cycles. These regions are considered as Low Oxygen Zones (LOZs) and, for the global ocean, they are frequently named Oxygen Minimum Zones (OMZs). The thresholds below which the oxygen deficiency has biological and biogeochemical impacts differ in terms of values and reporting units. For the biogeochemistry, it is the absence of oxygen that alters the biogeochemical cycling of N, P and Fe. The oxygen concentration threshold for impacts on living

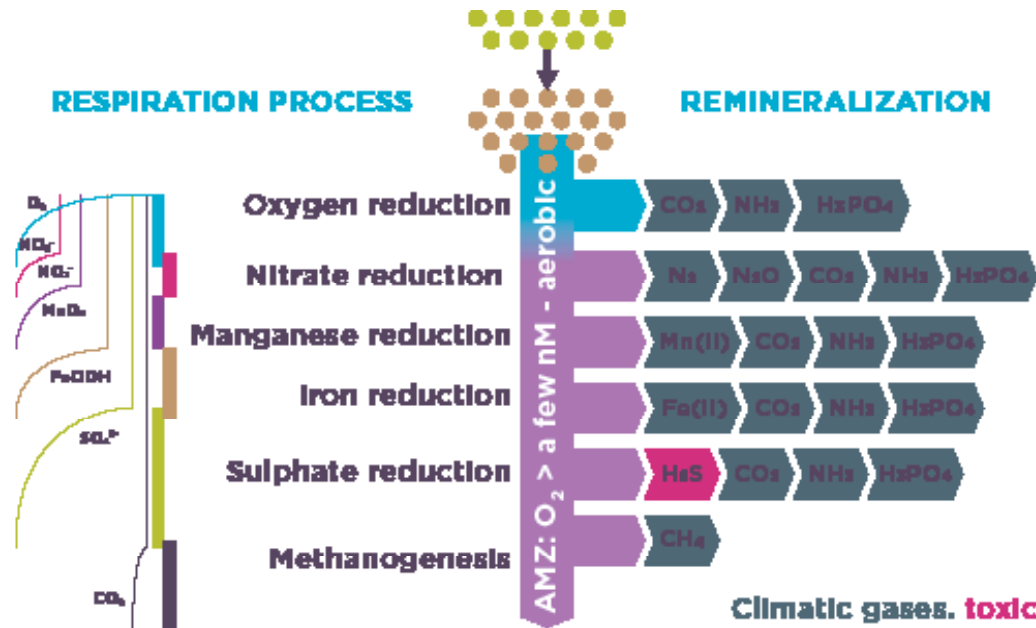


Figure 1.4 Succession of respiration processes in oxic and anoxic environments. In oxygenated waters, only oxic respiration occurs while in anoxic regions there is successively nitrate reduction (i.e. denitrification), manganese, iron, sulphate reduction and finally methanogenesis (Figure modified from Canfield & Thamdrup, 2009).

organisms varies somewhat across taxa. The definition of LOZs is based on fixed threshold values, with about $20 \mu\text{mol O}_2 \text{ kg}^{-1}$ (i.e. $\sim 5\%$ saturation) for OMZs and about $61 \mu\text{mol O}_2 \text{ kg}^{-1}$ for coastal LOZs. In extreme cases, oxygen can become completely depleted and the waters become anoxic and even euxinic when hydrogen sulphide, a toxic compound for most marine life (except some forms of bacteria), is produced.

1.3 Global / Regional differences in mechanisms

LOZs can be found in different ecosystems encompassing the open ocean, (semi)-enclosed seas, the estuary-coastal ocean continuum up to the edge of the continental shelf, and upwelling margins (Figure 1.3). The basic mechanisms responsible for the formation of low oxygen conditions differ across systems (e.g. Fennel & Testa, 2018). The configuration of the basin (e.g. open versus (semi)-enclosed), its bathymetry, and specifics of the land-sea-sediment-atmosphere interactions determine the residence time of waters and the level of biological production and hence the system's sensitivity to deoxygenation. Basically, low oxygen conditions naturally exist in the open ocean in regions without unusually high rates of O_2 utilization, but where the circulation is most sluggish and ventilation times are longest. The most poorly ventilated waters are found in the subsurface layers ($\sim 100 - 1000 \text{ m}$) of

the Tropical Ocean inside relatively stagnant cyclonic gyres that exist north and south of the equator in the eastern part of ocean basins (Karstensen et al., 2008). These OMZs are permanent features, but their upper boundaries are highly dynamic, and the analysis of long time series data have shown that their upper boundary is extending upward (Stramma et al., 2008). In some parts of the Eastern Tropical Pacific, recent observations made with sensors with detection limits of a few nM reveal the presence of an Anoxic Marine Zone (AMZ) between $100 - 500 \text{ m}$ inside the OMZs (Tiano et al., 2014). The absence of oxygen in these AMZs gives rise to peculiar microbial processes (Figure 1.4) that are described below.

Similarly, naturally poor ventilation due to restricted vertical circulation explains the deficiency of oxygen in some enclosed basins, such as the Baltic and Black Seas. In areas, like the Black Sea and the Cariaco basin, the degradation of organic matter leads to the production of a huge pool of hydrogen sulphide, a compound that is toxic for most animal life. In the Black Sea case, the opening of the Bosphorus strait $\sim 10\,000$ years ago, and the resulting intrusion of the salty Mediterranean waters, transformed the basin from a lake to the largest euxinic region ($4.7 \times 10^5 \text{ km}^3$ of sulphidic waters) in the world. Few aerobically-respiring animals are found in the waters between 100 m depth and the bottom.

The eastern branch of the main anti-cyclonic gyres located in both hemispheres in the Atlantic and Pacific Oceans leads to the occurrence of major upwelling zones along the eastern boundary of the ocean, i.e. Eastern Boundary Upwelling Systems (EBUS). These upwelling zones are located off Peru-Chile, Namibia, California and Senegal. They bring oxygen depleted and high nutrient waters from the open ocean OMZs onto the continental shelf. These upwelling zones have high levels of primary and secondary production that biologically support many of the world's important fisheries. They have very high oxygen consumption rates, and this is where the most intense and thick OMZs tend to be found. The degradation of the organic material consumes unusually large amounts of oxygen and can generate severe hypoxia and even anoxia with potential detrimental consequences for aerobically respiring living organisms. The variability of the oxygen conditions in EBUS depends on the intricate interplay between local (e.g. local wind mixing versus stratification) and remote (e.g. equatorial current) forcing. These, in turn, affect the ventilation mechanisms, the productivity of the region and the intensity of the upwelling (e.g. Bachèlery et al., 2015; Bettencourt et al., 2015).

The open ocean OMZs are naturally poorly ventilated and climate change is expected to further lower

ventilation. For instance, in the Black Sea, the depth of the oxygenated layer has dramatically decreased from 140 m in 1955 to 90 m in 2015 (Figure 1.5) very likely due to the reduced formation of well oxygenated waters in winter (Capet et al., 2016).

In parallel with the expansion of these naturally occurring oxygen deficient areas, anthropogenically-induced LOZs have also been rapidly increasing (Diaz & Rosenberg, 2008) (Figure 1.6). After the 1950s, the Haber-Bosh process offered a way to synthetically fix N to form ammonia at an industrial scale. This process has allowed for the mass production of synthetic fertilizers. The Haber-Bosh discovery and the increasing burning of fossil fuels have led to anthropogenic sources of newly created fixed N becoming two to three times larger than natural terrestrial sources resulting in substantial changes in the N cycle (Galloway et al., 2013). For coastal areas with large river inputs, it resulted in an increase in the delivery of fixed N by ~30 % from 1970 to 2000 (Seitzinger et al., 2010). Similarly, over the same period, dissolved inorganic phosphorus also increased by ~30%. This influx of nutrients leads to the eutrophication (over-enrichment) of the waters in the coastal zone. Eutrophication stimulates primary production and, to some extent, can be beneficial to fisheries. But if not well managed, eutrophication may

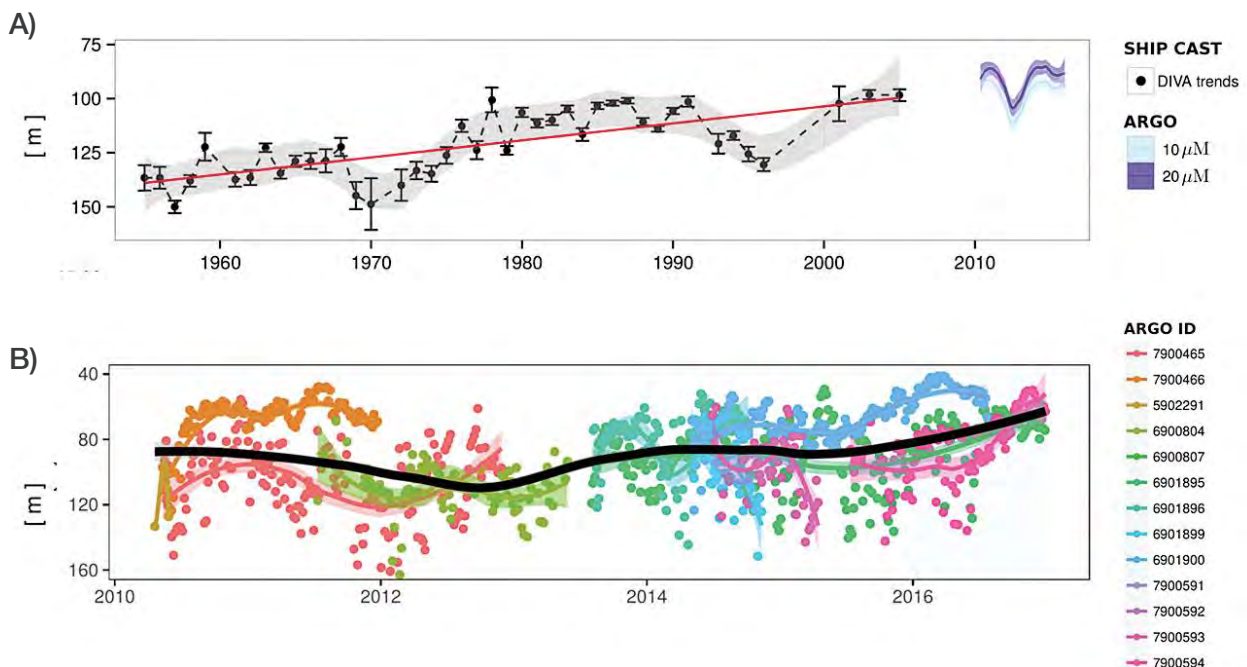


Figure 1.5 The surface oxygenated layer of the Black Sea has been shrinking from 140 m in 1955, 90 m in 2010-2015 and 72 m in 2016. A) trends of oxygen penetration depth deduced from (dots) the analysis of ship-based casts and (blue) ARGO floats. B) trend reconstructed from Argo floats over 2010-2016 (Figure from Capet et al., 2016).

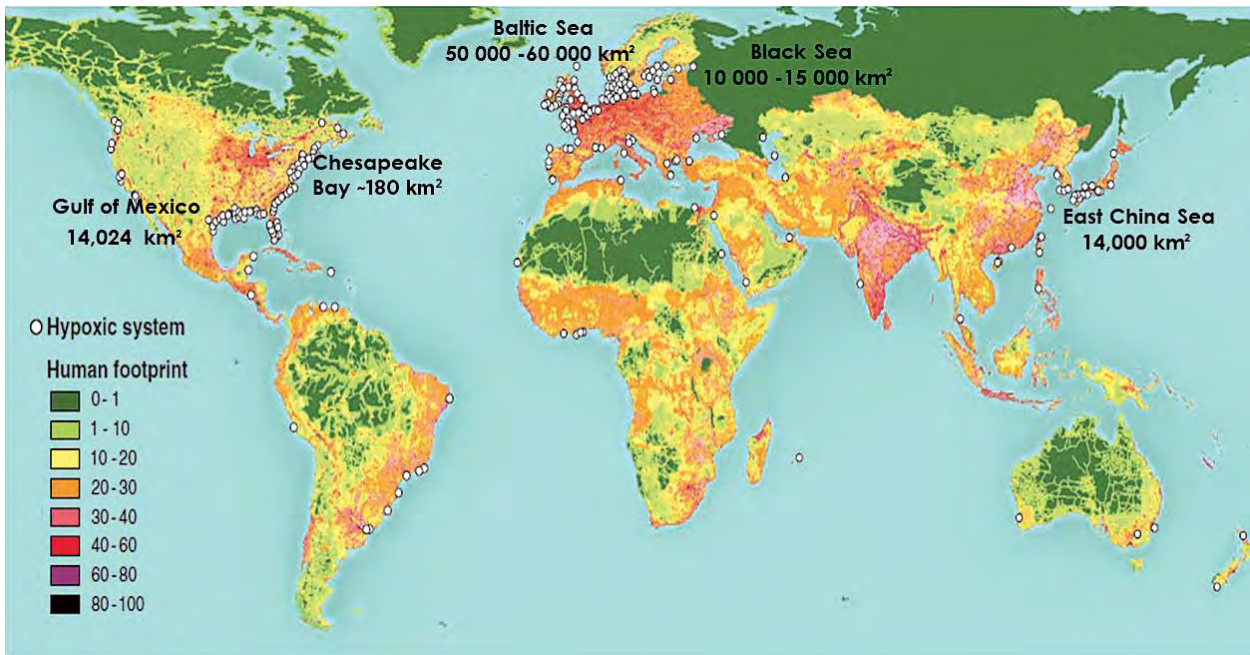


Figure 1.6 Global distribution of systems that have been reported as eutrophication (N and P enrichments)-associated LOZs. Their distribution matches the global human footprint (the normalized human influence is expressed as a percentage) in the Northern Hemisphere. For the Southern Hemisphere, the occurrence of dead zones is only recently being reported. Affected water bodies range from small coastal lagoons to large systems like the Baltic Sea, Black Sea, Kattegat, and East China Sea, and the Northern Gulf of Mexico. It should be noted that low oxygen zones can only be detected where monitoring is in place, and the uneven efforts in monitoring and research may contribute to the much higher number of low oxygen areas reported in the northern hemisphere (Figure from Diaz & Rosenberg, 2008).

lead to massive development of algae that produce large amounts of organic material that sink to the sea bed. When bottom waters are not well ventilated (e.g. in periods of vertical stratification), the oxygen consumed cannot be replaced and this leads to the creation of a LOZ. Coastal LOZs result from excessive external nutrients inputs from the rivers and once established, they are further stimulated by internal nutrients sources activated by the deoxygenation process (Figure 1.7). Indeed, the remobilization of bound P from the sediments in anoxic conditions will further aggravate the deoxygenation process by releasing P that further stimulates primary production. Even after a reduction of river nutrients, coastal systems require several years to recover because the sediment continues to consume large amounts of oxygen and can continue to leach out nutrients that accumulated during eutrophication (Conley et al., 2009).

1.4 Trends and impacts

1.4.1 Observations

The advent of autonomous platforms like Argo floats (Figure 1.8) and (wave) gliders has the potential to boost our knowledge of oxygen dynamics at the mesoscale

and even sub-mesoscale (1 to 100 km) (e.g. Pascual et al., 2017). Up to now, more than 100 000 oxygen profiles have been collected by Argo floats throughout the ocean, allowing depiction of the oxygen patterns over large areas. The inclusion of Argo oxygen data in global climatologies and trend estimation is promising but has not been done so far because of oxygen sensor calibration and data management issues.

Oxygen measurements at the very low concentrations ($< 5 \mu\text{mol O}_2 \text{ kg}^{-1}$) found in some parts of LOZs are technically challenging and the historical data at very low oxygen concentrations have been often suspect (Bianchi et al., 2012). Consequently, estimation of the extent and evolution of OMZs with particularly low oxygen concentrations at their core (e.g. AMZs) are still uncertain. Recent oxygen sensors with detection limits as low as a few nanomoles are now available and have changed our view of the biogeochemistry of OMZs (Tiano et al., 2014). The emergence of these new platforms and sensors makes possible the implementation of regional and global oxygen observatories targeted towards the monitoring and management of the deoxygenation process.

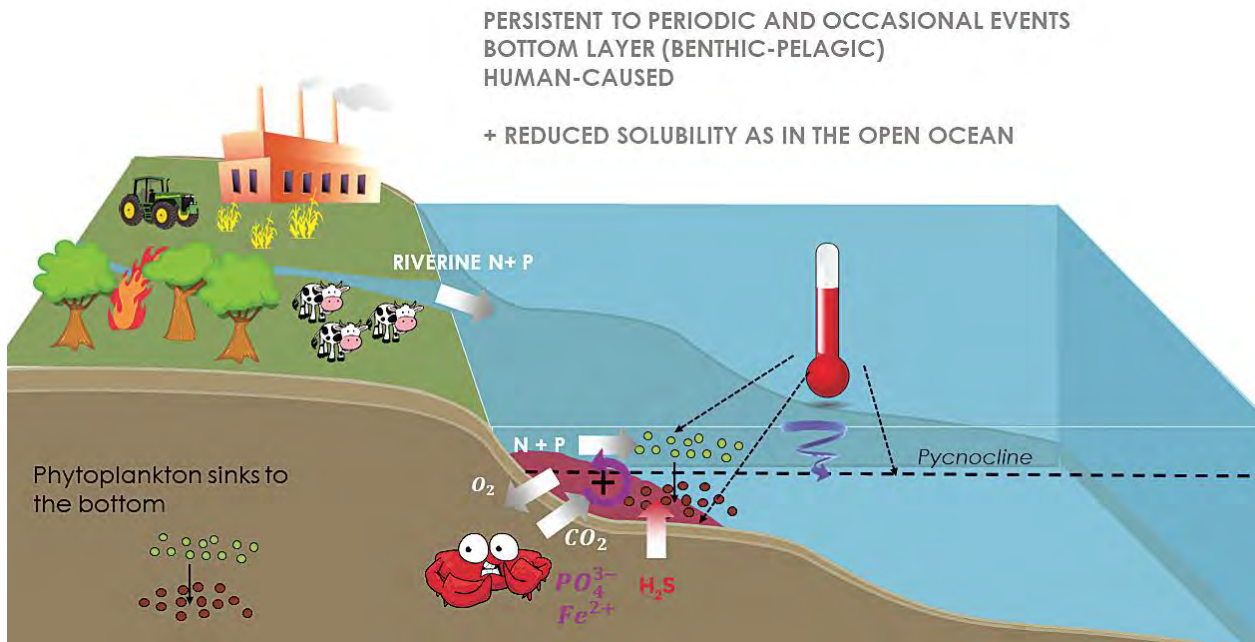


Figure 1.7 Schematic of the generation of a LOZ in the coastal area. Large nutrients discharges from the rivers stimulate intense primary production that sinks to the bottom where it is degraded consuming large amounts of oxygen. When the ventilation is not able to renew the oxygen consumed, a LOZ is generated and in extreme cases hydrogen sulphide escapes the sediment. Low oxygen conditions in bottom waters enhance the release of inorganic phosphorus that will stimulate primary production and hence feedbacks positively on the oxygen depletion.

Table 1.1 Oxygen Content and change per basin for the main areas affected by deoxygenation. Synthesis of the information provided by Schmidtko et al. (2017)

Basin	Oxygen decrease since 1960 (Pmol)	Change as percentage of global change (%)	Decrease as percentage of basin change since 1960 (%)	Causes
Global ocean	4.8 ± 2.1			Up to 1000 m: solubility plays a major role and explains 50% of the oxygen loss. Below 1000 m: changes in deep water formation and thermohaline circulation with natural variability superimposed are suggested to explain the oxygen loss.
North and Equatorial Pacific Ocean	1.9 ± 0.8	39.9 ± 17.2	3.8	Upper Layer: decline in the formation rates of North Pacific Intermediate waters due to warming changes on the time scales of Pacific Decadal Oscillation (PDO) are observed Below 1000 m: no impact of PDO has been found
Southern Ocean	0.8 ± 0.2	15.8 ± 4.9	2.1	Decline in deep water formation of Antarctic water masses due to changes in thermal buoyancy and in circumpolar wind patterns. Most pronounced in the Indian and Pacific sectors in parallel to the increase of salinity and temperature of the Antarctic Bottom Water of the circumpolar deep water.
South Atlantic Ocean	0.6 ± 0.1	12.4 ± 2.8	2.7	Reduced ventilation due to meridional overturning changes affect mainly the entire deep water column between north Atlantic deep water and Antarctic bottom water. Multi decadal variability.
Arctic Ocean	0.36 ± 0.15	7.6 ± 3.1	7.8	Reduced deep water ventilation due to a freshening and warming in the Canada Basin and Beaufort Sea. Increased consumption by enhanced biological activity due to sea ice reduction in summer.

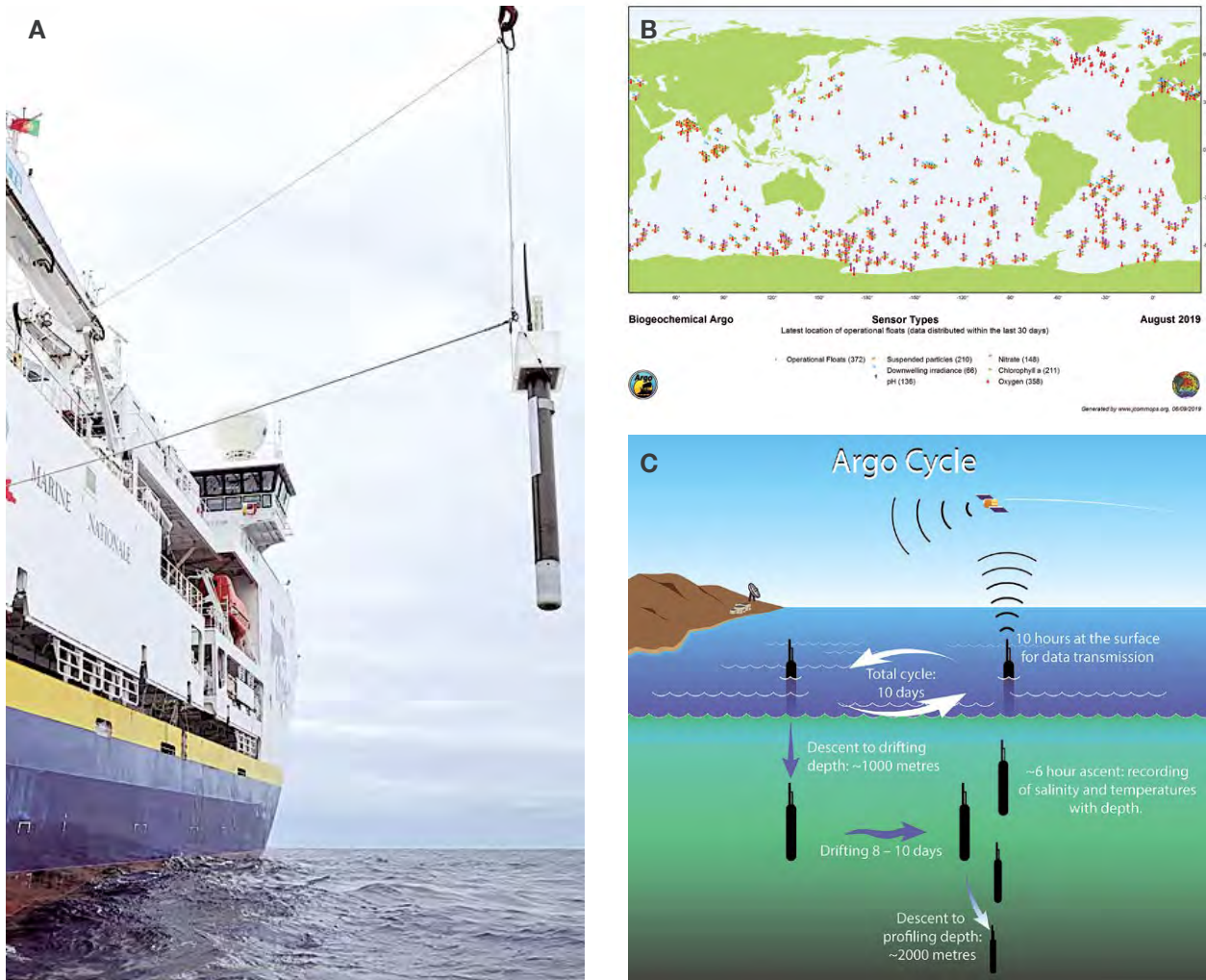


Figure 1.8 A) Deployment of an ARVOR float from the French R/V Pourquoi Pas; B) position of biogeochemical Argo floats in August 2019; C) schematics of an Argo profile cycle (sources: Map JCOMMOPS; photos : <http://www.argo.ucsd.edu/pictures.html> with courtesy of John Garrett, Skeptical Science for the Argo cycle).

1.4.2 Trends

Since the middle of the 20th century, the global and coastal ocean have had to face deoxygenation. In the global ocean, the oxygen content is decreasing and OMZs are expanding while in the coastal ocean, the occurrence of bottom LOZs is more and more reported.

Evidence shows that the oxygen balance in the global ocean has been perturbed during the last decades with the consequence that the oxygen inventory is globally decreasing (e.g. IPCC, 2013; Ito et al., 2017; Schmidtko et al., 2017; Stramma et al., 2008). Observations and model simulations agree that the ocean oxygen content has decreased by 1-2% since 1960. This decrease is not uniform but rather varies across ocean basins and depths (Table 1.1). The largest loss is observed at the depth of the main thermocline between 100-300 m in

the Tropical and North Pacific Ocean, the Southern and Arctic Ocean and the South Atlantic Ocean (Table 1.1).

Natural climate fluctuations can substantially contribute to the interannual to decadal variation in oxygen and can preclude unequivocal detection of any climate driven signal. This is particularly the case for the North Atlantic and North Pacific regions where the surface and subsurface oxygen concentrations are statistically linked with the North Atlantic Oscillations (NAO) and Pacific Decadal Oscillations (PDO) climate modes (Andrews et al., 2013; Duteil et al., 2018; Frölicher et al., 2009). Volcanic eruptions are another natural forcing that is superimposed onto the anthropogenic and internal drivers that govern oxygen variability. Volcanic eruptions enhance the amount of oxygen taken up by the ocean due to a cooling effect that reduces the stratification and increases solubility. The oxygen

inventory increases globally in the top 500 m, and this increase compensates for part of the human-induced decreasing trend in oxygen that follows an eruption (Frölicher et al., 2009). The identification of the causes of deoxygenation requires extracting the climate signal from the natural and internal variability of the ocean system. Models, supported by observational data, are essential for making this differentiation as, currently, the available observations alone do not allow sufficient differentiation of the different contributing drivers and signals.

Global warming is expected to further decrease the global ocean oxygen content directly because the solubility of oxygen is lower in warmer water (i.e. direct thermal effect) and indirectly through changes in ocean dynamics (e.g. increased stratification, decreased mixing layer subduction, convective mixing and deep-water formation, slowdown of the thermohaline circulation) that reduce ocean ventilation. These changes have affected the balance of the air-sea oxygen flux, reducing the amount of oxygen that goes from the atmosphere to the ocean and increasing the outgassing of oxygen from the ocean. A reduction of deep-water formation will affect the whole ocean after decades to hundreds of years (dependent on depth). These changes may also have an impact on key biogeochemical processes and hence the local production-consumption of oxygen in a way that is still not clearly understood. For the same level of global photosynthesis and respiration, the increased stratification reinforces the decoupling between the oxygen oversaturated surface waters and the undersaturated subsurface waters. This strengthened decoupling increases the outgassing of oxygen. Observations and modelling have been combined in order to determine the relative importance of these different mechanisms and how they have affected the oxygen dynamics of different ocean basins. Clearly, the different layers of the ocean respond to global warming with different time scales; the surface layer responding after just a few years, whilst the intermediate layers and the deep ocean adjust to surface conditions on 10 to 120 years (Karstensen et al., 2008) and millennial time scales, respectively. In addition, the mechanisms of deoxygenation differ regionally and in particular differ vertically within a system. Over the first 1000 m of the water column, ~50% of the oxygen loss can be attributed to solubility change, while below 1000 m, changes in ocean circulation and deep-water formations with natural variability superimposed explain the oxygen loss. Globally, it has been shown that the direct thermal effect can only explain a limited fraction (~15%) of the oxygen

decrease observed globally; the remaining part being imparted to indirect effects (Schmidtko et al., 2017).

Diaz and Rosenberg (2008) classified systems affected by oxygen deficiency according to the frequency of occurrence and duration of their low oxygen events. They found that since the 1960s the number of reported coastal LOZs has approximately doubled every ten years from ~25 in 1960 up to ~400 in 2007. Coastal LOZs exhibit different types of dynamics in response to the local aspects of primary production, stratification and mixing. Episodic events, with infrequent oxygen depletion (i.e. less than one event per year as defined by Diaz and Rosenberg, 2008), represent ~17% of the reported coastal LOZs and are the first signal that a region may potentially be shifting towards higher frequency oxygen deficiency. In small systems (e.g. river-estuary, bay, lagoon, inlet), oxygen depletion may appear several times per year lasting from a few hours to days or weeks. In these systems (~25%), local weather events and the periodic spring-neap-tidal cycles govern the variability of the primary production and the alternation between stratification and mixing periods. Low oxygen in about 50% of the reported LOZs occurs seasonally in summer-autumn when the seasonal thermocline or pycnocline is established and prevents the ventilation of bottom waters. The oxygen consumed by the degradation of the spring algal bloom cannot be replaced and a LOZ is generated in the benthic boundary layer. In systems prone to permanent stratification (8%), a persistent LOZ develops.

1.4.3 Projecting deoxygenation

Robust model projections under various scenarios of changes are needed for the global and coastal ocean in order to test in advance the potential impacts of mitigation strategies. The projection and forecasting of deoxygenation are based on state-of-the-art models that couple the physics and biogeochemistry, interact with the atmosphere and, in the coastal ocean, are linked with the land and the sediments. Mechanistic models are powerful tools to understand the underlying processes operating and to be able to then differentiate the causes of the oxygen decrease. While models used for projecting deoxygenation in the global and coastal ocean are quite similar in terms of formulations, their resolution in space and time, required accuracy, horizon of projections, and scenarios differ. A climate approach, with long term projections up to the end of the 21st century under global change scenarios, is needed for

the global ocean. Conversely, for the coastal ocean, a weather-based approach with medium to short term projections and forecasting is more appropriate: medium term projections (< 20 years) can support the implementation of regional river nutrients management strategies while, the setting up of a warning system, would require the implementation of an operational framework delivering near real time forecasts with a high accuracy.

Global models are able to reproduce the observed decline in the global oceanic oxygen inventory since 1960. Yet, they are not able to represent the spatial (region-specific) patterns of decrease and, in particular, the observed decline in the tropical thermocline. For the 21st century, an ensemble of models consistently predicts that continued global warming will worsen deoxygenation in the surface and deep ocean under the high mitigation (RCP 2.6) and business as usual (RCP 8.5) scenarios, with decrease of the global oxygen inventory of 1.81 ± 0.31 and $3.45 \pm 0.44\%$, respectively (Bopp et al., 2013). Yet, there is still little agreement in the simulated spatial distribution of low oxygen areas with concentrations less than $100 \mu\text{mol O}_2 \text{ kg}^{-1}$ (Cabre et al., 2015). This uncertainty limits our ability to reliably predict the impact of climate warming on the open-ocean OMZs and hence on oxygen sensitive biogeochemical processes including the N budget. The predictive skill of coarse resolution ocean models at low latitudes is limited by the need to resolve zonal currents thought to be important in supplying oxygen into the tropical OMZs (Brandt et al., 2010; Keeling et al., 2010; Stramma et al., 2010).

Looking at a longer time horizon; by 2150, the decreasing oxygen trend projected up to 2100 for the tropical intermediate (200-1000 m) reverses. The volume of OMZ is projected to shrink through 2300 with consequences on the N budget through a reduction of denitrification. This may potentially have important climate feedbacks through the reduced production and emission of N_2O to the atmosphere (Fu et al., 2018). Model simulations show that the causes for this oxygen increase are a reduction of export production combined with an intensified ventilation after 2200. Fu et al. (2018) suggest that at the end of the 21st century the projected expanding tropical OMZs do not reach a steady state but rather are in transition towards volume reduction.

Projecting oxygen levels in individual coastal water bodies requires modelling the variability of the ventilation

and primary production from hours to weeks in response to changing river discharges (e.g. fresh water, inorganic nutrients, suspended particles), local weather conditions (e.g. wind storms, flooding events, heat waves), interactions with offshore (e.g. advection, upwelling), oxygen consumption in the sediments, and possibly the influence of the spring-neap tidal cycle. Coastal and regional models have the ability to represent the oxygen dynamics at monthly to weekly time scales but their performances can be hampered by the quality of their boundary conditions, mainly river discharges and atmospheric forcing that do not have the required spatial and temporal resolutions. Coastal models are progressively evolving towards a structure that allows a seamless coupling of the river-estuary-coastal ocean continuum. This will offer an improved quantification of the export of nutrients, and, in particular of N and P, along the river-ocean dimension.

The mitigation of coastal deoxygenation requires the implementation of effective nutrient reduction strategies based on a dual reduction of N and P to control the level of eutrophication (Conley et al., 2009). The economic costs associated with the reduction of anthropogenic nutrients is substantial and thus it is crucial that the level of reduction in a given coastal system be based on a deep comprehension of the processes governing oxygen dynamics and the likely ecological benefits. Over the last decades, regional action plans have been implemented in order to reduce the amount of nutrients discharged to the coastal zone through better wastewater treatment and other best management practices. However, to date, the positive effects are not always as expected and some regions remain far from reaching their nutrient reduction targets as positive feedback mechanisms (i.e. enhanced release of iron-bound phosphate in low oxygen conditions) and sediment inertia continue to emit nutrients for several years after reduction (e.g. Capet et al., 2013; Conley, 2012; Rabalais et al., 2010). Even when the nutrients level returns to a reference state, some systems may not return to their initial reference but rather may go to a new ecological state due to the non-linearity of living systems (Duarte et al., 2009).

Nutrient management in agriculture, the reduction of P detergent, and the increasing connections of people to sewage plants with high levels of treatment will control the amount of river export of fixed N and dissolved inorganic P (Seitzinger et al., 2010). Based on four scenarios of socio-economic development and using

an indicator of coastal eutrophication potential (Billen & Garnier, 2007), Seitzinger et al. (2010) estimate that risk for coastal eutrophication in many regions of the world until at least 2030 will likely continue due to the increase in inorganic P and N and changes in the nutrient ratios of river exports. Warming is expected to further exacerbate the deoxygenation issue by intensifying respiration and reducing the ventilation process due to a reduced solubility and stronger, prolonged stratification.

1.4.4 Impacts

1.4.4.1 Impact on biogeochemistry and biogeochemical feedbacks

The transition to anaerobic conditions induces major changes in the biogeochemical cycling of essential elements like N, P and Fe in the water column and in the underlying sediments. Some of these modifications will further the deoxygenation process as positive feedback loops may establish and stimulate further oxygen consumption. Special microbial processes start to operate, such as anaerobic remineralization of organic matter by denitrification and anaerobic ammonium oxidation (anammox), leading to formation of dinitrogen gas N_2 (a component that is largely inaccessible for most organisms) and a net loss of bioavailable N in the ocean. Nitrous oxide (N_2O), a potent greenhouse gas, is formed as a byproduct during nitrification and as an intermediate product during denitrification (Bange, 2006). Because the oxygen thresholds that govern the microbial pathways to N_2O are not precisely known, the role of OMZs in the marine N_2O budget is debatable. In a warming world, the sign of change of the N_2O budget (e.g. Bianchi et al., 2012; Martinez et al., 2015) and the sign of the air-sea flux of N_2O are uncertain, as increased stratification is expected to prevent N_2O from reaching the surface ocean and escaping to the atmosphere (Martinez et al., 2015).

Estimates of the total loss of bioavailable N from the open ocean is currently estimated to be 0.005-0.006 Pmol N yr⁻¹ from the water column, and 0.01-0.02 Pmol N yr⁻¹ from sediments (Somes et al., 2013). Analysis and modelling of global benthic data also indicate that denitrification in sediments underlying high nutrient-low oxygen areas such as OMZs remove around three times as much N per unit of C deposited as sediments underlying highly oxygenated water, and account for approximately 10% (i.e. 0.001 Pmol N yr⁻¹) of global benthic denitrification (Bohlen et al., 2012).

The amount of this loss is significant in regards to the inventory of fixed N (~ 300 Pmol,) and if not compensated for by other sources, has the potential to affect the content of bioavailable N over a time scale of ~10 000 yrs (Gruber, 2016). It is not yet known whether the recently inferred quadrupling of oxygen-deficient waters (Schmidtke et al., 2017) has been accompanied by a corresponding increase in anaerobic remineralization and denitrification. In oxic conditions, Fe and P can be adsorbed on particles in the sediment and onto sinking marine aggregates. With the onset of oxygen deficient conditions, the P bound to Fe oxides is generally remobilized and released to the overlying water, where it has the potential to stimulate primary production and hence further the oxygen deficiency. Oxygen deficient regions are enriched in iron and, based on the Redfield ratio, have an excess of P relative to N. These conditions are expected to be favourable for the fixation of N_2 by photosynthetic bacteria (e.g. *Prochlorococcus*, *Synechococcus*) that produce fixed N and that can potentially compensate for the loss of fixed N by denitrification and anammox. The feedbacks that link N loss and N fixation remain enigmatic. It is not yet known whether, on what time scales and to what extent global rates of N fixation respond to changes in N loss processes that are likely associated with ongoing deoxygenation (Deutsch et al., 2007; Knapp et al., 2016; Landolfi et al., 2013).

1.4.4.2 Impact on living organisms

At 100% saturation, the amount of oxygen available in one litre of water is ~35 times less than that in an equivalent volume of air. This means that in order for a marine animal to extract the same amount of oxygen in support of metabolism, the organism must pass 35 times more volume of medium across their gas exchange surfaces (gills vs lungs) or have to be much more efficient in taking up oxygen than terrestrial organisms. Critical physiological processes like respiration depend on the flux of oxygen into marine organisms (Seibel, 2011). This flux is governed by the gradient in oxygen partial pressure (pO_2) across membranes and tissues. Because pO_2 incorporates the effects of temperature, salinity and hydrostatic pressure into one single number, pO_2 thresholds are expected to be universally applicable (Hofmann et al., 2011; Seibel, 2011). Currently, most of the experiments (e.g. Davidson et al., 2016; Stevens & Gobler, 2018; Vasquer & Duarte, 2008) have addressed the effect of O_2 concentrations (rather than pO_2) on living organisms. An absolute pO_2 threshold below

which aerobic life is not sustainable still remains to be determined.

Contrary to pO_2 , oxygen concentrations do not incorporate the effect of temperature, salinity and hydrostatic pressure. Consequently, species living in open ocean permanent OMZs do not have the same oxygen concentration thresholds as species experiencing seasonal oxygen depletion in the warmer coastal ecosystems (Hofmann et al., 2011). Nevertheless, a comparative analysis of experimentally derived oxygen concentration thresholds for benthic organisms shows that there is no one single oxygen concentration threshold but rather that this threshold value can exhibit significant variability when viewed across the high diversity of taxa found in the oceans. This analysis predicts that, as oxygen declines, the sequence of losses of benthic fauna during a low oxygen event should be initiated by the loss of fish, followed by crustaceans, then worms, echinoderms, and molluscs (Vasquer & Duarte, 2008).

These differences reflect differences in taxa traits describing their ability to adapt and to escape, such as mobility, life cycle dynamics, physiological tolerance,

and metabolic adaptation over hours to days (e.g. reduced activity, lowered heartbeat rate, shift to anaerobic metabolism) (e.g. Vasquer & Duarte, 2008). Species inhabiting the permanent open ocean OMZs have evolved to be adapted to these low oxygen concentrations; an example is the vampire squid (Figure 1.9) living off California with oxygen levels below $15 \mu\text{mol O}_2 \text{ kg}^{-1}$ (Seibel et al., 1999).

1.5 Ecosystem consequences: The challenge of scaling up from species to ecosystem

The development and extension of low oxygen areas degrade the living conditions and vertically contract the metabolically viable habitat for a large number of living species. It alters marine ecosystems and biogeochemical cycles by shifting the spatial distribution of species, altering trophic relationships by favouring low-oxygen tolerant species including invasive species and microbes, and excluding sensitive species with, in the case of severe oxygen deficiency, increased mortality of the most sensitive ones (Hofmann et al., 2011). Exposure of animals to low oxygen can induce movement (avoidance), reduce survival and growth, alter behaviour and prey-predator interactions, impair



Figure 1.9 Vampire squid, *Vampyroteuthis infernalis*, recovered from 700 m depth off the coast of southern California. This species possesses specific physiological adaptations that enable them to survive in the extreme, persistent hypoxia of the oxygen minimum layer. (Seibel et al., 1999, Photograph taken by B. Seibel).

reproduction, trigger epigenetic changes, disrupt life cycles, and cause mortality (Breitbart et al., 2018). Mobile species that have the capability to avoid low oxygen waters by swimming or crawling away may escape low oxygen conditions and accumulate in well oxygenated waters. They may become more vulnerable to fishers targeting these high oxygen refuge areas. Although short-term economic benefits may result, there is concern that these strategies can contribute to misinformed management, and potentially contribute to over-harvesting of affected stocks both in coastal areas (Craig & Bosman, 2013) and the open ocean (Stramma et al., 2012). For instance, observations show that the vertical expansion of the OMZs in the tropical north-east Atlantic restricts the migration depth of billfishes and tunas to a narrower surface layer, potentially increasing their vulnerability to surface fishing gear and distorting information used in fisheries management that could lead to over-harvesting (Stramma et al., 2012). This reduction of the migration depth of these fishes can be due to a reduction of their habitat or that of their prey due to the expansion of OMZs. In coastal areas, hypoxia modifies the structure of the benthos and may affect the bioturbating/bio-irrigating activities of the macrofauna with feedbacks on the biogeochemistry of the coastal waters that are not yet well understood.

The extrapolation to marine habitats of results from laboratory controlled-experiments is not direct for several reasons. For instance, the coastal LOZ is often associated with a high level of productivity (via eutrophication or upwelling) that can be beneficial for marine animals and partially compensate for the detrimental effects of low oxygen. Oxygen concentrations in the field are not constant but vary in response to potential intermittent mixing events, oxygen consumption and production from living communities. Multiple stressors like warming, deoxygenation and acidification can interact and generate synergistic or antagonistic effects that affect the isolation and detectability of oxygen effects (Vasquer & Duarte, 2008). Also, the description of the impact of low oxygen conditions at the scale of the ecosystem is mostly qualitative and speculative. The scaling-up of information obtained in the laboratory at species level to robust quantitative information at the level of the ecosystem (~ several hundreds of kilometres) requires the development of a suite of advanced methodologies. Data analysis and simulation models provide maps of oxygen values, and appropriate transfer functions have to be devised in order to translate the consequences

of a LOZ on ecosystem functions. If appropriately parameterized, high trophic levels models can make the link with fisheries. For the biogeochemistry, some important parameterizations are still missing (e.g. N-fixation, N₂O pathways) as well as the impact of oxygen deficiencies on living organisms that mediate biogeochemical cycling (e.g. in the benthic ecosystem). The transfer of information on the environment provided by numerical models that basically address the low trophic levels up to the ecosystem faces several limitations. These include the limited capabilities of current models to simulate low oxygen values (< 20 µM), their rather coarse resolution (~ >1 km), the choice of the appropriate indicator of oxygen deficiency (concentration versus pO₂, duration of the event), the presence of other stressors (e.g. warming, acidification) that are expected to affect the lethal oxygen threshold (Vaquer-Sunyer & Duarte, 2008).

1.6 Ecosystem services consequences

Deoxygenation effects on ecosystem services are well documented in several areas and suggestive but not well quantified in many other possible pathways. This is partly due to the dynamic and localized aspects of deoxygenation, and also because of the difficulty in isolating oxygen effects from the effects of other co-varying stressors such as temperature and acidification. The challenges in isolating and quantifying the ecological effects of low oxygen (and consequently its effects on ecosystem services) should not be misinterpreted as all effects are small; effects of low oxygen can be important but hidden with other stressors and may be very important episodically.

Ecosystem services are typically divided into four categories: Provisioning (e.g. food, fresh water), Cultural (aesthetic, spiritual, education), Regulating (e.g. disease, biodiversity, water purification), and Supporting (e.g. productivity, nutrient cycling). Provisioning services have received significant attention to date, with a focus on deoxygenation effects on fisheries. Modelling analyses of fisheries demonstrate that in those situations when hypoxia alone may have small to moderate population-level effects on biomass of fish and shellfish available for harvest, the effects become large or amplified when hypoxia is combined with other stressors. A prevalent effect of deoxygenation is changes in fishing locations in response to fine-scale distribution changes due to hypoxia that affect the catchability and bio-economics of fishing. Catchabilities are relied upon for effective

fisheries management and not including their effects can result in ill-informed management analyses and incorrect harvesting advice.

Cultural services are an understudied area in ecosystem services in general. Spiritual, therapeutic, and aesthetic values remain difficult to quantify. One area of deoxygenation effects on cultural services is related to fisheries and is when deoxygenation, often in tandem with other stressors, affects traditional harvests of fish or shellfish used by indigenous peoples for spiritual purposes (Lynn et al., 2013). The potential for loss of valuable cultural services is illustrated by a recent bioeconomic analysis for the Chesapeake Bay. The loss was illustrated by showing the economic benefits that would result from improving water quality from today's conditions. The focus was on how management actions would lead to improved water quality that would result in increased recreational activities. Massey et al. (2017) roughly estimated that if the management targets on water quality were realized the benefits (in dollars) of improved water quality (including, but not limited to, higher oxygen) attributed to recreational use outside of fishing can be on the order of hundreds of millions of dollars annually. While this analysis is not a straightforward assessment of the impact of deoxygenation effects on cultural services, the results suggest that such assessments should be pursued.

The negative effects of deoxygenation on key regulating and supporting services continue to be areas of intense investigation. Alterations of benthic diversity and community structure (regulating services) due to low oxygen have been well documented (Diaz & Rosenberg, 2001; Levin et al., 2009). Another likely pathway is the loss of coral and seagrass cover due to low oxygen decreasing erosion control and water purification. How low oxygen affects the supporting services aspects of ecosystem services in terms of changes to biogeochemical cycling and the magnitude and food web pathways of productivity in coastal and open ocean ecosystems is becoming clearer but still further studies are required before generalizations can be made (Shepherd et al., 2017).

As ecology, economics, and social sciences continue to merge into integrated, coupled, natural and human systems analyses (Liu et al., 2007, 2015), the quantification of how deoxygenation and other environmental stressors affect ecosystem services will become more common.

1.7 Conclusions / Recommendations

Since about 1960, ocean deoxygenation has been occurring in the global and coastal ocean and is expected to worsen in a warming world with consequences for living organisms and on regional and global budgets of essential elements.

Better understanding of the deoxygenation process can be achieved by access to accurate observations and to furthering the reliability and coupling capabilities of physical, biogeochemical, plankton and benthic foodwebs, and upper trophic level models. Rapid advancement is being made in each of the modelling types, as well as in how best to couple them, in order to generate "climate to fish" models (Rose et al., 2010) that include oxygen effects. A regular monitoring of the state of the ocean with respect to oxygen based on observations and modelling offers new knowledge on the fundamental processes like global circulation, photosynthesis, respiration and interactions with the atmosphere. Keeling and Manning (2014) found that a better estimation of the oxygen air-sea flux would offer a better estimation of the Earth carbon budget of the order of 0.5 Pg C yr⁻¹. Indeed, the recent understanding that the air-sea flux of oxygen is probably not balanced, but rather reveals a net outgassing of oxygen from the ocean to the atmosphere leads to a revision of the global carbon budget and, in particular, the partitioning of the ocean and land carbon sinks.

Oxygen maps (climatologies) are regularly produced for the global ocean based essentially on ship-based data (e.g. Schmidtko et al., 2017; Stramma et al., 2008). Once quality checked, the oxygen time series delivered by Argo floats have the potential to enhance these climatologies by providing a high frequency signal. The lack of openly available oxygen data from the coastal ocean in a centralized database prevents a similar global mapping of oxygen for the coastal ocean. This would be needed in order to update the inventory of Diaz and Rosenberg (2008) and to reassess the state of deoxygenation in coastal waters.

The success of combating deoxygenation relies on our capacity to understand and anticipate its consequences in an environment affected by local, regional, and global processes. State-of-the-art models have capabilities to simulate the deoxygenation process in the global and coastal ocean, and their parameterizations and formulations should continuously evolve based on

new knowledge. Model development needs new observations and dedicated experiments, in particular in low oxygen and anoxic waters that are particularly challenging to measure and to model. Oxygen levels act as a “switch” for nutrient cycling and availability. The detailed nature of these thresholds and their ecological and biogeochemical implications are still a matter of intense scientific investigation.

For both the global and coastal ocean, an estimation of the uncertainty that accompanies projections of mean state is critical for management purposes. With this aim, ensemble approaches combining the projections of various models are promising, especially for the global ocean (e.g. Bopp et al., 2013); a similar process is emerging for the regional ocean as well (Meier et al., 2011). International platforms and programmes like IPCC (Intergovernmental Panel for Climate Change), IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services), the WCRP (World Climate Research Programme) CMIP (Coupled Model Intercomparison Project) project and the European Copernicus Marine Environment Service (CMEMS) promote the capacity to produce and evaluate ecological forecasts and long-term projections. Evidence has shown that the evolution of the oxygen levels is not a straightforward function of temperature but rather depends on the subtle interactions between physical and biogeochemical mechanisms whose balance can evolve in answer to anthropogenic forcings and over time scales of centuries (e.g. Jaccard & Gallbraith, 2012).

An enhanced understanding of the long-term response to climate warming of oxygen supply versus demand since the industrial revolution would improve our capabilities to project future changes (e.g. Deutsch et al., 2014).

A process that engages a dialogue between decision makers and scientists is necessary to foster communication between the two communities and to assure the saliency of model projections. Recently, IOC-UNESCO established the Global Ocean Oxygen Network (GO₂NE), a global network of ocean oxygen scientists, including experimentalists, modellers and field scientists, to promote scientific collaboration and public outreach (e.g. Breitburg et al., 2018).

1.8 References

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"The decline in the oceanic oxygen content can affect ocean nutrient cycles and the marine habitat, with potentially detrimental consequences for fisheries, ecosystems and coastal economies."

Chapter 2.1 authors

Global and regional case studies of ocean deoxygenation 2

No other chemical parameter is of such importance to marine life as dissolved oxygen. The equilibrium state of the ocean-atmosphere system has recently become perturbed, with the ocean becoming a source of oxygen for the atmosphere, even though its oxygen inventory is only about 0.6% of that of the atmosphere. Different analyses conclude that the global ocean oxygen content has decreased by 1-2% since the middle of the 20th century. While the biogeochemical and physical changes associated with ocean warming, deoxygenation and acidification occur all over the world's ocean, the imprint of these global stressors has a strong regional and local nature, a theme which is explored in this chapter.

In the following sections of this chapter global and regional evidence for ocean deoxygenation is explored in more details. Perhaps the most familiar regions of the ocean subject to low oxygen are the Baltic Sea and Black Sea. These are the world's largest enclosed low oxygen marine ecosystems. While the deep basin of the Black Sea is naturally anoxic, the low oxygen conditions currently observed in the Baltic Sea have been caused by human activities and are the result of enhanced nutrient inputs from land, exacerbated by global warming.

In the open ocean the eastern boundary upwelling systems are one of the ocean's most productive biomes, supporting one fifth of the world's wild marine fish harvest. As naturally oxygen-poor systems, these upwelling system are especially vulnerable to any changes in global ocean deoxygenation and so what happens to the oxygen content of them ultimately will ripple out and affect many hundreds of millions of dependent people. In the Atlantic, oxygen concentrations at mid-ocean depths have decreased during the last 60 years, partly due to ocean warming, partly as a result of decreased mixing and ventilation. Elsewhere the low-oxygen zones of the Indian Ocean are expected to expand and intensify.



2.1 Global evidence of ocean deoxygenation

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Summary

- The global oxygen inventory has decreased by ~2% over the period 1960 to 2010, this finding is supported by regional time series data that indicate a continuous decrease in oceanic dissolved oxygen.
- Ocean model simulations predict a decline in the dissolved oxygen inventory of the global ocean of 1 to 7% by the year 2100, caused by a combination of a warming-induced decline in oxygen solubility and reduced ventilation of the deep ocean.
- Open-ocean deoxygenation is resulting mainly from a warming ocean, increased stratification and changing circulation which interact with eutrophication-induced hypoxia (oxygen concentration below ~60 to 120 $\mu\text{mol O}_2 \text{ kg}^{-1}$) and biological activity in shelf regions.
- Climate change related longer-term oxygen trends are masked by oxygen variability on a range of different spatial and temporal scales.
- The decline in the oceanic oxygen content can affect ocean nutrient cycles and the marine habitat, with potentially detrimental consequences for fisheries, ecosystems and coastal economies.
- Oxygen loss is closely related to ocean warming and acidification caused by CO_2 increase driven by CO_2 emissions as well as biogeochemical consequences related to anthropogenic fertilization of the ocean; hence a combined effort investigating the different stressors will be most beneficial to understand future ocean changes.

Global deoxygenation effects	Consequences
Continuous loss of global oceanic dissolved oxygen content.	<ul style="list-style-type: none"> • First ecosystem changes can be observed, habitat compression occurs and large-scale changes in ecosystems are expected for the future.
Increasing deoxygenation and anoxia occurs in large areas of the continental shelves.	<ul style="list-style-type: none"> • Reduced fish catches with decreasing economic profit in coastal states are expected.
Deoxygenation is overlain by climate variability, interactions and understanding of impacts is limited.	<ul style="list-style-type: none"> • Periods with enhanced, reduced or even increased deoxygenation might appear, and predictions of the future deoxygenation are insecure.
Open ocean oxygen loss is closely connected to ocean warming and acidification caused by CO ₂ increase driven by CO ₂ emissions.	<ul style="list-style-type: none"> • Continuous CO₂ emissions will increase deoxygenation, warming, and acidification of the ocean.
Specific ecosystem services can be negatively affected by combined deoxygenation, pollution and ocean acidification.	<ul style="list-style-type: none"> • Negative impacts are expected on biological regulation, nutrient cycling and fertility, food, ornamental resources (like corals, pearls, shell material), tourism and recreation.

2.1.1 Introduction

Despite its far-reaching consequences for humanity, the focus on climate change impacts on the ocean lags behind the concern for impacts on the atmosphere and land (Allison & Bassett, 2015). In the ocean a reduction in ventilation and decrease of oceanic dissolved oxygen are two of the less obvious but important expected indirect consequences of climate change on the ocean (Shepherd et al., 2017). Deoxygenation of the open ocean is one of the major manifestations of global change. It accompanies ocean warming and ocean acidification as one of the three major oceanic consequences of rising atmospheric CO₂ levels (Levin & Breitburg, 2015). In addition, agricultural runoff and human waste cause decreasing oxygen concentrations in estuaries and coastal areas as well as the adjacent open ocean.

Oxygen is distributed in the ocean through an intimate interplay of physics and biology. Oxygen is transported by ocean circulation and mixing processes from the well-ventilated surface into the depths of the ocean interior. The ocean surface layers are saturated with oxygen due to atmospheric exchange and photosynthesis, primarily by phytoplankton. Oxygen is consumed by all animals throughout the ocean, but the majority of consumption occurs by bacterial respiration of organic matter. Both the supply and consumption of oxygen are severely modulated by climate change in ways that are not yet fully understood (Levin, 2018). On the continental shelf, nutrient input and eutrophication-induced hypoxia influences the oxygen concentration and hence the coastal ecosystem. Variations in marine oxygen concentrations can induce major changes to remineralization processes and associated sources and

sinks of important nutrient elements such as nitrogen, phosphorus and iron in the water column and underlying sediments (Oschlies et al., 2018). For instance, radically different microbial and chemical processes operate at low oxygen levels, such as anaerobic remineralization of organic matter by denitrification, leading to a net loss of fixed nitrogen from the ocean. Therefore, oxygen levels can act as a 'switch' for nutrient cycling and availability.

For the past several hundred million years, oxygen concentrations in Earth's atmosphere have been comparatively high (e.g. Mills et al., 2016). However, parts of the ocean seem never to have been far from anoxia (oxygen depleted) and have occasionally suffered major oceanic anoxic events (OAEs). In the past OAEs seem to have been promoted by warm climates, and some have been associated with major environmental crises and global-scale disturbances in the carbon cycle (Watson, 2016). Palaeo-records from the late Permian and Cretaceous provide evidence for past periods of dramatically reduced oceanic oxygen levels, and these had major consequences for marine ecosystems leading to mass extinctions. Major low-oxygen events in the past were primarily associated with warmer climates and higher atmospheric CO₂ levels. Hence deoxygenation, accompanying the present changes in climate, has to be understood in detail to be able to predict future ocean changes and propose societal actions that can help to avoid or minimize future anthropogenic inputs to oceanic deoxygenation events.

2.1.2 Geographic definition

Until recently knowledge of ocean deoxygenation was based on local time series of individual measurements

or from geographically restricted areas of oxygen data collections. In recent years the various data for the entire world ocean from the surface to the ocean bottom were used to investigate the trends in oxygen from both measurements as well as numerical model runs. The computed oxygen inventory for the whole world ocean from the sea surface to the ocean bottom varies for the different ocean basins and reflects oceanic volume, bathymetry and deep-water ventilation rates (Schmidtko et al., 2017). The largest oxygen inventories exist in the well-ventilated deep Atlantic Ocean (Figure 2.1.1A).

In the eastern Pacific and Atlantic Oceans as well as in the northern Indian Ocean the oxygen concentration is lower at mid ocean depths due to weak water renewal by sluggish ocean circulation. These regions are often called oxygen minimum zones (OMZs), e.g. marked in Figure 2.1.1 by the $80 \mu\text{mol O}_2 \text{ kg}^{-1}$ contour. In the eastern portions of ocean basins, the sluggish circulation is caused by the asymmetric shape of the subtropical gyres, which lead to weak ventilated regions at the eastern sides equatorward of the subtropical gyres, sometimes referred to as shadow zones (see Box 2.1.1). Formation of well oxygenated deep water can be

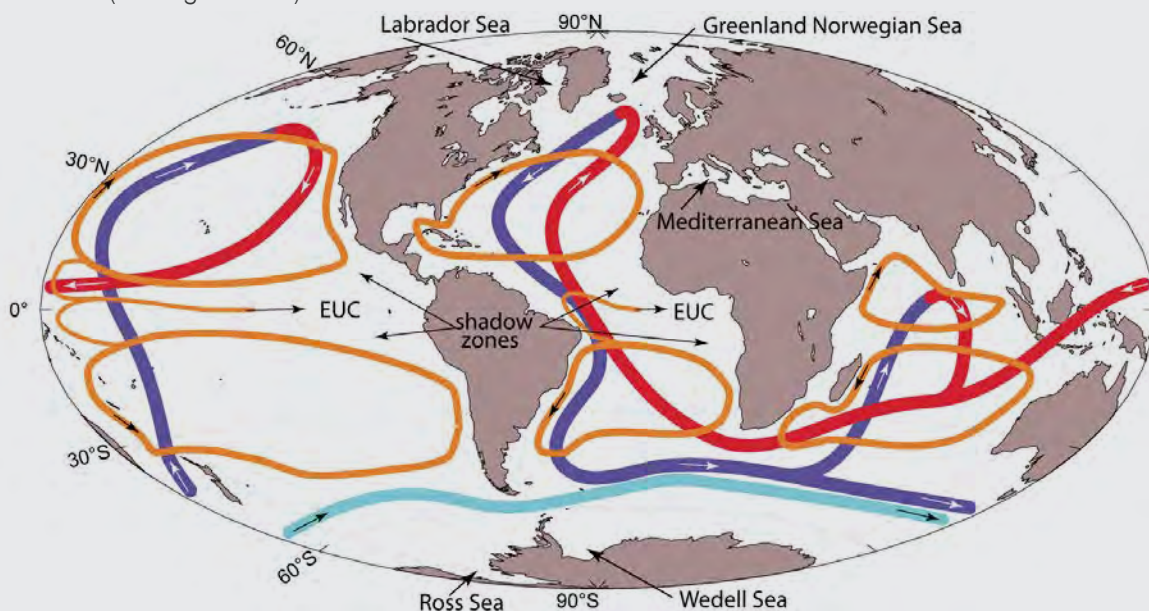
reduced by ocean surface warming in two ways: by a reduction in ventilation volume, and by a temperature increase of the water formed. Formation of this deep water that drives thermohaline ocean circulation on a global scale takes place in a few areas: the Greenland-Norwegian Sea, the Labrador Sea, the Mediterranean Sea, the Weddell Sea and the Ross Sea (see Box 2.1.1). These are the source regions ventilating the deep ocean basins via deep western boundary currents. These deep currents later upwell and form near-surface currents that complete the thermohaline circulation pattern.

2.1.3 Trends and impacts

Ocean models predict a decline of total dissolved oxygen in the global ocean in the order of 1 to 7% by the year 2100, caused by a combination of warming-induced decrease in oxygen solubility and reduced ventilation of the deep ocean (e.g. Keeling et al., 2010; Oschlies et al., 2018; Schmidtko et al., 2017). Oxygen trends, variability and impacts based on measurements are often analysed locally or across small geographical regions and should be used to verify the model results.

Box 2.1.1 Major ocean circulation features

The distribution and changes in oxygen are related to the large-scale wind driven and thermohaline ocean circulation (Box Figure 2.1.1)



Box Figure 2.1.1 Schematic distribution of the wind driven subtropical gyres (orange) and their contribution to the Equatorial Undercurrent (EUC) and the warm (red) and cold (blue) components of the thermohaline overturning circulation. The cool Antarctic Circumpolar Current (light blue). The shadow zones of the Pacific and Atlantic oceans are marked by arrows as well as the Labrador Sea, the Greenland-Norwegian Sea, the Mediterranean Sea, the Ross Sea, and the Weddell Sea.

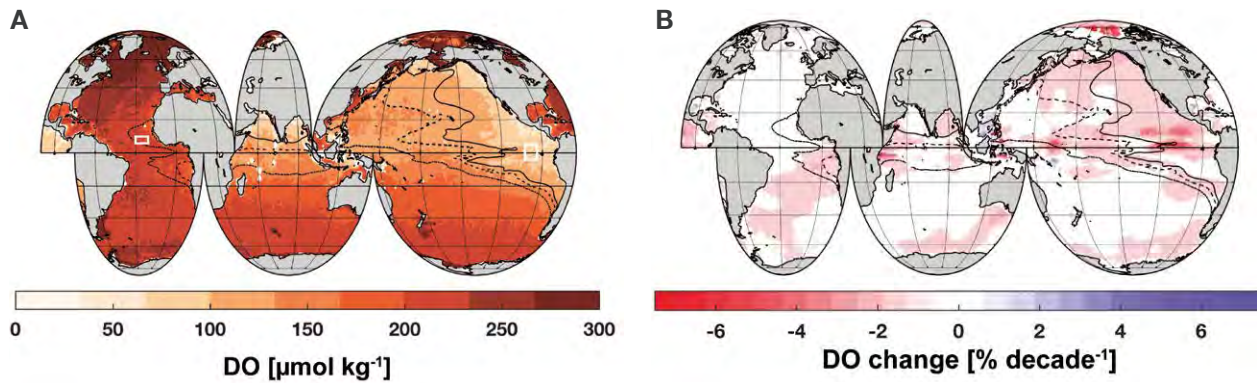


Figure 2.1.1 A): Global ocean top to bottom oxygen inventory (colour coded) with lines indicating boundaries of oxygen-minimum zones (OMZs), dash-dotted regions with less than $80 \mu\text{mol kg}^{-1}$ oxygen anywhere within the water column; dashed lines and solid lines similarly represent regions with less than $40 \mu\text{mol kg}^{-1}$ oxygen and $20 \mu\text{mol kg}^{-1}$ oxygen respectively. B): Change in dissolved oxygen per decade in % for the time period 1960 to 2010, based on Schmidtko et al. (2017). Areas 5°N - 5°S , 105° - 115°W and 10° - 14°N , 20° - 30°W used here are marked in white in A).

Despite data limitations, it is feasible to detect significant oxygen changes over time in some regions. These studies cover different time frames and regions (Keeling et al., 2010). Regional observational data (Stramma et al., 2008) indicate a continuous decrease in oceanic dissolved oxygen content in most regions of the global ocean. Despite the already low oxygen content in the tropical ocean, a decrease of oxygen was observed for selected regions in all three tropical ocean basins for the period 1960 to 2008 (Stramma et al., 2008). These time series reveal vertical and horizontal expansion of the intermediate-depth low-oxygen zones and reduced oxygen content in the OMZ cores, where the oxygen concentration is lowest.

Despite limited data some large-scale analyses have been undertaken based on measurements in the literature. A recent and comprehensive analysis of observed oxygen changes indicates a 2% (i.e. 96 Tmol yr^{-1} ($\text{Tmol} = 10^{12} \text{ mol}$)) decline of total global ocean oxygen content over the 50 year period 1960 to 2010 (Schmidtko et al., 2017). Five distinct regions with significant oxygen loss stand out that cannot be directly attributed to solubility changes alone. These are the tropical regions of all basins, which contain most of the upper-ocean OMZ, the North Pacific, the South Atlantic, the Southern Ocean and the Arctic Ocean (see Figure 2.1.1B). Different drivers for the oxygen decrease in these regions have been proposed (Schmidtko et al., 2017). For the upper (0 - 1200 m depth) North Pacific a decline in North Pacific Intermediate Water formation is thought to be the main cause of decreasing oxygen content, whereas for the deep (1200 m to ocean bottom) South Atlantic a reduced or changing ventilation process as well as multi-decadal variability seem to be responsible

(Schmidtko et al., 2017). The amount of oxygen lost globally in the upper ocean has been estimated to be about $26 \text{ Tmol O}_2 \text{ yr}^{-1}$ (0 to 1200 m layer for 1960 to 2010; Schmidtko et al., 2017) similar to the $24 \text{ Tmol O}_2 \text{ yr}^{-1}$ (0 to 1000 m for 1958 to 2015) estimated by Ito et al. (2017). A larger decrease reported for the 100 – 1000 m layer of $55 \text{ Tmol O}_2 \text{ yr}^{-1}$ between the 1970s and 1990s (Helm et al., 2011) is probably related to the strength of the Pacific Decadal Oscillation during this time period.

Circulation in the thermocline (~ upper few hundred metres of the ocean) is predominantly wind-driven and therefore particularly sensitive to changes in wind patterns, which in turn are highly associated with major climate modes such as Pacific Decadal Oscillation (PDO) and El Niño-Southern Oscillation (ENSO) in the Pacific Ocean and North Atlantic Oscillation (NAO) and Atlantic Meridional Mode (AMM) in the Atlantic. Hence these climate modes have a strong potential influence on the changes in the upper ocean oxygen content. For example for the overall time period of positive and negative PDO (1960 to 2008) in the tropical eastern Pacific (5°S to 5°N , 105°W to 115°W ; area D in Stramma et al. (2008); see Figure 2.1.1) the oxygen decrease is $0.23 \mu\text{mol O}_2 \text{ kg}^{-1} \text{ yr}^{-1}$ in the 200 to 600 m depth layer but for the time period of mainly positive PDO (1979 to 2008) a much stronger oxygen decrease occurs ($0.64 \mu\text{mol O}_2 \text{ kg}^{-1} \text{ yr}^{-1}$, Figure 2.1.2).

Global warming leads to upper ocean warming, and less dissolved oxygen can therefore be stored in the surface layer due to a reduced oxygen solubility in warmer water. A tight relationship between oxygen inventories and ocean heat content was observed from measurements for the upper 1000 m (Ito et al., 2017). Temperature

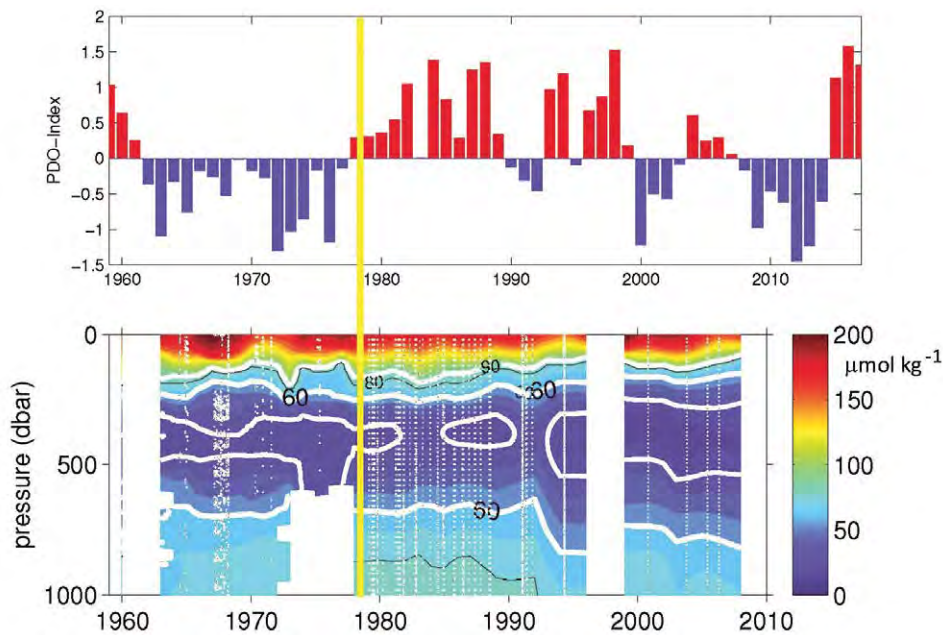


Figure 2.1.2 Annual mean Pacific Decadal Oscillation Index (<http://ds.data.jma.go.jp/tcc/tcc/products/elnino/decadal/annpdo.txt>) and dissolved oxygen concentration ($\mu\text{mol kg}^{-1}$ versus time in the eastern equatorial Pacific Ocean (5°S to 5°N , 105° to 115°W (area D in Stramma et al., 2008)). The yellow line marks the shift from the negative to the positive PDO phase.

profiles in the Japan Sea show a warming by as much as $0.1 - 0.5^{\circ}\text{C}$ in the upper 1000 m and by 0.01°C below 2000 m for a 30 year period and an associated oxygen decrease in the deep layer (Watanabe et al., 2003). Furthermore, warmer waters are less dense and enhance ocean stratification and consequently less oxygen-rich waters reach the deep ocean. A reduced oxygen supply in midwater depths, in the absence of any major change in the midwater microbial community, leads to a decreased oxygen concentration at a given depth, and ultimately to vertical expansion of the OMZs and the low-oxygen zone above them. In effect, this vertical expansion reduces the volume of the well-oxygenated epipelagic surface zone, thus reducing habitat extent of many fishes with high oxygen demand (Figure 2.1.3).

Another important driver of decreased oxygen content in coastal oceans is eutrophication-induced hypoxia that results from addition of excess nutrients into the ocean. The number of such coastal zone sites has increased by an order of magnitude since the 1960s (Diaz & Rosenberg, 2008) and oxygen decline rates are more severe in a 30 km band near the coast than in the open ocean (Gilbert et al., 2010). Near eastern shelf-breaks, poleward undercurrents such as the California and Peru-Chile Undercurrent in the Pacific Ocean and the Mauritania and Angola Currents in the Atlantic carry oxygen-poor water from expanding tropical OMZs

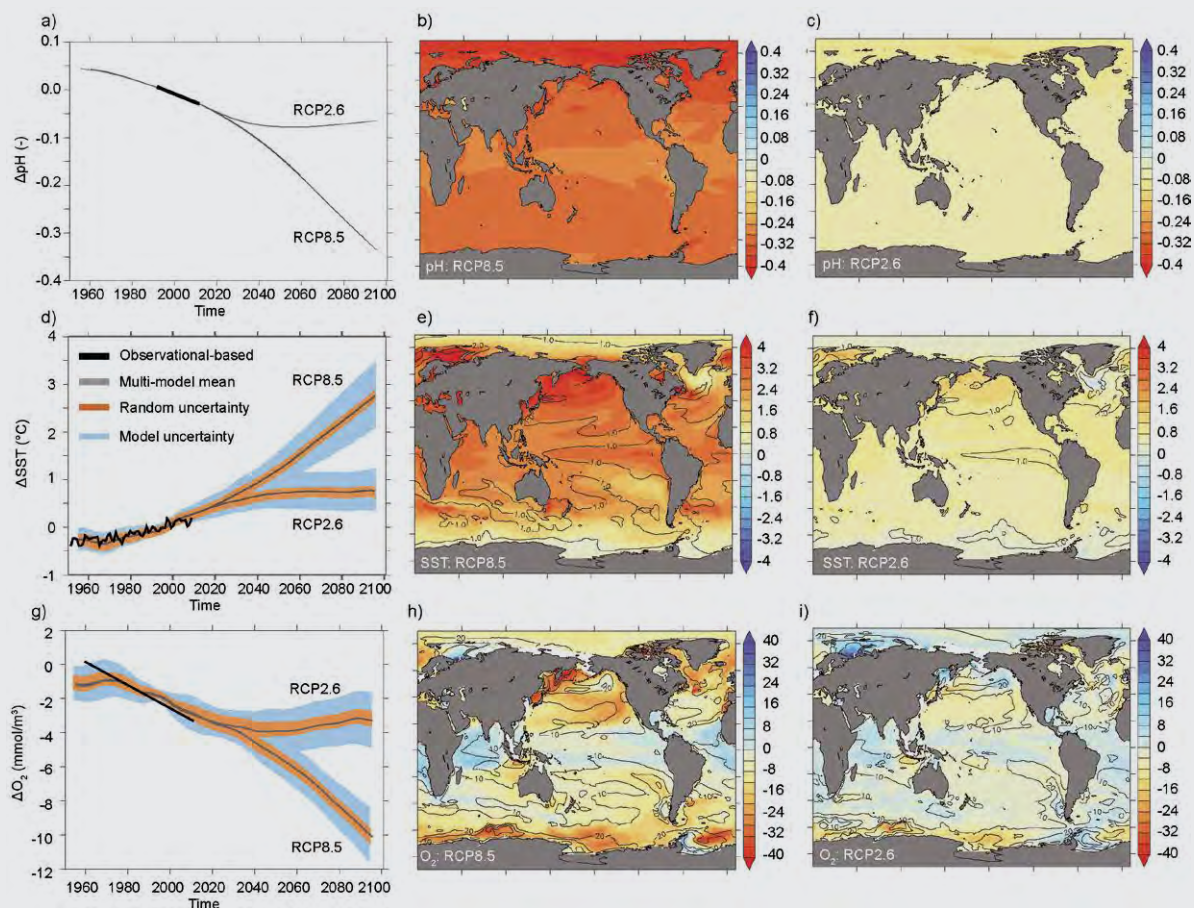
toward the subtropics, where it can interact, often through wind-driven upwelling processes, with both natural and eutrophication-induced hypoxic zones on the inner shelves. This occurs for example off Peru, Chile, Namibia and the western Indian margin (Figure 2.1.3; Stramma et al., 2010). In the eastern Pacific these oxygen-poor upwelled waters are corrosive (low pH) and undersaturated with respect to aragonite, exacerbating the stress imposed on the exposed ecosystem (Feely et al., 2008). It is important to point out that the unusually high productivity of such shelf regions depends on wind-driven upwelling. Upwelling of deoxygenated and corrosive water will impact the largest fisheries on the planet, e.g. that for Peruvian anchoveta.

Results of numerical biogeochemical Earth system models reveal that the magnitude of the observed change is consistent with CO_2 -induced climate change. However, the correlation between pattern of simulated and observed oxygen change is negative for the subtropical and tropical upper ocean, indicating that the models do not correctly reproduce the current processes responsible for observed regional oxygen changes (Stramma et al., 2012a). Particularly in the tropical thermocline, a region which features open-ocean oxygen minimum zones, observations indicate a general oxygen decline, whereas most of the state-of-the-art models simulate increasing oxygen levels in these OMZs. Wind-driven changes in the low-latitude

Box 2.1.2 Future projections based on projected greenhouse gas emissions

Model projections into the future depend on the projected greenhouse gas emissions. Representative Concentration Pathways (RCPs) are four greenhouse gas concentration trajectories which describe possible climate futures that are considered possible depending on the scale of greenhouse gas emissions in the years to come. They are RCP2.6, RCP4.5, RCP6 and RCP8.5 reflecting a range of possible greenhouse gas-caused radiative forcing values in the year 2100 relative to pre-industrial values of +2.6, +4.5, +6.0 and +8.5 W m^{-2} (difference between insolation absorbed by the Earth and energy radiated back to space). RCP2.6 is compatible with the Paris Agreement and assumes that global annual greenhouse gas emissions peak between 2010-2020, with emissions declining substantially thereafter. In RCP8.5 emissions continue to rise throughout the 21st century, often called 'business as usual'. The key greenhouse gases emitted by human activities are 76% carbon dioxide, 16% methane, 6% nitrous oxide and 2% fluorinated gases (IPCC, 2014).

To assess internal variability and model scenario uncertainties, a combination of several Earth System Models (Frölicher et al., 2016) was used, and the results project a decrease of surface pH, increase of sea surface temperature (SST), and oxygen loss in most ocean basins in the 100 to 600 m layer by 2100 for the RCP2.6 and the RCP8.5 scenarios (Box Figure 2.1.2). Hence even the most optimistic scenario (RCP2.6) would lead to lower ocean surface pH, as well as ocean warming and deoxygenation in the future (Box Figure 2.1.2 c, f, i). By the end of the 21st century pH is projected to decrease (in pH units) by 0.29 ± 0.005 (RCP8.5) and 0.07 ± 0.005 (RCP2.6), SST is projected to increase by $2.39 \pm 0.50^\circ\text{C}$ (RCP8.5) and $0.75 \pm 0.30^\circ\text{C}$ (RCP2.6), and oxygen concentrations averaged over 100-600 m depth are projected to decrease by $6.98 \pm 1.02 \text{ mmol m}^{-3}$ (RCP8.5) and $1.29 \pm 1.06 \text{ mmol m}^{-3}$ (RCP2.6). (Those oxygen units are equivalent to $\mu\text{mol L}^{-1}$ and $\sim\mu\text{mol kg}^{-1}$).



Box Figure 2.1.2 Time series and spatial patterns of simulated change in surface pH, sea surface temperature ($^\circ\text{C}$), and oxygen concentration (mmol m^{-3}) averaged over 100 to 600 m depth. Simulated spatial patterns of multi-model mean changes in year 2095 for the (middle column) RCP8.5 scenario and right column RCP2.6 scenario (Reprinted with permission from Frölicher et al., 2016 (© Wiley and Sons)).

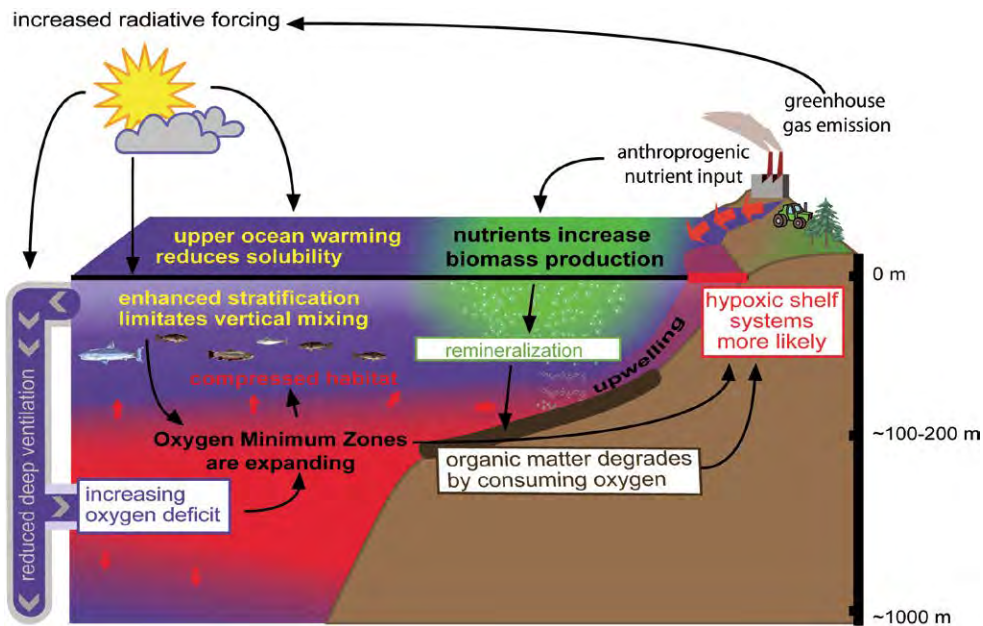


Figure 2.1.3 Schematic of interactions of open ocean oxygen minimum zone (OMZ, red) with hypoxic shelf system and dead zones on continental shelves of eastern ocean boundaries (modified after Stramma et al., 2010).

oceanic ventilation are identified as a possible factor contributing to the apparent discrepancies during the past decades. Other factors relevant to model-data discrepancies are the roles of equatorial jets, lateral and diapycnal mixing processes, changes in the wind-driven circulation, atmospheric nutrient supply and some poorly constrained biogeochemical processes (Oschlies et al., 2017). The process associated with the largest changes in simulated oxygen trend was variability in the wind forcing, particularly during the period prior to the oxygen content evaluation. Thus, a better observational constraint on the wind fields before the 1960s will help to yield more robust simulations of oxygen changes during the 50 years between 1960 and 2010 (Oschlies et al., 2017). Continued development and refinement of this more nuanced modelling approach thus holds great promise to more accurately predict future changes



Figure 2.1.4 Humboldt (jumbo) squid (*Dosidiscus gigas*) at night - Gulf of California' © robertharding/Alamy stock photo.

in ocean oxygen on a regional scale and resolve some observation-model discrepancies.

2.1.4 Ecosystem consequences

Oxygen influences biological processes at the most fundamental level. Changes in temperature, oxygen content, and to a lesser degree some other ocean biogeochemical properties directly affect the ecophysiology of marine water-breathing organisms with regard to distribution, phenology and productivity (Cheung et al., 2012). Expanding OMZs benefit microbes and life forms adapted to hypoxia while restricting the ranges of most other species. Eutrophication as a result of coastal pollution exacerbates this problem, through organic matter which increases metabolic consumption in deeper coastal areas (Gattuso et al., 2015). Moreover, higher temperatures lead to community-level shifts to smaller Eukarya, Bacteria and Archaea under conditions of diminished oxygen (see e.g. Gattuso et al., 2015) and also increase sensitivity of various fish and invertebrates to hypoxia, thereby limiting the depth distribution of those species not adapted to hypoxic conditions. In the tropical Atlantic, for example, the expansion of the OMZ reduced the available habitat for tropical pelagic fishes (Stramma et al., 2012b). In addition, the maximum size of exploited fishes decreases with rising temperature and decreasing oxygen level, ultimately reducing potential fish yields (Baudron et al., 2014) which is in agreement with current model predictions (e.g. Cheung et al., 2012).



Figure 2.1.5 Owlfish (*Bathylagus miller*) Monterey Bay © 2001 MBARI.

Conversely, hypoxia-adapted species may benefit, as illustrated by the range-expansion of Humboldt squid (Figure 2.1.4), a species which is well adapted to hypoxia (Stewart et al., 2014). Increases in jellyfish blooms have been linked to eutrophication and hypoxia and lowered pH; such blooms may indirectly promote hypoxia by preying on zooplankton, leaving more unconsumed phytoplankton to sink and degrade via microbial consumption (Purcell et al., 2001). Some species will potentially benefit from a habitat expansion, these include, for example, larger animals that permanently inhabit the OMZ and include species with extremely low metabolic rates, e.g. the vampire squid and the mysid shrimp which have enhanced oxygen extraction and transport abilities and the bathylagid owlfishes (Figure 2.1.5), the pelagic worm *Poebobius meseres* (Christiansen et al., 2018) and filter-feeding tunicates (e.g. Pacific transparent sea squirt, or common sea grape) (Gilly et al., 2013). The impact of habitat compression was also quantified by the change in proportion of zooplankton biomass in the upper water column (Wishner et al., 2013). The vertical repositioning of biomass layers and the increased depth range of low oxygen water that diel vertical migrators and sinking particles must transit in an expanded OMZ, could have widespread effects on species distribution, the biological pump, and benthic-pelagic coupling (Wishner et al., 2013).

Future projections of potential stressors of ocean ecosystems, such as deoxygenation, warming, acidification, and changes in ocean productivity, remain vague due to incomplete understanding of fundamental mechanisms behind these processes, internal climate variability, and divergent carbon-emission scenarios (Frölicher et al., 2016). Nevertheless, it is clear that future oxygen changes will be strongly dependent on and

mostly negatively impacted by future global greenhouse gas emissions (see Box 2.1.2).

2.1.5 Societal consequences

Deoxygenation especially in shelf and coastal waters has and will lead to more societal consequences. Productivity will be decreased both for capture fisheries and aquaculture. Fish and shellfish species that support regional human needs for protein are scarce and vulnerable to hypoxic waters, a problem particularly severe for artisanal fisheries without the capability of relocating in response to hypoxic or anoxic events that cause mortality and changes in distributions of fisheries species (Levin & Breitburg, 2015). Human communities, especially in developing nations, that depend heavily on coastal fishery resources for food, economic security, and traditional culture are at particular risk from shifts in ocean primary production and species habitat ranges (Gattuso et al., 2015).

Ecosystem services comprise the entire range of benefits that nature provides to human communities and can be classified in four major categories: supporting services, provisioning services, regulating services and cultural services (see Cooley, 2012). Specific ecosystem services could be negatively affected by pollution, warming, ocean acidification, and deoxygenation. Services that are very likely to be negatively impacted by all stressors include: the supporting services of biodiversity, biological regulation, nutrient cycling, and fertility of marine organisms; the provisioning services of food, building materials, ornamental resources (e.g. coral, pearls, shell material, aquarium fish); and all the cultural ecosystem services of spiritual benefits, tourism and recreation, aesthetic benefits, and opportunities for education and research (Cooley, 2012).

Established, emerging, and new ocean industries are directly influenced by oceanic deoxygenation. Negative influences are listed with regard to fisheries, aquaculture, pharmaceuticals and chemical industries, tourism, and assimilation of nutrients; whilst positive influences are seen only with regard to technology R & D (Allison & Bassett, 2015).

Societal responses to climate change range from individual adaptive decisions, to attempts by representatives of sovereign states to reach a global consensus on reducing greenhouse gas emissions (Allison & Bassett, 2015). O'Neill and Nicholson-Cole



Figure 2.1.6 A menhaden (*Brevoortia tyrannus*) fish kill due to severe hypoxia – near anoxia in Greenwich Bay (Narragansett Bay, Rhode island) © Chris Deacutis.

(2009) have shown that non-threatening images that engage everyday emotions, such as a picture of a community mobilizing to protect their local environment, are more likely to inspire wider citizen action to address climate change impacts than are fear-inducing representations of a climate catastrophe. For example, pollutants mostly from wastewater treatment facilities resulted in poor water quality and deoxygenation in Narragansett Bay over the past decades. The pollution led to algal blooms and a lack of dissolved oxygen in the bay. Following a large fish kill in 2003 (Figure 2.1.6) wastewater treatment plants reduced the amount of nitrogen discharge into the water and in some parts of the Bay the oxygen returned to normal levels by 2014 leading to better water quality and a healthier marine habitat that resulted in increased home prices in this region (Jepsen, 2017).

2.1.6 Implication of continuing ocean deoxygenation

As deoxygenation is closely connected to global warming and CO₂ increase, a continuation and possibly acceleration of the current rate of ocean deoxygenation is expected. An area in the eastern tropical Atlantic,

where repeated measurements have been made in recent years indicates that the oxygen concentration continuously decreased in the open ocean in the 50 to 300 m layer by 0.49 $\mu\text{mol kg}^{-1}\text{yr}^{-1}$ for the period 1960 to 2016 (Figure 2.1.7). Excess nutrients from land can stimulate further biogeochemical activity and push open-ocean ecosystems into more severe hypoxic conditions. At the same time, future warmer estuarine and ocean waters resulted in an increasing number of eutrophic coastal sites approaching hypoxic tipping points, thus worsening the severity and spatial extent of oxygen depletion in systems with historically occurring hypoxia (Levin & Breitburg, 2015). Harmful algal blooms might be augmented from nutrients released in bottom water due to hypoxia (Davidson et al., 2014) with severe consequences for pelagic fishes and invertebrates that provide important fisheries for humans and prey for marine mammals.

Shoaling of the upper boundaries of the OMZs accompanies horizontal OMZ expansion, and decreased oxygen at shallower depths can affect all marine organisms through multiple direct and indirect mechanisms. Effects include altered microbial processes that produce and consume key nutrients and gases, changes in predator-prey dynamics, and shifts in the abundance and accessibility of commercially fished species (Gilly et al., 2013). Microbial communities will be greatly affected by the expansion and shoaling of OMZs. Three key changes in microbial communities and microbe-mediated biogeochemical cycles are likely to be consequences of OMZ expansion, intensification, and shoaling: alteration of the N cycle, the emergence of sulphur (S) cycling, and the creation of new low-oxygen habitats (Gilly et al., 2013). The removal of nitrogen can be a limiting nutrient in upwelling areas, phytoplankton growth and surface production would be reduced. In OMZs sometimes sulphate seems to be reduced to sulphide, which is toxic to most organisms. Deeper low-oxygen habitats will expand as OMZ shoals with effects on carbon, nitrogen and sulphur cycling, but the ultimate biogeochemical outcome is difficult to predict (Gilly et al., 2013).

2.1.7 Conclusions / Recommendations

Deoxygenation is an ongoing process and is expected to continue as increasing global temperatures reduces the capacity of the ocean to hold oxygen, decreases the degree of mixing in the upper water column and reduces the ocean overturning circulation. The current

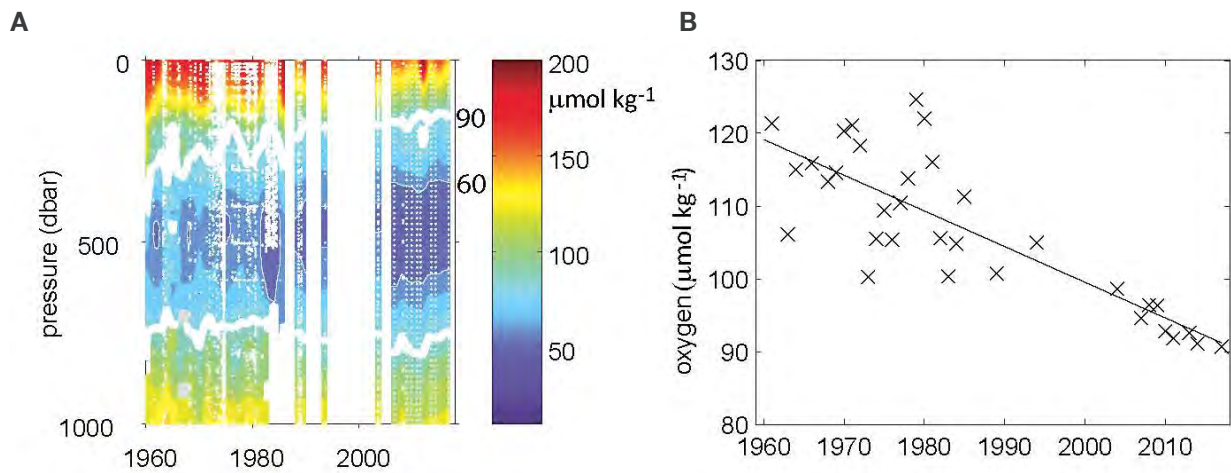


Figure 2.1.7 A) Dissolved oxygen concentration ($\mu\text{mol kg}^{-1}$) versus time in the eastern tropical Atlantic Ocean (10° to 14°N , 20° to 30°W (area A in Stramma et al., 2008)) extended with cruises until September 2016; and B) mean oxygen content of the layer 50 to 300 m with a decreasing linear trend of $0.49 \mu\text{mol kg}^{-1} \text{ yr}^{-1}$ for the period 1960 to 2016.

understanding of both the causes and consequences of reduced oxygen in the ocean and our ability to represent them in models especially in the low latitudes are inadequate. The reasons for the discrepancies between simulations and observations currently remain unclear (Shepherd et al., 2017).

Accelerated oxygen loss in both the open ocean and coastal waters is generating complex biological responses. The phenomena in the open ocean and in shelf regions are highly interconnected, and investigations in both areas need to be linked more closely in the future to address ocean deoxygenation.

Spatial patterns of oxygen change differ considerably between observed and modelled estimates. Within models the primary uncertainty of ocean deoxygenation in the subsurface tropical ocean is due to a compensation between decreasing oxygen saturation due to warming and decreasing apparent oxygen utilization (difference between oxygen saturation and measured oxygen concentration) due to increased ventilation of the corresponding water masses (Bopp et al., 2017). Model improvements are needed for better simulations to understand oxygen changes and consequently improve the quality of projections further into a changing future (Oschlies et al., 2017).

Detecting time-varying trends in ocean properties and processes requires consistent, high-quality measurements. Ocean time-series as well as spatial monitoring provide vital information needed for assessing oxygen-related ecosystem change. Some

of the most important contributions to emerge from the ocean time-series programmes are reconstructions of biogeochemical rate processes based on annual mass balance of properties such as dissolved oxygen, dissolved inorganic carbon, nitrate and nitrogen and carbon isotopes. Future studies that seek mechanistic understanding of ecological interactions underlying the biogeochemical dynamics should be encouraged (Church et al., 2013).

As CO_2 increases in the atmosphere and the ocean, this is a driver for ocean warming and acidification, and closely related with deoxygenation. Investigations of the biological effects of a single, isolated driver are problematic, in that they can produce misleading inferences about different organism's responses in a multivariate natural environment. Essentially, interactive (additive, synergistic, or antagonistic) effects are generally not predictable from single-driver studies. In some cases, hypoxic conditions can mediate negative effects of ocean acidification, however, ocean acidification and hypoxia increase heat sensitivity, and oxygen loss combined with warming is projected to lead to the contraction of metabolically viable habitats of marine animals on a global scale (see Gattuso et al., 2015). Growing evidence suggests that interactions with other environmental factors, such as irradiance, nutrient availability, geographical location and species community composition, can strongly modulate the biological effects of warming, ocean acidification and hypoxia (see Gattuso et al., 2015).

Understanding the impact of climate change, as well as society's diverse perspectives and multiscale responses to the changing ocean, requires a correspondingly diverse body of scholarship in the physical, biological, and social sciences as well as humanities. This can ensure that the research that informs climate policy leads to a plurality of values and viewpoints and may enable the concerns of maritime societies and economic sectors to be heard in key adaptation and mitigation discussions (Allison & Bassett, 2015).

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We wish to thank William F. Gilly, Thomas Frölicher and John M. Baxter for helpful comments and improvements on this text and the support by the German Research Foundation (DFG) as part of the research project SFB 754 'Climate-Biogeochemistry Interactions in the Tropical Ocean'.

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2.2 Evidence for ocean deoxygenation and its patterns: Atlantic Ocean

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Summary

- No other chemical parameter is of such importance to all higher marine life as dissolved oxygen. From available data it is obvious that oxygen-limited areas have expanded throughout most of the Atlantic during the last 50 to 100 years and are clearly related to human activities.
- Oxygen limited waters, hypoxic and even anoxic conditions are now found in many coastal areas in the Atlantic Ocean including in connected seas like the Mediterranean, the Black Sea, the North Sea and the Baltic Sea, and the Gulf of Mexico.
- Sediment studies show that anoxic conditions have been present in deep waters in the past, long before anthropogenic activities started to have an influence on the marine environment. However, the present observed deoxygenation in coastal and offshore areas is clearly linked to human activities such as input of nutrients and organic matter, and increasing temperatures as a result of climate change.
- The expanding oxygen minimum zones affect the entire Atlantic ocean ecosystem, its biodiversity and productivity.
- In addition to many coastal waters, oxygen limited waters are also found at mid-water depths (typically 300-1000 m) in the Atlantic Ocean basins, particularly the Equatorial and South Atlantic. The oxygen concentrations in these areas have decreased during the last 60 years, partly due to ocean warming, and partly as a result of decreased mixing and ventilation.
- Continued spreading of deoxygenated areas in the Atlantic, as well as the rest of the world ocean, must be considered a most serious environmental problem with enormous potential impacts on biodiversity and human societies.

Atlantic Ocean deoxygenation	Potential consequences
Oxygen limited areas have expanded over most of the Atlantic Ocean during the last 50 to 100 years.	<ul style="list-style-type: none"> If the conditions continue to deteriorate a number of human ocean and coastal activities are in jeopardy including fishing, aquaculture and coastal tourism.
Human activities are the reasons for the expanding oxygen limited areas.	<ul style="list-style-type: none"> If the release of nutrients, oxygen depleting organic substances and greenhouse gases are not dealt with, the deoxygenated areas will expand as well as extend into deeper parts of the Atlantic Ocean.
Consequences can now more often be noted in many coastal areas and marginal seas where the smell of anoxic water is a regular phenomenon.	<ul style="list-style-type: none"> Coastal areas will lose fisheries, tourism and may even be uninhabitable to marine life.
In addition to large parts of the coastal waters of the Atlantic, over the last 60 years large ocean basins such as the Equatorial and southern Atlantic are being affected by decreasing oxygen levels.	<ul style="list-style-type: none"> If the deoxygenation of entire ocean basins continue human life will be seriously threatened, not only in coastal areas but everywhere on the planet.

2.2.1 Introduction

The Atlantic Ocean, including marginal seas like the Mediterranean, Gulf of Guinea, Black Sea, North Sea, Baltic Sea, and Gulf of Mexico, is the second largest body of water on the planet. The surface area of about 106 million km² with an average depth is about 3600 m, and a maximum depth of 8500 m. The Atlantic Ocean is the drainage basin for more land area than any other ocean basin. Seven of the world's ten largest rivers empty into the Atlantic Ocean. The Atlantic Ocean basin is the only part of the world ocean with significant water exchange with the Arctic Ocean.

There are more and longer data series of physical/chemical and biological parameters from the Atlantic (particularly the North Atlantic) than from any other part of the world ocean. Such data series of measurements in some cases stretch as far back as 150 years.

In the Atlantic Ocean, as in most of the world ocean, the oxygen concentrations in the water column are generally characterized as slightly supersaturated in the surface water, more-or-less undersaturated at intermediate depth, and with higher levels of oxygen, although still undersaturated, in deeper waters. This difference in the oxygen concentration is a reflection of the production and uptake of oxygen through photosynthesis and air-sea gas exchange near the surface, and the consumption through respiration and degradation processes below. Deeper waters tend to have higher oxygen levels because of supply of well-oxygenated bottom waters and low degradation rates. These well-oxygenated bottom waters originate from down-welling/thermohaline circulation in polar

regions. The oxygen-minimum zone typically occurs at depths between 300 and 1200 m which is the zone where the permanent thermocline is found. A number of other physical processes also influence the levels of oxygen at a particular depth in the ocean, such as circulation, and down- and up-welling. The Atlantic is characterized by massive down-welling in the North Atlantic and Norwegian Sea. Here North Atlantic Deep Water (NADW) is formed which feeds the upwelling in many other regions of the world ocean. There is also significant although less pronounced down-welling in the South Atlantic near Antarctica.

Upwelling areas are found in several parts of the Atlantic Ocean (Figure 2.2.1). At these sites nutrient rich deep water is brought up to the surface through a combination of wind and Ekman drift and the Coriolis force. Ekman drift is the process where winds generate currents and due to such currents upwelling occurs, a process called the Coriolis effect. This deep water may, however, be oxygen limited or hypoxic and such waters are found often around 100 to 300m depth and sometimes even at the surface. Pronounced upwelling areas are found for example off the south-west coast of Africa where the Benguela Current brings pulses of hypoxic deepwater to the surface along the coast of South Africa, Namibia and Angola (Arntz et al., 2006; Mohrholz et al., 2008; Monteiro et al., 2006, 2008; Prochazka et al., 2005) (Figure 2.2.1). The Canary Current is a wind-driven surface current which is part of the North Atlantic Gyre. Along the north-west African coast off Mauretania and West Sahara the Canary Current, due to the Ekman drift, produces a pronounced upwelling which brings oxygen-depleted but nutrient-rich deep water to the surface (Gyory et al., 2007; Hempel, 1982). Furthermore, seasonal upwelling

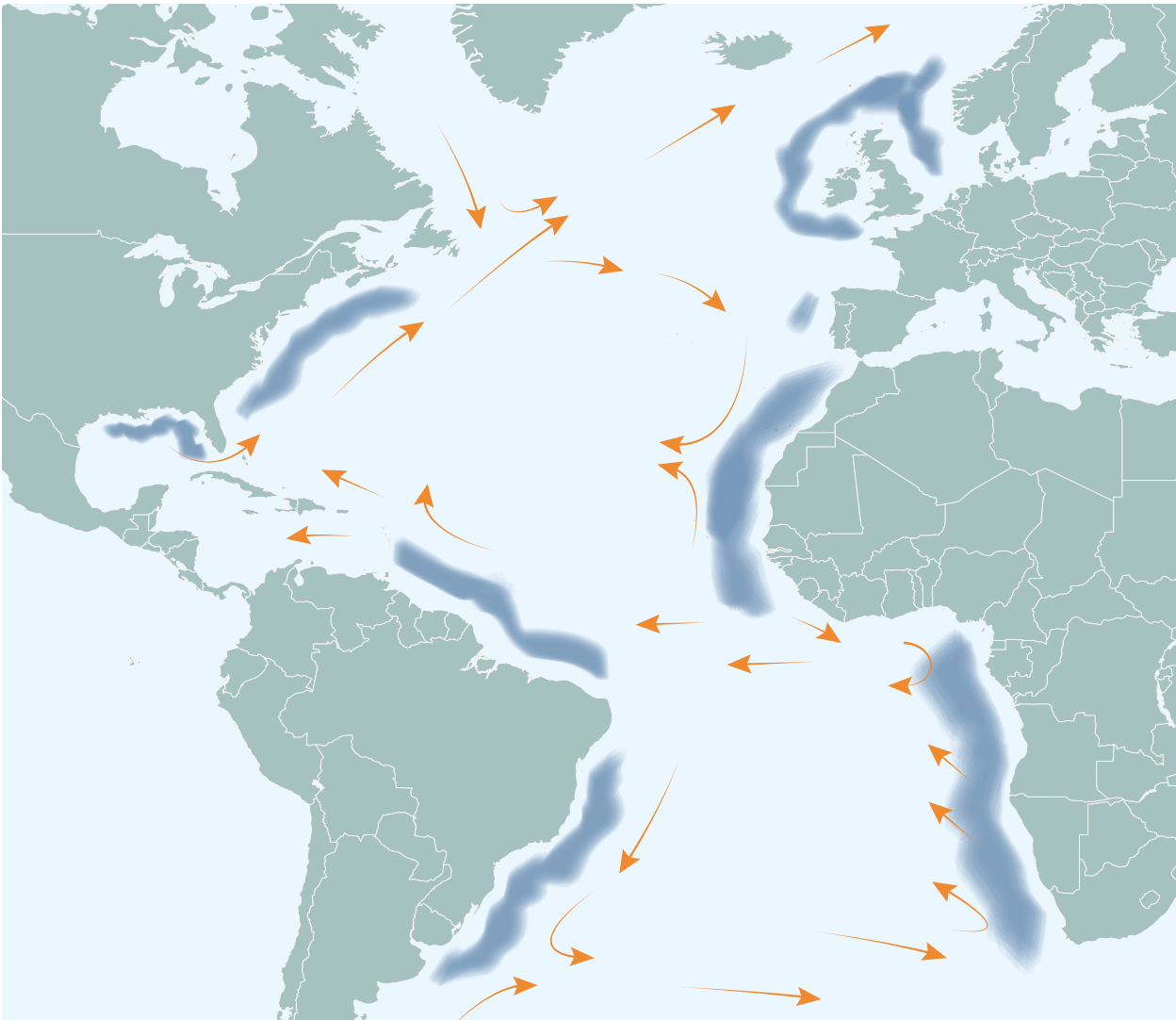


Figure 2.2.1 The Atlantic Ocean with areas of permanent or seasonal upwelling of deep water (dark blue areas). Such areas are common in the basins along the western coasts of the Europe and Africa but occurs also along large parts of the coastline in Europe and North America as well as in the Baltic and Black Seas. Major surface currents are also illustrated (orange arrows).

areas related to the West African monsoon are found in the central equatorial Atlantic Ocean, typically occurring from May through September (Christian & Murtugudde, 2003). The area affected by this upwelling may be as large as 2 million km² (Subramaniam et al., 2013).

2.2.2 Trends and impacts

2.2.2.1 Coastal areas

Under natural conditions shallow waters on the continental shelf generally tend to have higher concentrations of oxygen because of higher primary productivity and being better ventilated. However, a number of anthropogenic activities affect the levels of oxygen in coastal oceanic waters. Coastal waters are affected by forestry, agriculture and urbanization which

often leads to increased concentrations of nutrients and organic matter (e.g. Seitzinger et al., 2010; Sinha et al., 2017). This leads to eutrophication which results in increased decomposition and decreased oxygen concentrations (hypoxia) which may further lead to anoxia (no oxygen). There are numerous reports of such conditions along much of the world's coastlines (see for example reviews by Diaz & Rosenberg (2008) and Rabalais et al. (2014), as well as the assessments carried out by the World Resources Institute (2010)). In the Atlantic Ocean region eutrophic conditions are nowadays more or less permanent in parts of the Gulf of Guinea, Abidjan Lagoon, along the Atlantic coast of Spain and Portugal, English Channel, Wadden Sea, Kattegat and Skagerrak, up to 40% of the Baltic proper, Bay of Gdansk, Gulf of Riga, the Black Sea including Azov Sea and Sea of Marmara.

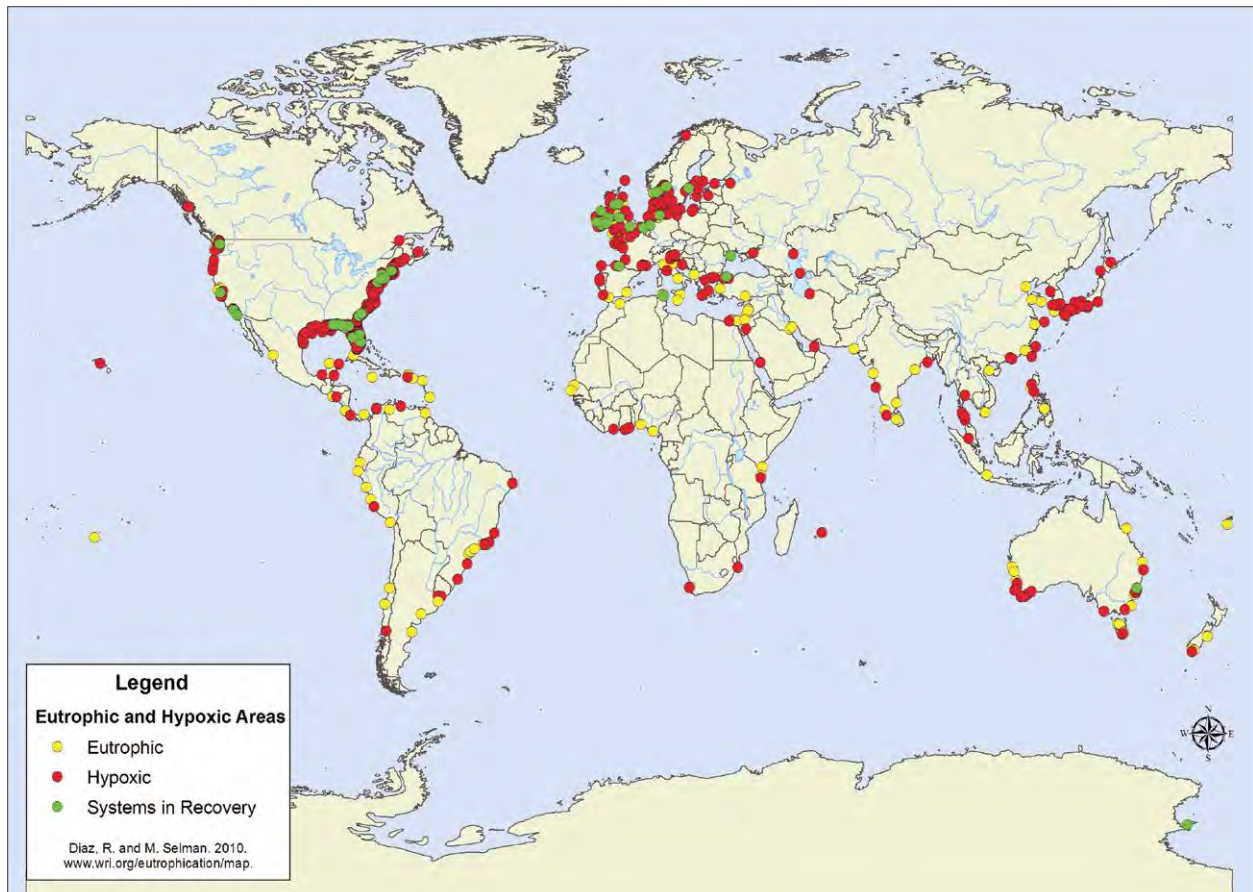


Figure 2.2.2 Map showing the distribution of 415 hypoxic and eutrophic coastal systems worldwide. Most of these areas are found in the Atlantic. From WRI (2010).

A contributing factor to decreasing oxygen concentrations is the increasing ocean water temperature. Global warming results in increasing water temperatures particularly in surface waters, which also leads to decreasing dissolved oxygen concentrations as warmer water holds less oxygen. In the Baltic Sea where the relative importance of physical forcing versus eutrophication is debated, analysis of oxygen and salinity profiles collected over the last 115 years show that increasing temperatures over the last two decades has contributed to worsening oxygen conditions (Carstensen et al., 2014). In the Baltic Sea, oxygen deficient waters have expanded from 5000 to 60,000 km² over the last century making it the largest anthropogenically induced hypoxic area in the world. Increasing water temperatures will also increase the tendency for stratification of the water mass which will decrease the tendency for mixing of the water mass.

However, due to human activities on land, higher rates of degradation are also a characteristic feature of shallow waters. Increased loads of nutrients and organic matter due to runoff from drainage areas affect the oxygen

conditions in many coastal areas, particularly near major rivers or in enclosed or semi-enclosed sea areas. In the Atlantic Ocean depressed oxygen levels as a result of increased outflow of organic matter and nutrients have been observed along most of the coastal areas. In some cases, the deoxygenation is temporary and affects relatively small areas. However, there is an increasing number of large coastal areas that are more-or-less permanently affected by hypoxia or anoxia. Recovery from prolonged periods of anoxia takes many years (Diaz & Rosenberg, 2008; Pearson & Rosenberg, 1978).

The World Resources Institute published a global assessment of the number of eutrophic and hypoxic coastal areas around the world in 2010 (Figure 2.2.2). In total 762 areas were impacted by eutrophication and / or hypoxia (World Resources Institute, 2010). Of these about 300 were to be found in the Atlantic including the Mediterranean, Black, North and Baltic Seas (Figure 2.2.3).

The northern Gulf of Mexico is another example of an area impacted by hypoxia and eutrophication (Rabalais

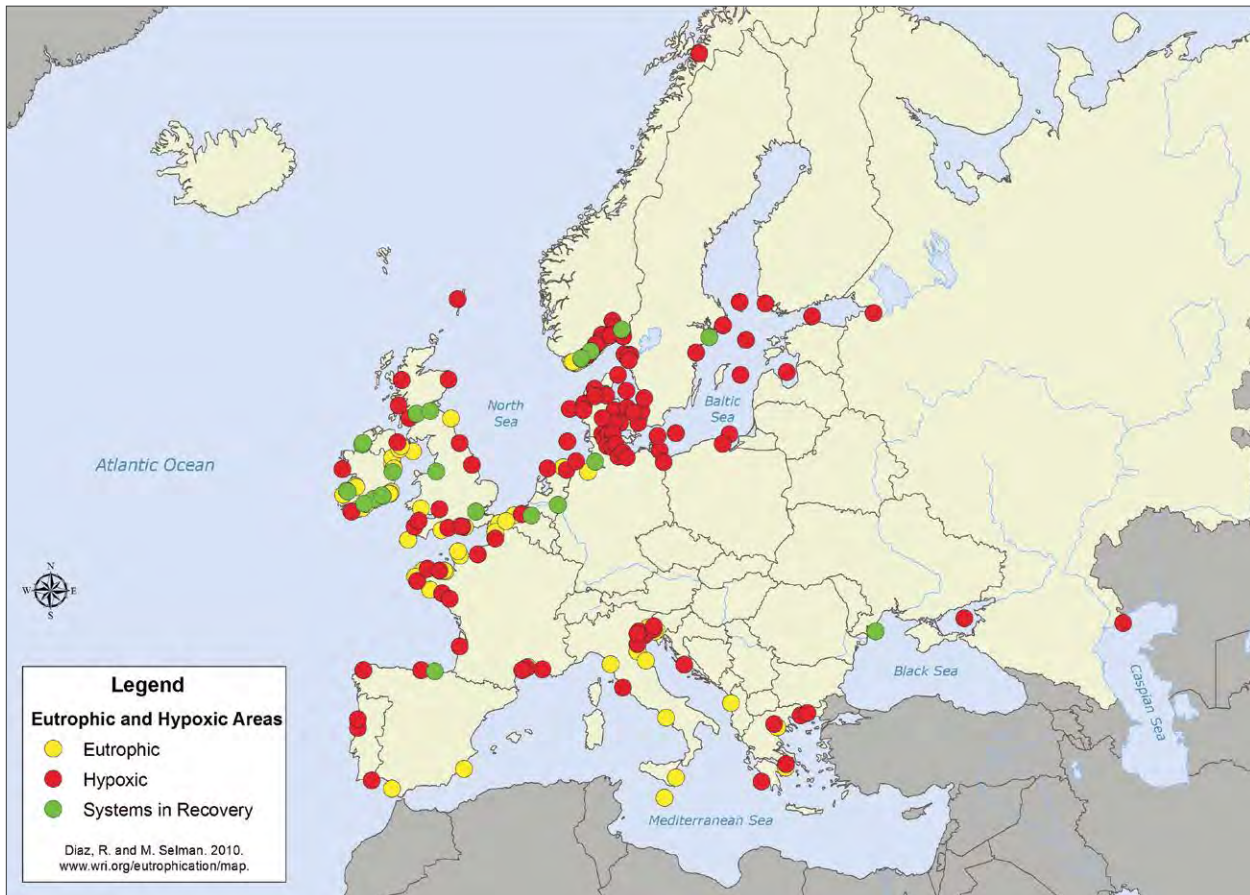


Figure 2.2.3 Map showing the distribution of hypoxic and eutrophic coastal systems in Europe. From WRI (2010).

et al., 2014) (Figure 2.2.4). The average size of the hypoxic zone in the northern Gulf of Mexico over the past 30 years (1985-2014) has been estimated at about 13,650 km². Another large coastal area affected by hypoxic conditions in North America is the Chesapeake Bay which covers about 11,000 km². As a result of reductions in the input of nutrients from surrounding areas and increasing ambient temperatures and sea-level rise the oxygen concentrations in bottom waters are projected to increase while the oxygen levels at mid-depths will decrease. However, with the precipitation over land predicted to increase, there will be larger volumes of winter and spring fresh water inflow and nutrient loads leading to increased primary production. The combined effect of this multitude of factors is predicted to further lower the dissolved oxygen throughout the Chesapeake Bay (Irby et al., 2017).

Parts of the eastern and southern North Sea including the Skagerrak, the Kattegat, the Sound (the strait between Sweden and Denmark) and the Wadden Sea are examples of areas increasingly affected by hypoxia although a slight recovery was seen recently in

the Kattegat (OSPAR Commission, 2017). In addition, the Baltic Sea is an extreme example of a marginal sea where extensive areas (as much as 30-40%) are affected by hypoxia at mid-depths (30 to 150 m) and anoxia in the deeper water (e.g. Lindberg, 2016).

Even more affected by hypoxia and anoxia was the Black Sea till the early 1990s when up to nearly 90% of the water volume was affected (Paleari et al., 2005) by anoxic conditions. However, the release of nutrients from surrounding areas has decreased since then and the environmental conditions in the Black Sea appear to have improved, although the improvement is unstable, and complete recovery may take a very long time (Jessen et al., 2017). Jessen et al. (2017) conclude that the bottom water oxygen concentration is a key factor in determining the biogeochemistry of the sediments and overlying waters. Hypoxic conditions prevent bioturbation and decrease remineralization rates even within short periods of a few days. However, Capet et al. (2016) point out the importance of dedicated monitoring in areas such as the Black Sea where seasonal fluctuations and the heterogeneous

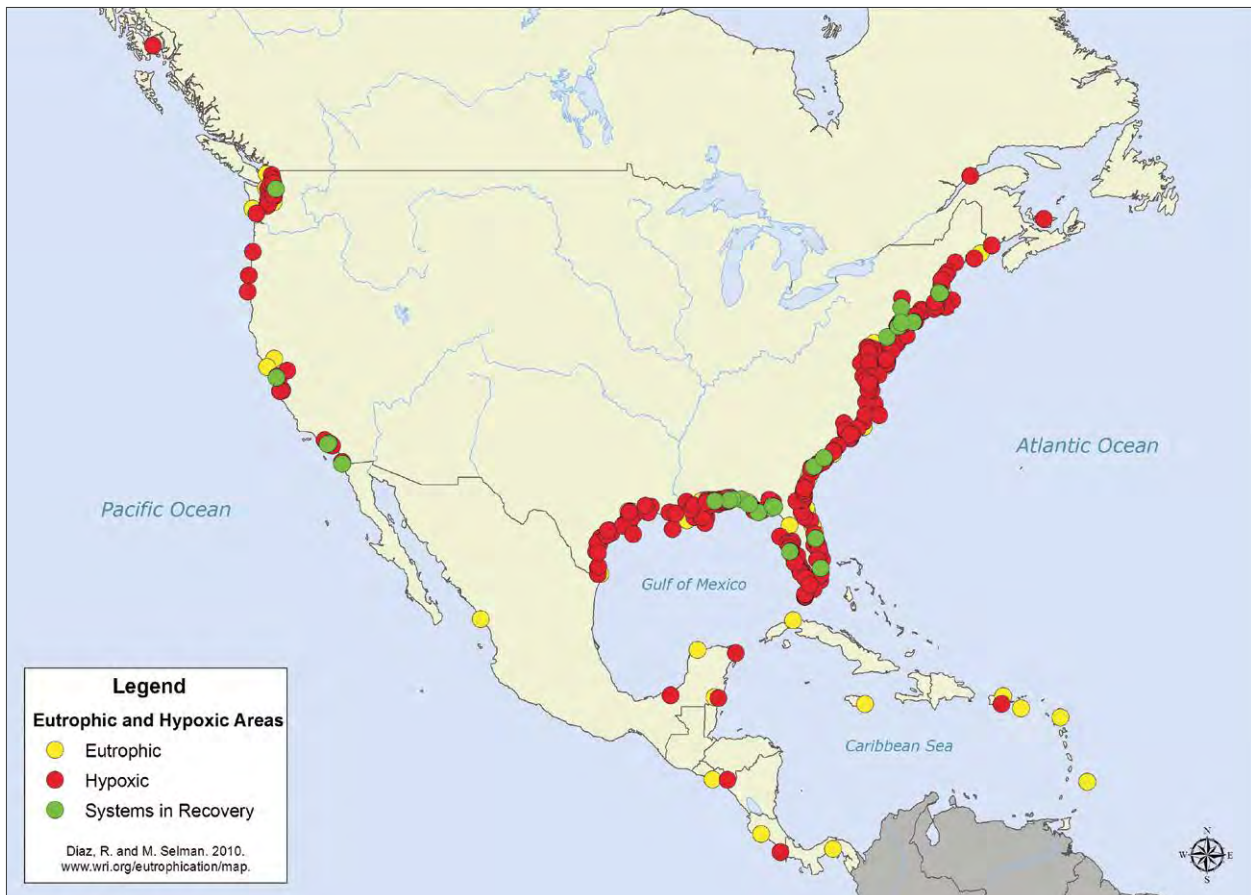


Figure 2.2.4 Map showing the distribution of hypoxic and eutrophic coastal systems from coastal North America. From WRI (2010).

spatial distribution complicates the interpretation of information from different data sets, and conclude that the reported recovery of the Black Sea after 1995 probably overestimated the trends and that hypoxic events have been recurring.

2.2.2.2 Offshore Atlantic Ocean

Models for the future development of the oxygen concentrations in the Atlantic project a 1 to 7% decline by the year 2100 (Keeling et al., 2010; Long et al., 2016). This decline would be caused by a combination of a warming-induced decline in oxygen solubility and reduced ventilation of the deep ocean.

Generally, over the Atlantic Ocean there are large subsurface oxygen minimum zones (OMZs) offshore, particularly in the eastern tropical and subtropical Atlantic. Oxygen poor waters have far-reaching ecological impacts as key fauna such as bottom-living invertebrates that normally are responsible for the degradation of organic matter and fish cannot survive in these hypoxic zones (e.g. Bianucci et al., 2016; Brennan et al., 2016) (Figure 2.2.5). There has been a significant

increase in the vertical expansion of these low-oxygen zones at intermediate depth in the eastern parts of the tropical Atlantic both south and north of the equator (Stramma et al., 2008, 2010). Schmidtko et al. (2017) assessed the global oceanic oxygen content during the past five decades for the different basins in the Atlantic Ocean.

The loss in ocean oxygen is spread over the entire deep-water column between the North Atlantic deep water and Antarctic bottom water, with 12.4% of the global ocean oxygen loss over the 50 years (i.e. from 1960) occurring in the South Atlantic (Table 2.2.1; Figure 2.2.6). The change is in line with the theory of reduced ventilation due to meridional overturning changes, and that this reduced ventilation has provided less oxygenated waters in recent years, particularly in mid-latitudes in both hemispheres, as well as in tropical areas. That multi-decadal basin-scale variability in combination with the slow-down in oceanic overturning of the deep water and a potential increase in biological consumption is supported by other work (Broecker et al., 1999; Keller et al., 2016). In the upper water column, warming and the resulting decrease in solubility



Figure 2.2.5 Atlantic wolffish (*Anarhichas lupus*) has a critical oxygen level of 5.69–6.64 mg L⁻¹. © Nature Picture Library / Alamy stock photo.

and biological consumption is most likely the reason for the loss in oxygen which, measured over the entire global ocean corresponds to over 2% since the 1960s (Schmidtko et al., 2017).

The long-term trends in dissolved oxygen in eight regions (Labrador Sea, Irminger Sea, Iceland Basin, Rockall Through and the Western European Basin North, Newfoundland Basin, North American Basin, Mid Atlantic Region, and Western European Basin South) covering the entire North Atlantic during the 50 years from 1960–2009 were analysed based on three different data sets (Stendardo & Gruber, 2012). The results showed a significant decrease in oxygen in the upper and mid-depth waters in almost all regions over the five decades. However, over the same period the deep water and water from Labrador entering into the North Atlantic increased in oxygen concentrations to a limited extent in two regions of the North Atlantic. Stendardo and Gruber (2012) concluded that the oxygen decreases in the mid-water of the northern

and eastern regions were largely driven by changes in circulation and/or ventilation, while the decreases observed in the upper layer and the oxygen increases in the deep water and the Labrador water were driven by changes in solubility. Comparing the oxygen trends with those of the oceanic heat content for the different regions and water depths the figures largely overlap and are larger than what would be expected from solubility alone. Hence biological parameters such as production and respiration as well as factors related to ventilation and circulation probably play roles in explaining this.

Santos et al. (2016) showed that the explanation to the declining oxygen concentrations is more complicated than simply warming. Their study showed that deoxygenated Antarctic mid-water directly impacts the thickness of the oxygen minimum zones in the eastern tropical South Atlantic (ETSA) and the eastern tropical North Atlantic (ETNA). The investigation using data since the 1960s showed the thickness of the oxygen minimum zones has increased by $2.58 \pm 0.67 \text{ m y}^{-1}$ (ETSA) and $3.37 \pm 0.73 \text{ m y}^{-1}$ (ETNA), and that the oxygen levels had decreased correspondingly while the temperatures has increased. However, an analysis of the Antarctic Intermediate Water (AAIW) source region revealed a temperature increase of 1.9 °C and a dissolved oxygen decrease of $\sim 46 \mu\text{mol kg}^{-1}$ over the study period of 60 years. This would indicate a decrease in oxygen solubility of up to $\sim 15 \mu\text{mol kg}^{-1}$ and thus the observed warming explains only 31% of the observed oxygen decline. This suggests that a reduction in ventilation, ocean circulation and thermal stratification as well as productivity changes and altered respiration and mineralization may have also contributed to the decrease in dissolved oxygen levels.

Table 2.2.1 Atlantic Ocean: Volume, oxygen content and change and solubility related to changes per basin and depth. The decreasing oxygen content is particularly pronounced in the South Atlantic (modified from Schmidtko et al., 2017)

Atlantic Ocean area	Volume (10 ⁶ km ³)	Oxygen content (Pmol)	Solubility (rel. oxygen change (Tmol dec ⁻¹))	Change in % of global change in the entire world ocean
North Atlantic	111.6	26.86 ±0.05	-0.4	0.9
0–1200 m	34.04	6.90 ±0.02	-9.8	2.7
1200 m–bottom	77.02	19.96 ±0.03	-9.3	1.8
Eq. Atlantic	74.19	15.89 ±0.04	-11.1	7.5
0–1200 m	20.62	2.76 ±0.02	-7.8	2.3
1200 m–bottom	53.58	13.13 ±0.02	-3.3	5.2
South Atlantic	100.84	22.39 ±0.05	-30.0	12.4
0–1200 m	27.72	5.98 ±0.02	-26.2	1.4
1200 m–bottom	73.12	16.41 ±0.03	-3.8	11.0



Figure 2.2.6 Map illustrating the area of decreasing oxygen content down to 1200m which is particularly pronounced in the South Atlantic (modified from Schmidtko et al., 2017).

Sediment cores from the deep North Atlantic have revealed millennial changes in the oxygen concentrations (Hoogakker et al., 2016). Interglacial changes in bottom water (1-2 km deep) in the north-east Atlantic have been linked to decreased ventilation related to changes in oceanic circulation and biological productivity. Hoogakker et al. (2016) showed that glacial cold events may be associated with lower seawater oxygen levels across the North Atlantic and suggested that lower oxygen concentrations in the deep water can be linked to increased export of organic material from the surface waters and its subsequent remineralization in the water column.

Hypoxia interrupted by periodic anoxia will fundamentally alter the benthic ecosystem and its ability to process carbon. Studies show that under normal oxygen conditions most of the organic matter sinking to the sea bed is consumed and recycled. Usually only a minor part of the organic matter gets buried in the ocean floor, most of it is remineralized and fed back to the ecosystem. However, declining oxygen levels and short hypoxic periods will completely change the picture and more than 50% of the organic matter will not be remineralized, significantly influencing the carbon storage in the sea floor for decades (Jessen et al., 2017).

2.2.3 Ecosystem consequences

Oxygen is an essential element for all higher life and the implications of continued spreading of deoxygenated areas in the Atlantic Ocean must be considered a most serious environmental problem. It has fundamental implications on ocean productivity, biodiversity, biogeochemical cycles and the global climate.

The response to declining oxygen will vary depending on sensitivity of different species and different life stages. The responses may be death or sub-lethal effects such as behavioural or physiological, that may manifest as reduced growth or impaired reproduction. Furthermore, the oxygen available to organisms depends on the temperature of the water (low temperature means increased solubility), pressure (high pressure increases solubility), and salinity (high salinity means lower solubility).

Declining concentrations of oxygen not only have direct and often dramatic effects on higher organisms such as fish and shellfish, but decreased oxygen levels also affect a number of important biogeochemical reactions and cycling in the marine environment. Hence the cycling of nutrients, metals, sulphide and carbon are affected. For example, hypoxia and anoxic conditions prevents the sequestration of phosphorus in the sediment. As a consequence, even if the input of phosphorus is eliminated, under hypoxic conditions phosphorus remains in the ecosystem and continues to fuel primary productivity resulting in massive algal blooms, perhaps for decades, for example as in the central Baltic Sea, the Black Sea, parts of the North Sea and the Cariaco Basin (Ahtiainen et al., 2014; Jokinen et al., 2018; Kemp et al., 1990; Nixon et al., 1996; Ye et al., 2016). These blooms of algae may in some cases be harmful (HABs). The extent of hypoxia also affects the loss of fixed nitrogen in the ocean via denitrification, thereby influencing the supply of nitrate which is a limiting nutrient over much of the ocean (e.g. Gruber, 2004). This will have negative consequences on ocean productivity. The concentrations of oxygen also influence the production of nitrous oxide (N_2O) which is a powerful greenhouse gas. Production of this gas will increase under hypoxic conditions both from denitrification and nitrification (Codispoti et al., 2001; Keeling et al., 2010). Results from investigations off the western Indian Shelf during periods of hypoxic, suboxic and anoxic waters produced a maximum surface N_2O saturation of >8000%. The studies showed the sensitivity of denitrification to small

changes in the ocean dissolved oxygen, and that small changes in dissolved O_2 concentrations can change the N_2O emission from the ocean rapidly.

The ecological consequences of the decline in oxygen levels in marine areas are dramatic. Hypoxia impoverishes the ecosystem with only the most tolerant and opportunistic species remaining, and anoxia eliminates all higher life. Pelagic species may, to a certain extent, be able to avoid hypoxic conditions and indeed this is why fish stocks are still present in places such as the Black Sea and the Baltic Sea. Fish such as cod and herring simply move to surface waters as hypoxia spreads in deeper waters. However, species living on or near the sea bed will not be able to survive such conditions. Also, although adult cod may be able to survive, eggs and larvae may not as the situation in the Baltic Sea shows (e.g. Nissling, 1994). The response pattern of benthic communities to hypoxia has been described by Pearson and Rosenberg (1978). As dissolved oxygen declines to $<0.7 \text{ ml L}^{-1}$ and extends through time, mass mortality of both more sensitive and the more tolerant species will take place. If anoxia occurs all benthos will die. The process of recovery from such conditions follows a different path from when oxygen is declining. The conceptual model for benthic community responses to hypoxia and anoxia and the recovery from such conditions has been described in the Pearson-Rosenberg model (Pearson & Rosenberg, 1978).

2.2.4 Societal consequences of continued deoxygenation

The socio-economic consequences of continued deoxygenation of the Atlantic Ocean are enormous and difficult to comprehend. Fundamental changes will take place affecting biological as well as chemical factors in the ocean and in the longer term also life on land will suffer as biogeochemical cycles including that of carbon and oxygen are affected. Initially, and this is already happening, fisheries suffer from the consequences of hypoxia and anoxia in the pelagic and benthic zones (Table 2.2.2). As the oxygen minimum zones are expanding the habitats for fish and shellfish are compressed. In the tropical Atlantic some populations of tuna, billfish and marlin have experienced a 15% reduction in their vertical habitat range between 1960 and 2010 as a result of the expansion of the oxygen minimum zones (Stramma et al., 2011). Organisms that require high oxygen levels are losing habitat while more tolerant species

Table 2.2.2 The typical effects of hypoxic/anoxic conditions

Before deoxygenation	Under low-oxygen condition
<ul style="list-style-type: none"> • Diverse ecosystem including demersal species • Benthic life consisting of fish and shellfish 	<ul style="list-style-type: none"> • Impoverished ecosystem • Only pelagic fish in surface waters • No deep-water/benthic life
<ul style="list-style-type: none"> • Well-oxygenated deep water • Well-flushed water body 	<ul style="list-style-type: none"> • Hypoxic/anoxic deep-water

will expand. The effects are manifested as decreased catches of benthic species and increased catches of upper-pelagic fast-growing species, a reflection of a switch to shorter food chains; clear signs of such effects have been seen in the Baltic Sea, the Black Sea and in other parts of the North Atlantic (e.g. Bianucci et al., 2016; Brennan et al., 2016). It is reasonable to assume that, as deoxygenation progresses, fisheries in coastal as well as offshore areas will be affected with implications on the food supply to many millions of people.

As oxygen levels continue to decrease and reach hypoxic conditions the available habitats for aerobic organisms decrease rapidly (Deutsch et al., 2011). The spatial extent of hypoxia is highly sensitive to small changes in the oxygen content with maximum responses at suboxic levels where anaerobic processes predominate. Areas most at risk in the Atlantic are the eastern tropical/subtropical basin as well as mid-latitudes. Based on model simulations widespread hypoxia is forecasted in these areas between 2014 and 2030 (Long et al., 2016).

Potentially the societal consequences of the effects of ocean deoxygenation on the global climate is, however, even more serious but much more information is needed to fully understand the implications. As the oxygen concentrations are decreasing the nutrient cycling is affected and as this is taking place on such a large scale it has implications for the global biogeochemistry and climate. Oxygen is directly linked to the carbon cycle via photosynthesis and respiration, hence the rate at which organic material is produced, distributed and recycled. Understanding how the ocean ecosystems are changing with global warming is clearly linked with the CO₂ concentrations in the atmosphere and the ability of the ocean as well as land to serve as carbon sinks.

2.2.5 Conclusions / Recommendations

Hypoxic and anoxic conditions are found in many coastal areas in the Atlantic Ocean including in

connected seas like the Mediterranean, the Black Sea, the Baltic Sea and Gulf of Mexico. From available data it is obvious that these oxygen-limited areas have expanded dramatically during the last 50 to 100 years. In coastal areas there are several good examples that conditions can improve, provided the input of nutrients and organic matter from land can be controlled. At local and regional levels, there are therefore good reasons to build sewage treatment plants and improve management of drainage water from land in order to reduce these substances as far as possible.

The expanding oxygen minimum zones affect the entire marine ecosystem, its biodiversity and productivity. In addition, there are several links to global climate change. Oxygen limited waters are also found at mid-water levels in most of the Atlantic Ocean basins, usually at 300 to 1000 m depth. The oxygen concentrations in these areas have decreased during the last 60 years, partly due to ocean warming, partly as a result of decreased mixing and ventilation. Continued spreading of deoxygenated areas in the Atlantic Ocean must be considered a most serious environmental problem. There is no other parameter of such importance to all higher life as dissolved oxygen. To be able to manage the declining oxygen levels in offshore areas global action is needed. The clear links to the atmospheric concentrations of carbon dioxide would strongly suggest that the issue of deoxygenation of the ocean must be dealt with within the framework of the climate change negotiations.

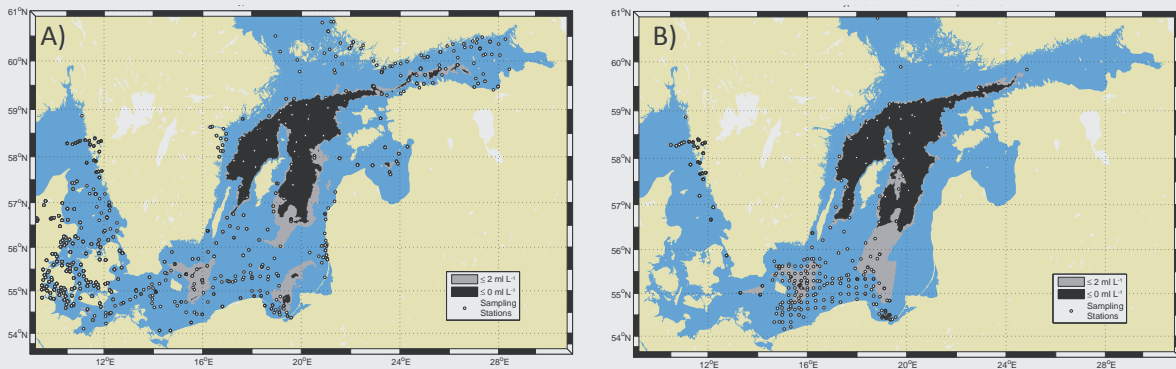
Understanding of the relative importance of autotrophic and respiratory processes, as well as physical processes (e.g. mixing and currents) in deep and mid-water oxygen dynamics requires more data than what are currently available.

Also, knowledge regarding the impacts of climate change on physical processes, oxygen deficiency and oxygen consumption is poor in large parts of the Atlantic Ocean. In order to better distinguish between the effects of nutrient enrichment and changes in seawater

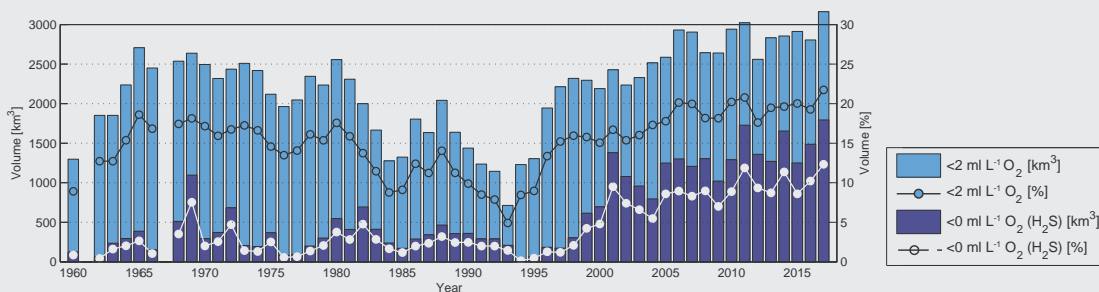
Box 2.2.1 The Baltic Sea and deoxygenation

The Baltic Sea has been affected by deoxygenation and anoxic conditions since it was formed after the last glaciation. Geologists have detected periods of anoxic conditions at the sea bed since the Littorina Sea about 8000 years ago. The Littorina Sea was a brackish water marginal sea which existed for about 4000 years before the present Baltic Sea. However, since the early 1900s local outbreaks or hypoxia have become more frequent and since 1950 large areas, up to 100 000 km² have been affected by anoxia in the deep and intermediate waters from the sea bed up to 50 to 80 m depth (Box Figures 2.2.1.1 – 2.2.1.3). The water column in the Baltic Sea is highly stratified due to large inflows of fresh water from surrounding land areas and low and infrequent inflow of Atlantic water. As a consequence, the surface water is only some 6 to 8 Practical Salinity Unit (PSU) while the deep water is 15 to 20 PSU. The halocline is at about 40 m in the southern Baltic Sea and about 80 m in the north. The anoxia in deep waters contributes to the mobilization of nutrients from the seabed sediment which results in massive algal/bacterial blooms during the summer months.

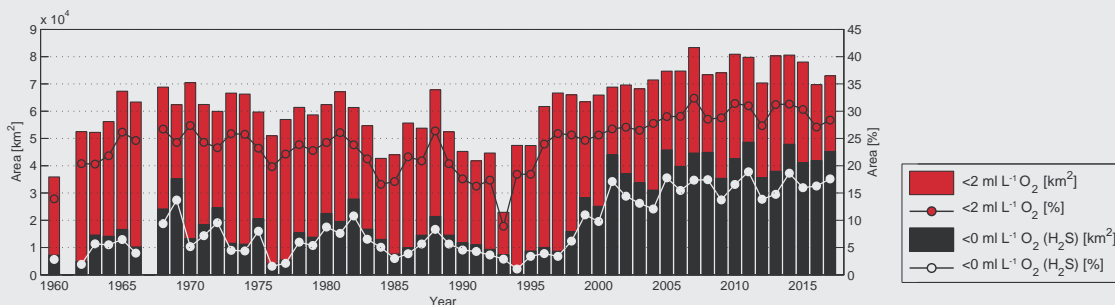
The increasing problems with hypoxia and anoxia during the last 100 years have been related to the release of nutrients and organic substances from the drainage area. Based on a catchment-sea coupled model system and numerical experiments based on meteorological and hydrological forcing data and scenarios, it is projected future changes will lead to increasing problems with hypoxia and decreasing pH (Omstedt et al., 2012).



Box Figure 2.2.1.1 The Baltic Sea with Gulf of Finland, Gulf of Riga, the Sound, the Belt Sea and the Kattegat. The maps show the extent of hypoxic and anoxic water in the autumn (A) 2016, (B) 2017. From SMHI 2017 (www.smhi.se).



Box Figure 2.2.1.2 Aerial extent of anoxic and hypoxic conditions in the Baltic Proper including the Gulf of Finland and the Gulf of Riga from 1960 to 2017. Results from 1961 and 1967 have been removed as data from deep basins are missing. From SMHI, Report Oceanography 63, 2017.



Box Figure 2.2.1.3 Volume of anoxic and hypoxic deep water in the Baltic Proper, Gulf of Finland and Gulf of Riga 1960-2017. Results from 1961 and 1967 have been removed as data from deep basins are missing. From SMHI, Report Oceanography 63, 2017.

temperature as a result of climate change more data series are needed. Since oxygen deficiency is localized and often short-lived, modelling can help in identifying hotspots.

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2.3 Evidence for ocean deoxygenation and its patterns: Indian Ocean

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Summary

- Analysis of available data for the past five decades indicates a generally lower and more variable rate of deoxygenation in the North Indian Ocean than in other oceanic areas (i.e. substantial oxygen loss in the upper 300 m in the western Arabian Sea, mixed trends in the central Arabian Sea, and a slight decline in the Bay of Bengal).
- There is no clear evidence for expansion/intensification of the functionally-anoxic oxygen minimum zone (OMZ) in the Arabian Sea, where microbes decompose organic matter via anaerobic pathways, but slight oxygen loss might have brought the relatively more oxygenated Bay of Bengal OMZ close to anoxia.
- Preliminary analysis suggests substantial decrease in oxygen levels below 400 m in the northern Red Sea.
- Emerging hypoxia in conjunction with an increase in organic load in response to eutrophication in the Persian Gulf may lead to expansion/intensification of the Arabian Sea OMZ.
- The world's largest naturally-formed shallow hypoxic zone along India's west coast is more intense now as compared to 1970s; seasonal oxygen-deficiency off Oman and eastern India is also more severe. Hypoxia/anoxia has developed in several Indian estuaries, bays and ports and in some estuaries of western Australia as a result of human activities.
- There is a severe lack of information from potential hotspots, including the mouths of the Indus, Ganges-Brahmaputra, and Irrawaddy rivers. Capacity building and networking are needed to expand/improve monitoring of deoxygenation and other impacts of global change in the region.

Human induced change	Potential consequences
The bulk of excess heat retained by the Earth due to greenhouse warming being absorbed by the ocean.	<ul style="list-style-type: none"> • Ocean deoxygenation occurring at all depths due to: <ul style="list-style-type: none"> ◦ lower solubility of oxygen in warmer waters. ◦ stronger vertical stratification (steeper temperature gradient) inhibiting diffusion of O₂ from surface to deep ocean. ◦ more sluggish deep circulation reducing oxygen supply to deep waters.
Increase in nutrient inputs to the ocean through river runoff and atmospheric deposition.	<ul style="list-style-type: none"> • Nutrient over-enrichment (eutrophication) promoting algal blooms, enhancing O₂ demand and causing development of hundreds of coastal hypoxic (dead) zones as well as intensification of naturally formed low-O₂ zones.
Low - O ₂ zones of the Indian Ocean expected to expand and intensify due to above-mentioned human-induced changes. w	<ul style="list-style-type: none"> • Expansion of volume of hypoxic (O₂<1.4 ml L⁻¹) water has many deleterious effects on marine life including: (i) loss of habitat; (ii) changes in food webs; (iii) reduced growth and reproduction; (iv) physiological stress; (v) migration; (vi) vulnerability to predation; (vii) disruption of life cycles; and, in extreme cases, (ix) mortality. • The northern Indian Ocean contains about 2/3 of the global continental margin area in contact with very low O₂ (<0.2 ml L⁻¹) waters, and also houses the world's largest naturally-formed shallow low-O₂ zone (off western India). With countries surrounding its semi-enclosed basins, accounting for about a quarter of the global human population, its environment, biodiversity and living resources, are most vulnerable to human-induced changes, especially deoxygenation. • When dissolved O₂ is depleted below detection levels, as happens within a large volume of waters at mid-depths within the oxygen minimum zone (OMZ) of the Arabian Sea, the microbial community respire anaerobically, predominantly utilizing nitrate, an essential nutrient, converting it to inert molecular nitrogen (N₂) and nitrous oxide (N₂O), a potent greenhouse gas. While N₂ produced through this process (denitrification) modulates reactive nitrogen balance and marine biological productivity, oceanic N₂O emissions play an important role in Earth's radiation balance. • The OMZ of the Bay of Bengal retains some O₂ in minute traces but enough to inhibit large-scale denitrification. The volume of water containing traces of O₂ (<0.2 ml L⁻¹) in the northern Indian Ocean is much larger than the volume of functionally-anoxic OMZ of the Arabian Sea. This in conjunction with the extreme sensitivity of denitrification to vanishingly low O₂ levels underlines the non-linear response of N₂ and N₂O production to ocean deoxygenation. Thus, expansion and intensification of oceanic OMZs are expected to have large impacts on productivity as a result of reactive nitrogen loss, and on climate through enhanced production of N₂O.

2.3.1 Introduction

Unlike the Pacific and Atlantic Oceans, the Indian Ocean is bound by the Eurasian landmass at nearly tropical latitudes (~25°N, Figure 2.3.1), which has a profound impact on regional climate and oceanography. Differential heating and cooling of land and sea give rise to the unique phenomenon of monsoons, manifested by complete reversals of atmospheric and surface oceanic circulations every six months north of about 10°S latitude (Wyrski, 1973). The monsoons also greatly affect the

chemistry and biology of the Indian Ocean. During the summer or south-west monsoon (SWM), strong winds blow anomalously from the south-west, being strongest in the western Arabian Sea where they drive a vigorous western boundary current and uplift sea water from depth that is rich in nutrient salts. This water spreads far and wide eastward, fertilizing the nutrient-impooverished surface layer and promoting growth of algae that form the base of rich and diverse food webs (Naqvi et al., 2006a). In other ocean basins, this process, called upwelling, occurs along eastern boundaries (i.e. off Namibia and



Figure 2.3.1 Map showing the Indian Ocean and important locations/features mentioned in the text. While the southern boundary of the Indian Ocean is arbitrarily fixed at 60°S latitude, longitudes 20°E and 146.82°E, corresponding to the southern tips of South Africa and Tasmania (Australia), are taken to separate the Indian Ocean from the Atlantic and the Pacific, respectively (https://www.iho.int/mtg_docs/com_wg/S-23WG/S-23WG_Misc/Draft_2002/Draft_2002.htm). This chapter largely focuses on the Indian Ocean north of the equator. The dark blue area in the Arabian Sea marks the functionally anoxic zone defined by concentration of nitrite, a proxy of anoxia, exceeding $0.2 \mu\text{M}$ within the oxygen minimum layer (from Naqvi, 1991).

Mauritania in the Atlantic, and off California and Peru-Chile in the Pacific). As compared to the Arabian Sea, upwelling is much weaker in the Bay of Bengal, partly because of weaker winds and partly because the Bay of Bengal receives enormous runoff from a number of rivers as well as a large amount of rainfall that greatly affects its hydrography and circulation (Naqvi et al., 2006a). The two basins are also differently affected by the winter or north-east monsoon (NEM), when cool, dry continental winds blow from the north-east causing convective mixing and consequently winter algal blooms in the Arabian Sea. This does not happen in the Bay of Bengal, where the upper water column is more strongly

stratified because of low salinities, inhibiting convection (Naqvi et al., 2006a). Consequently, the Arabian Sea is far more productive than the Bay of Bengal on an annual basis (Qasim, 1977).

The other unique feature of the Indian Ocean geography is that it is connected to the Pacific Ocean through the Indonesian seas, which allows the inflow of warmer, low-salinity water (the Indonesian Throughflow) from the Pacific that drives the anomalous poleward-flowing eastern boundary current (the Leeuwin Current), and is primarily responsible for the absence of large-scale upwelling off western Australia (Schott & McCreary,

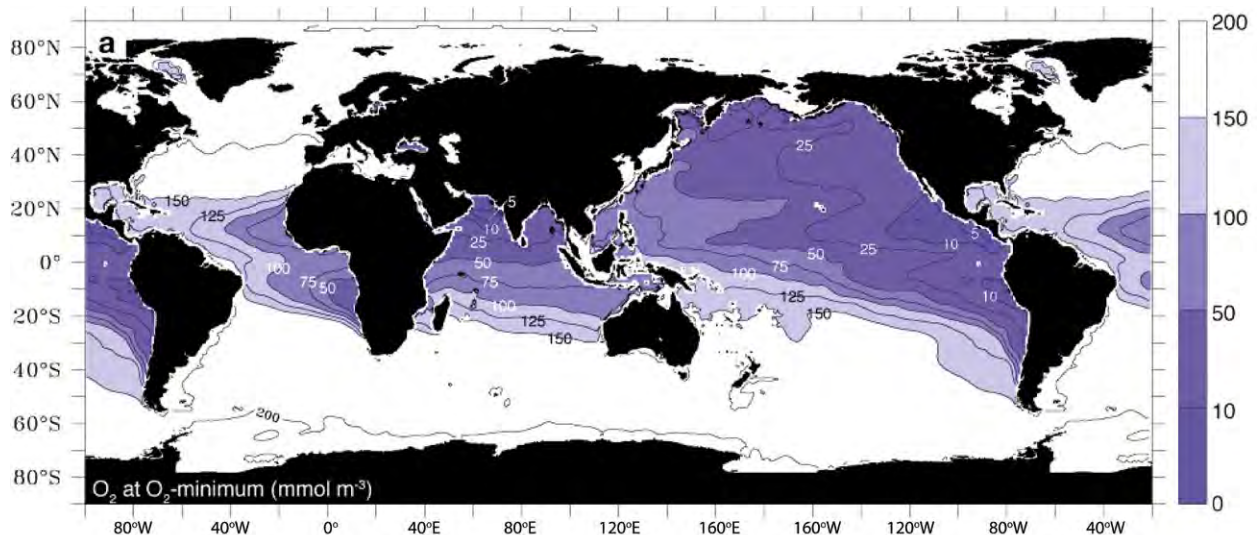


Figure 2.3.2 Distribution of dissolved O_2 (μM) at its minimum (after Keeling et al., 2010). The depth of the minimum varies, but in the northern Indian Ocean the lowest O_2 concentrations are generally found below ~ 150 m and above 800 m (Wyrтки, 1971). Note the anomalous location of the oxygen minimum zones in the northern Indian Ocean. Oxygen supply from the south is indicated by the northward tilt of contours along the western boundary (off Africa and Arabia).

2001). The biogeochemistry of this region is, therefore, completely different from its counterparts in the Pacific and Atlantic Oceans (in the equator-bound Humboldt Current and Benguela Current, respectively).

The low-latitude northern boundary of the Indian Ocean also drastically influences deep water circulation and renewal. As the dense, deep waters are mostly formed in cold, polar areas, the deep Indian Ocean can only be ventilated by waters flowing northward from the Southern Hemisphere. Although two sources of dense intermediate waters do exist in the Mediterranean-type marginal seas - the Persian Gulf and the Red Sea that are located in highly arid zones and receive little river runoff - most of the ventilation below the surface layer in the upper kilometre of the Indian Ocean occurs through waters formed close to or just north of the Polar Front (around 50°S latitude) in the Southern Indian Ocean (Swallow, 1984). These waters do not flow directly northwards but take a circuitous route; carried by the anti-clockwise flow of the southern subtropical Indian Ocean, these waters are fed into the complex equatorial current system of the Indian Ocean from where they cross the equator in the western Indian Ocean during the SWM (Swallow, 1984).

Deviations in patterns of surface and deep currents and related biological productivity in the Indian Ocean from those observed in the Atlantic and Pacific Oceans also result in unusual distribution of dissolved oxygen (O_2) in the Indian Ocean (Wyrтки, 1971). Like other oceanic areas, the water column in the Indian Ocean

also contains mid-depth O_2 concentration minima, maintained by a combination of relatively high O_2 demand by microbes that decompose organic matter sinking from the surface, and restricted O_2 supply as a result of sluggish deep-water circulation and mixing. What is unusual is that while the so-called oxygen minimum zones (OMZs), located in the tropics, are most intense along the eastern boundaries of the Pacific and Atlantic Oceans, they occur along the northern boundary of the Indian Ocean (Figure 2.3.2).

The northward tilt of O_2 contours in the western Indian Ocean (Wyrтки, 1971) is because, as mentioned above, cross-equatorial flow of relatively oxygenated intermediate waters of southern origin occurs only in the west; despite this, O_2 deficiency is clearly more severe in the north-western Indian Ocean than in the north-eastern Indian Ocean (Figure 2.3.2). This is also supported by the distribution of chemical proxies of anoxia. For example, the upper 1/3 or so of the OMZ of the Arabian Sea is distinguished by the accumulation of nitrite (NO_2^-), a transient species of nitrogen usually not present much below the surface layer. This feature, called the secondary nitrite maximum (SNM), is ubiquitous to almost all intense OMZs, but it is not seen in the Bay of Bengal (Naqvi et al., 2006a). The SNM is believed to be produced by bacteria that decompose organic matter using nitrate (NO_3^-), the most abundant form of reactive nitrogen in the sea, once O_2 gets fully consumed. Recent measurements have shown that O_2 levels associated with the SNM are below the detection limit (a few nanomol per litre) of the best O_2 sensor

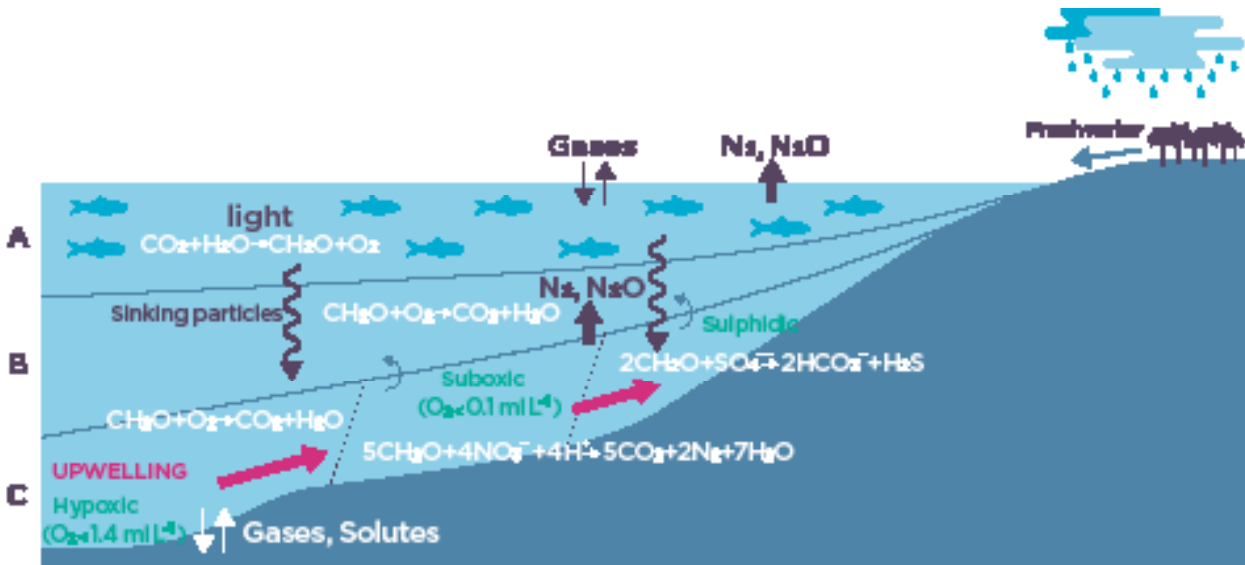


Figure 2.3.3 A schematic representation of processes occurring in the world's largest naturally formed coastal hypoxic zone off the west coast of India (eastern Arabian Sea) in late summer and early autumn. The water column over the shelf can be broadly divided into three layers. (A) The upper layer is warm and has low salinity because of intense monsoon rainfall; being in contact with the atmosphere, it is also well oxygenated. (B) The middle layer is a transient zone where salinity (\uparrow), temperature (\downarrow), density (\uparrow) and O_2 (\downarrow) change rapidly with depth. This layer acts as a barrier, strongly inhibiting mixing of the overlying and underlying waters. (C) The lower, near-bottom layer comprises cold, saline water that is derived through upwelling from the oxygen minimum zone (OMZ) located offshore. The little O_2 it initially contained gets used up over the shelf by bacteria that decompose copious organic matter sinking from the surface. Removal of O_2 triggers microbial conversion of nitrate (NO_3^-) to gaseous nitrogen (N_2) (denitrification). Unusually large amounts of nitrous oxide (N_2O) are also produced through denitrification ($5CH_2O + 4NO_3^- \rightarrow 5CO_2 + 2N_2O + 5H_2O$) making this region a hotspot for oceanic N_2O emissions. As this water ascends further and loses all NO_3^- , sulphate reduction sets in, producing obnoxious and toxic hydrogen sulphide (H_2S). Conditions in the deep layer are harsh for higher life forms including fish.

(Switchable Trace Oxygen, STOX) presently available (Thamdrup et al., 2012). Nitrite is further converted to elemental nitrogen (N_2), with nitrous oxide (N_2O), laughing gas, being another intermediate of this reaction chain, called denitrification (Deuser, 1975). This process is also known to occur in several other anaerobic environments, such as groundwaters and soils. Denitrification is of immense geochemical importance because it regulates the N_2 inventory of the atmosphere; but for this process, N_2 , the most abundant (78%) gas in the Earth's atmosphere would be depleted in a few tens of million years (Deuser, 1975). In addition to denitrification, N_2 can also be produced by microbes that oxidize ammonium (NH_4^+), another common nitrogen species, with NO_2^- in the absence of O_2 . Although the relative importance of anaerobic ammonium oxidation (Anammox) and denitrification continues to be debated (Lam et al., 2011; Ward et al., 2009), both processes require anoxic conditions. It is estimated that the Arabian Sea accounts for at least 1/3 of the global N_2 production in oceanic OMZs (Codispoti et al., 2001; Naqvi, 1987). Surprisingly, the SNM zone, where most of this loss is believed to occur, is located in the central and north-eastern parts of the Arabian Sea (Figure 2.3.1), that are biologically less productive than the upwelling centres off Somalia and Arabia, underscoring the importance of circulation in the

formation and sustenance of SNM (Naqvi, 1991). While the biogeochemistry of OMZs is dominated by nitrogen cycling, the OMZs also affect cycling of several other elements, such as manganese, iron, iodine and sulphur (Briertburg et al., 2018). Thus, changes in the volume and intensity of OMZs are potentially of global significance.

Based on physical considerations alone (poorer ventilation), the OMZ is expected to be more intense in the Bay of Bengal than in the Arabian Sea. The OMZ in the latter region is indeed *nearly* devoid of dissolved O_2 ; however, unlike the Arabian Sea it does not support large-scale anaerobic respiration as evident from the absence of SNM (Naqvi et al., 2006a) and associated N_2 production (Bristow et al., 2017). This is in large part due to the fact that the Bay of Bengal is considerably less productive than the Arabian Sea (Qasim, 1977) as a result of much weaker coastal upwelling and strong stratification that restricts nutrient entrainment from subsurface waters into the sun-lit surface layer through wind-induced and convective mixing. However, rivers also bring large quantities of particulate organic carbon (POC) to the Bay of Bengal along with enormous amounts of lithogenic material, and it is hypothesized that incorporation of dense mineral material into particle aggregates facilitates rapid sedimentation of POC to

the sea floor with less degradation in the water column (Ittekkot et al., 1992; Rao et al., 1994).

The extent and intensity of deoxygenation in the estuarine, coastal and shelf waters of the Indian Ocean also vary regionally. In the western Arabian Sea, strong seasonal upwelling brings up low O_2 waters over the shelf off the Somali and Arabian coasts. However, vigorous circulation means the upwelled waters do not stay long enough over the narrow shelves to allow the development of intense anoxia. Over the western Indian shelf, upwelling is much weaker, and the upwelled waters rarely reach the surface because of the presence of a thin (5-10 m) low-salinity lens that is formed as a result of intense monsoon rainfall (Figure 2.3.3). With the cold, high-salinity, O_2 -depleted water capped by the warm, low-salinity surface layer, bottom waters with O_2 content below 0.5 ml L^{-1} ($22.3 \text{ } \mu\text{M}$; $1 \text{ ml L}^{-1} = 44.6 \text{ } \mu\text{M}$), about 10% of value expected if these waters were in equilibrium with the atmosphere, seasonally cover the entire shelf (area $\sim 200,000 \text{ km}^2$), making it the largest shallow water O_2 deficient zone in the world (Naqvi et al., 2000). The bottom waters over the inner shelf experience some of the most extreme anaerobic phenomena, including denitrification and reduction of sulphate to noxious and toxic hydrogen sulphide (H_2S), another pathway of organic matter degradation, observed along an open coast anywhere in the world. Sulphate reduction is activated when NO_3^- also gets fully consumed by microbes. Such conditions do not occur in the Bay of Bengal despite immense river runoff which has been postulated to be highly enriched in nutrients (Seitzinger et al., 2002). This is perhaps due to reduction of nutrient loads in freshwater ecosystems before the river water reaches the sea (Naqvi et al., 2018).

The low O_2 systems described above are naturally-formed and have existed in the geological past, albeit with varying intensity driven by natural climate variability (Reichert et al., 1998). These systems are expected to be highly sensitive to human-induced climatic and environmental changes of both global and regional nature, such as warming and eutrophication, one major effect of which is ocean deoxygenation (Breitburg et al., 2018). In the following sections, an attempt is made to document ongoing trends of further deoxygenation in and around these systems and their potential ecological and socio-economic consequences. While ocean deoxygenation is global and would obviously occur in other parts of the Indian Ocean as well, this

chapter focuses largely on the northern basins, not only because being already affected by severe O_2 deficiency these basins are most vulnerable to human-induced deoxygenation, but also because sufficient data are available from these basins to discern ongoing changes. Information from the equatorial and southern parts of the Indian Ocean is mentioned briefly, where available.

2.3.2 Trends and impacts

2.3.2.1 Open-ocean

Analysis of global data sets has revealed steady declines in subsurface O_2 concentrations since 1960 in many parts of the ocean, especially close to OMZs in the tropics (Helm et al., 2011; Stramma et al., 2008). The rate of O_2 loss has been reported to be highest ($0.34 \text{ } \mu\text{mol kg}^{-1} \text{ yr}^{-1}$) in the North Pacific and lowest ($0.09 \text{ } \mu\text{mol kg}^{-1} \text{ yr}^{-1}$) in the equatorial Indian Ocean. In a more detailed follow-up study, Schmidtko et al. (2017) demonstrated that the ocean has already lost over 2% (4.8 petamol) of its O_2 content (227.4 petamol) since 1960 (1 peta or $10^{15} \text{ mol} = 32 \text{ billion tonne of } O_2$). The computed O_2 decline rate was highest ($0.210 \pm 0.125 \text{ petamol per decade}$) for the equatorial Pacific followed by the North Pacific ($0.173 \pm 0.040 \text{ petamol per decade}$), with these two regions accounting for $\sim 40\%$ of the global oceanic O_2 loss rate ($0.961 \pm 0.429 \text{ petamol per decade}$). In contrast, the combined contribution by the equatorial Indian Ocean ($0.055 \pm 0.049 \text{ petamol per decade}$) and the southern Indian Ocean ($0.027 \pm 0.034 \text{ petamol per decade}$) was just 8.5%. Based on Schmidtko et al. (2007; Figure 1), the change in dissolved O_2 in the Arabian Sea and Bay of Bengal put together would be $\ll 0.055 \text{ petamol per decade}$. Their results also indicated a substantial decrease in O_2 along the west coast of India, in the Gulfs of Aden and Oman, and in parts of the northern Bay of Bengal. As in most other areas, the decreases in O_2 concentration in the upper water column appear to have been driven primarily by lower O_2 solubility in warming sea water. In deeper water, however, the O_2 decrease was attributed to basin-scale multi-decadal variability, slow-down of oceanic overturning circulation and enhanced remineralization. Significantly, the highest rate of decrease in the equatorial Indian Ocean was recorded along the western boundary (off Africa) where more oxygenated intermediate waters of southern origin cross the equator (Swallow, 1984). Since these waters are responsible for $\sim 90\%$ of O_2 supply to OMZs of the North Indian Ocean, the observed loss of O_2 in the western equatorial Indian Ocean has potentially

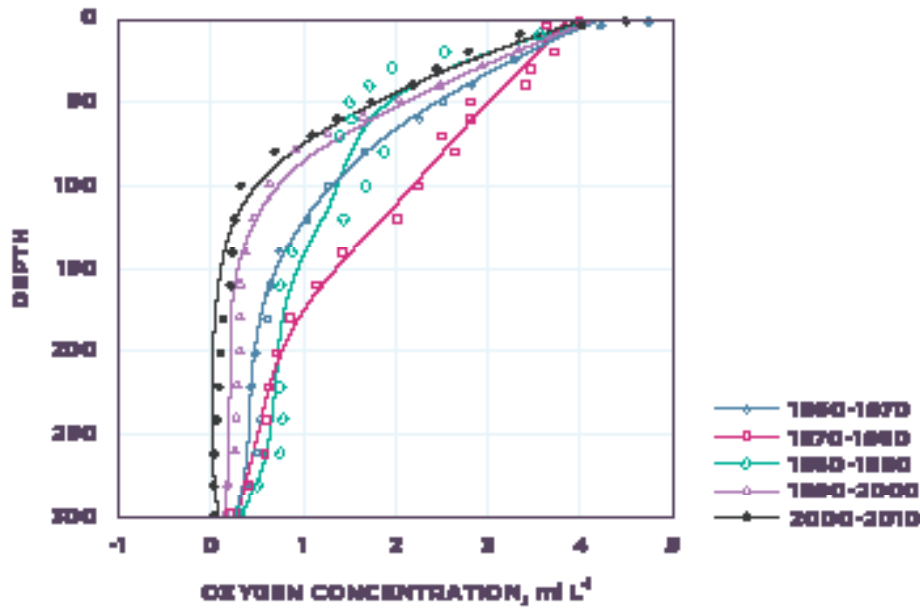


Figure 2.3.4 Decadal changes in oxygen content in the upper 300 metres in the western Arabian Sea (after Piontkovski & Al-Oufi, 2015).

important implications for future intensification of these OMZs.

2.3.2.1.1 Arabian Sea and Gulf of Oman

Three recent studies have specifically dealt with changes in dissolved O_2 in the upper water column of the north-western Indian Ocean over the past few decades. Two of these (Piontkovski & Al-Oufi, 2015; Queste et al., 2017) focused on the western Arabian Sea and the Gulf

of Oman. The western Arabian Sea contains the world's only major western boundary upwelling system where, as stated earlier, low O_2 waters are brought up to the continental shelves during the SWM. Analysis of data from this region collected during 53 cruises conducted from 1960 to 2008 revealed significant decadal changes in the upper 300 metres. While the water temperature has risen by ~ 1.5 °C over five decades, the oxycline (the horizon below the surface where O_2 concentration begins to fall rapidly) shoaled up at a rate of ~ 19 m per decade. Significantly, the observed decrease in O_2 concentration within the OMZ is quite large during the SWM, when waters derived from the southern hemisphere ventilate the OMZ, with the most recent data (for 2000-2010) indicating near anoxic conditions (Figure 2.3.4). In a more recent study, Queste et al. (2017) combined historical data with recent time series measurements made with automated gliders equipped with O_2 sensors to show that within the core of the OMZ in the Gulf of Oman O_2 levels have fallen from $6\text{--}12 \mu\text{mol kg}^{-1}$ at the time of the International Indian Ocean Expedition (IIOE) in the 1960s to $< 2 \mu\text{mol kg}^{-1}$ in recent times. Although, this shift is subtle, and could to some extent be accounted for by the improved quality of recent data, it is potentially significant given the above-mentioned sensitivity of respiratory processes to vanishingly low O_2 levels.

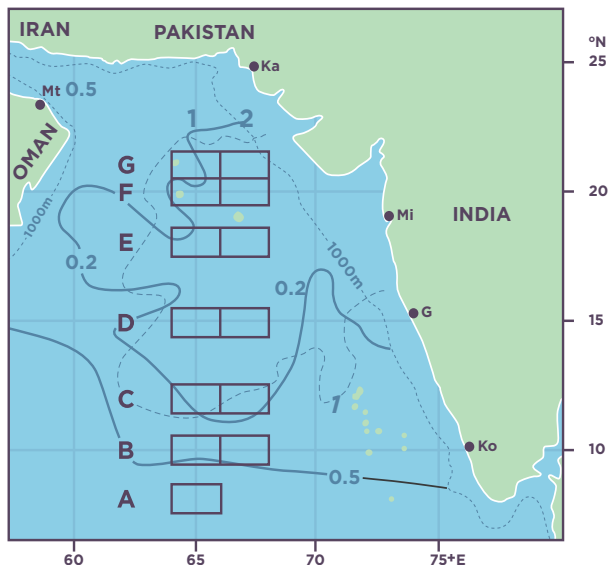


Figure 2.3.5 “Boxes” selected by Barse et al. (2014) to investigate decadal changes within the oxygen minimum zone of the Arabian Sea. The left boxes are numbered “1” while the right boxes are numbered “2”. Oxygen distribution at 200 m is shown by the 0.2 and 0.5 mL l^{-1} contours (solid) from Wyrski (1971); the zone of denitrification is demarcated by the $1 \mu\text{M}$ nitrite contour (dashed) from Naqvi (1991).

The third investigation (Barse et al., 2014) that concentrated on the more intense OMZ in the central Arabian Sea yielded less clear trends. This study utilized discrete O_2 measurements made between 1959 and

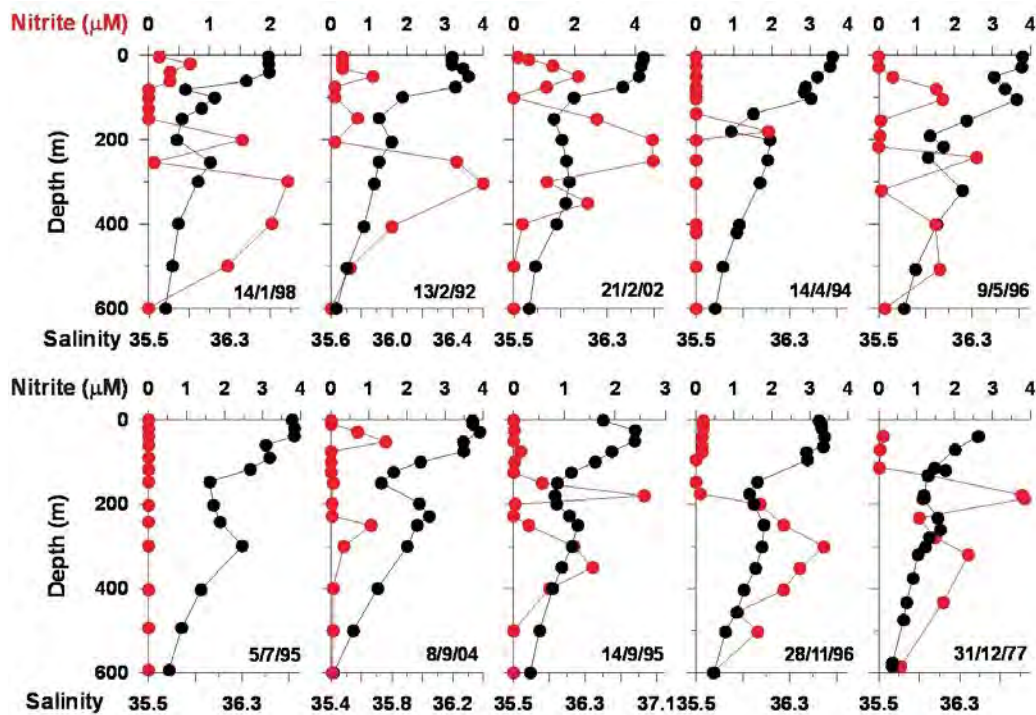


Figure 2.3.6 Vertical profiles of nitrite (red symbols) and salinity (black symbols) at a fixed site (Lat. 19.75°N, Long. 64.62°E) sampled repeatedly between 1977 and 2004 (arranged by month of visit). The station is located close to the north-western boundary of denitrification zone and the observed variability is largely caused by the flow of the high salinity water mass originating in the Persian Gulf (modified from Banse et al., 2014).

2004 near 150, 200, 300, 400, and 500 m water depths at stations located within zonally-paired boxes of 1° latitude x 2° longitude that were centred at 8, 10, 12, 15, 18, 20, and 21°N latitudes along 65° and 67°E longitudes (Figure 2.3.5). Except for 8 – 12°N, all boxes were located within the zone having SNM. On many recent cruises in the Arabian Sea (e.g. US JGOFS Arabian Sea Process Study, 1994-1995; Morrison et al., 1999), O₂ analysis by the automated Winkler procedure involved photometric end-point detection. As this technique yields consistently lower values (by ~0.04 ml L⁻¹) than manual titrations involving visual end point detection, Banse et al. (2014) only considered O₂ data generated with the latter procedure to minimize analytical bias. However, about a quarter of the O₂ data used might still have been accompanied by substantial NO₂⁻ (Karl Banse, pers. comm.), but exclusion of these data is unlikely to alter the major conclusions of this study.

Linear regression analysis, carried out for each depth and box separately for NEM and SWM to see if the O₂ concentration varied systematically with time, revealed conflicting trends (Banse et al., 2014). Within the three southern boxes (A-C), located at 8-12°N, outside the OMZ having SNM, O₂ concentration seemingly increased with time in the majority of cases, although

the correlation was significant at $p \leq 0.1$ on only three occasions. In contrast, within the OMZ the overwhelming trend was of declining O₂ concentrations with time in all boxes except F2, G1 and G2, situated at 20-21°N during both monsoon seasons. Although the median value for significant positive slopes (~-0.12 μM yr⁻¹), was close to the lower range of rates of O₂ decline reported by Stramma et al. (2008), it was somewhat higher than the concentrations measured within the SNM (<0.090 μM) with the STOX sensor (Jensen et al., 2011; note that the limit of detection of the sensor was higher on this cruise). An important result of this study was that the long-term declining trends within the OMZ were different during the NEM and SWM seasons with a more pronounced decrease occurring during the NEM when O₂ concentrations were slightly higher. The seasonal variability points to O₂ supply to the OMZ through vertical mixing and horizontal advection. Within the three northern boxes (F2, G1 and G2), although the majority of slopes were positive, none of them were statistically significant, with the maximal rate of increase being only ~0.10 μM yr⁻¹.

Banse et al. (2014) also used NO₂⁻ (within the SNM) as a proxy of functional anoxia (Thamdrup et al., 2012). Nitrite concentration broadly reflects the extent of

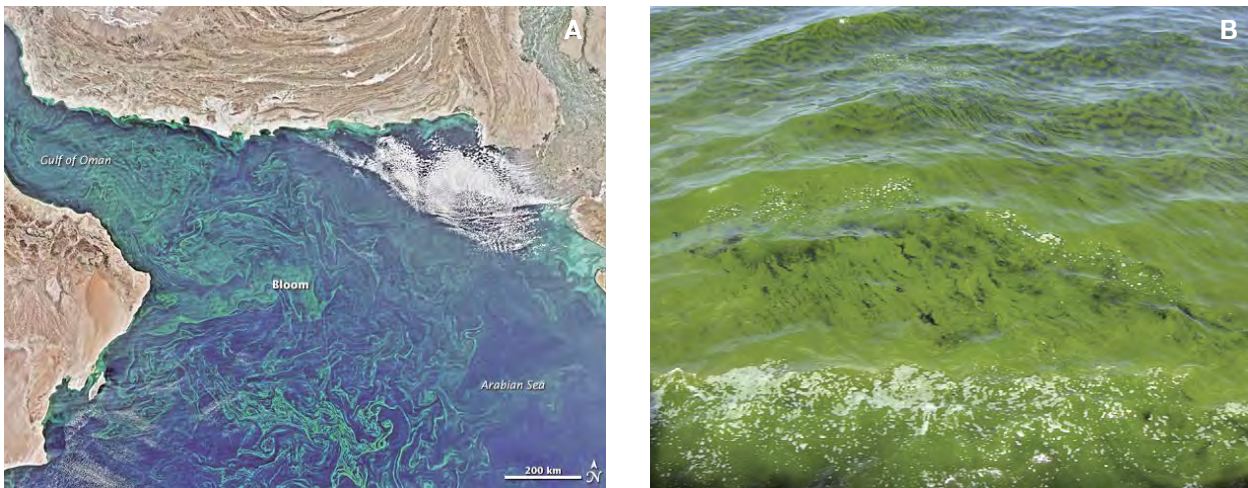


Figure 2.3.7 A) Convective mixing in winter leads to the development of phytoplankton blooms in the northern Arabian Sea, which are identifiable by satellite-based ocean colour measurements. Source: Image obtained on 14.02.2015 by the Moderate Resolution Imaging Spectrometer (MODIS) on NASA's Aqua satellite (<https://earthobservatory.nasa.gov/images/85718/winter-blooms-in-the-Arabian-Sea>). Earlier algal blooms in this region largely comprised diatoms, the major group of phytoplankton with glassy shells. Diatoms were grazed by copepods that were, in turn, eaten by fish. B) Replacement of diatoms by larger sized dinoflagellates (*Noctiluca scintillans* bloom in February 2009 (from <http://helgagomes.com>)), attributed to incursions of low O_2 waters into the surface layer (Gomes et al., 2014), may disrupt this important food chain. Instead the photosynthesized organic matter may now end up as 'useless' salps and jellyfish with potentially large socio-economic consequences.

denitrification (Bulow et al., 2010; Naqvi, 1991) or the intensity of the OMZ. The SNM in the Arabian Sea has been known to occur since 1933/34 (Gilson, 1937), which implies that parts of the OMZ in the Arabian Sea have been functionally anoxic for at least 80 years. Repeat measurements at two locations - 19.75°N , 64.62°E , going back to 1977 (Figure 2.3.6), and $\sim 15^\circ\text{N}$, 68°E , going back to 1979 (data not shown) - showed large interannual changes in NO_2^- concentration but no secular long-term trend. The amplitude of variability was larger at the former site, it being closer to the north-western boundary of the denitrification zone and to a large extent affected by the warm, saline outflow from the Persian Gulf that serves as a source of O_2 to the OMZ (Codispoti et al., 2001). Consequently, at depths where this water mass is found, as identified by its characteristic salinity maximum, NO_2^- and salinity were inversely related (Banse et al., 2014). Linear regression analysis between NO_2^- concentration and year of measurement yielded both negative and positive slopes, with the number of positive slopes exceeding that of negative values indicating that the NO_2^- concentration mostly increased with time, i.e. OMZ intensified. The Arabian Sea was extensively surveyed during the Joint Global Ocean Flux Study (JGOFS) project. Utilizing the data collected during the US JGOFS cruises, Rixen et al. (2014) demonstrated that the area with NO_2^- concentrations exceeding $2 \mu\text{M}$ was 63% larger in 1995 than what was estimated from the earlier data (Naqvi, 1991). However, Rixen et al. (2014) also pointed out that these observations

probably indicated considerable seasonal and interannual variations in denitrification rather than a secular trend of increase. Combining this data set with their own observations made in September-October, 2007, Rixen et al. (2014) showed that the seasonal and interannual variations were driven by the monsoons. During the SWM, the boundary of the denitrification zone, determined by a complex interplay between circulation and productivity, moved eastward as a result of advection of the more oxygenated water across the equator in the western Indian Ocean. Reversal of circulation during the NEM led to westward expansion of the denitrification zone. Rixen et al. (2014) proposed that during those years when the SWM was weaker, the denitrification zone expanded toward the west, and vice versa. The sedimentary records presented by Rixen et al. (2014) indicated an intensification of denitrification in the Arabian Sea during the past few thousand years, supporting this view (see also Kessarkar et al., 2018), but the longer sedimentary records show the opposite trend (Altabet et al., 2002). Thus, it is still not clear whether or not denitrification in the Arabian Sea has intensified in recent decades. In any case, the monsoons play an important role in regulating the intensity of the OMZ and the associated biogeochemical transformations, and since global warming is projected to impact the SWM significantly (Turner & Annamalai (2012), and references therein), this represents an additional region-specific human-induced forcing that may potentially modify O_2 distribution in the North Indian Ocean.

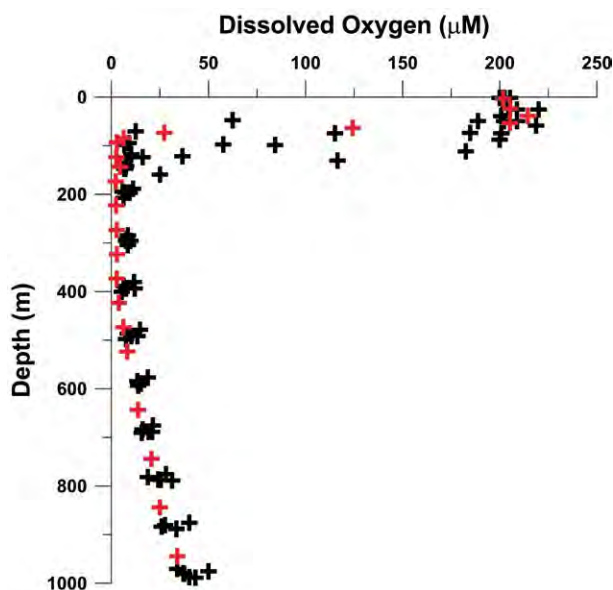


Figure 2.3.8 Comparison of O_2 distribution in the northern Bay of Bengal in the vicinity of Lat. $18^\circ N$, Long. $89^\circ E$ based on sampling in April 1963 (black symbols) and April 2007 (red symbols).

It has been reported that global warming has already led to an intensification of upwelling in the western Arabian Sea (Goes et al., 2005). These authors analysed satellite data off Somalia to demonstrate an increase in phytoplankton biomass by over 350% from 1997 to 2003. It was suggested that the increase in productivity of the Arabian Sea would have far-reaching consequences for the OMZ. However, intensification of upwelling and a consequent increase in phytoplankton biomass have not been confirmed either from satellite data or by *in situ* measurements by subsequent workers (e.g. Naqvi et al., 2010). An expansion of the OMZ has been invoked by Gomes et al. (2014) to explain a radical shift in the composition of winter phytoplankton blooms in the Arabian Sea, where the dinoflagellate *Noctiluca scintillans* was reported to have replaced diatoms over the past decade (Figure 2.3.7). The remarkable ability of its endosymbiont *Pedinomonas noctilucae* to fix carbon under hypoxic conditions is believed to give *Noctiluca* an ecological advantage over other phytoplankton. However, incursions of low O_2 waters into the surface layer in winter have not been subsequently verified (Prakash et al., 2017).

2.3.2.1.2 Bay of Bengal

Reliable O_2 data from the Bay of Bengal date back only to the International Indian Ocean Expedition (IIOE) in the early 1960s. In order to determine whether any change in O_2 concentration has occurred since that time, unpublished O_2 data collected on a cruise of R.V. *Anton Bruun* in the vicinity of Lat. $18^\circ N$, Long. $89^\circ E$ during 20-22 April 1963 are compared in Figure 2.3.8 with measurements made on a cruise of R.V. *Roger Revelle* at about the same time of the year 44 years later. Besides being located in the northern Bay where the OMZ is most intense, the choice of this location was determined by data availability over a long period. The *Anton Bruun* occupied five stations within latitudes $17.1-20.07^\circ N$ and longitudes $88.4-90.28^\circ E$. In 1963, O_2 concentrations, measured with visual end point detection within the depth range $\sim 200-400$ m averaged $8.33 \pm 2.11 \mu M$ ($0.187 \pm 0.047 \text{ ml L}^{-1}$), with a minimum of $5.36 \mu M$ (0.12 ml L^{-1}). Corresponding average and minimum values observed on the *Roger Revelle* Sta. 199 (Lat. $18^\circ N$, Long. $89.85^\circ E$) sampled on 27 April 2007 were $2.63 \pm 0.26 \mu M$ ($0.059 \pm 0.006 \text{ ml L}^{-1}$) and $2.26 \mu M$ (0.051 ml L^{-1}), respectively, based on automated Winkler titrations. Even after allowing for the difference ($1.8 \mu M$ or $\sim 0.04 \text{ ml L}^{-1}$) between the two techniques, the decrease, even though small, is still significant considering, as in the case of Gulf Oman, the extreme sensitivity of anaerobic respiratory pathways to minor changes in O_2 in the low range. More recent data at this site (collected in January-February 2014 on board R.V. *Sagar Kanya*) using STOX sensors yielded a minimum O_2 concentration of 36 nM (0.0008 ml L^{-1} - Bristow et al., 2017). Elsewhere, O_2 concentrations fell below the detection limit of the sensor ($7-12 \text{ nM}$) in six samples; otherwise O_2 was always present, albeit in traces ($10-200 \text{ nM}$), within the OMZ at all seven stations sampled.

Broad anoxic zones, characterized by SNM, were not observed, except for a thin layer having secondary NO_2^- up to 180 nM at Lat. $18^\circ N$, Long. $89^\circ E$. Despite the absence of SNM, Bristow et al. (2017) recorded the presence of $2-3 \mu M$ of excess N_2 within the Bay of Bengal OMZ. This quantity is an order of magnitude smaller than the N_2 excess found within the Arabian Sea OMZ (Naqvi et al., 2006b), but it still indicates some biological N_2 production. Moreover, analysis of microbial genes revealed adequate presence of microbes capable of denitrification and Anammox that were not very different from other OMZs, and incubations of samples with isotopically labelled nitrogen compounds

demonstrated a potential for Anammox, provided NO_2^- was present. This means that while the system is primed for the conversion of reactive nitrogen to N_2 , rates of the processes involved (denitrification and Anammox) are far lower within the OMZ of the Bay of Bengal compared to other OMZs that contain SNM. Bristow et al. (2017) proposed that traces of O_2 present facilitate NO_2^- oxidation to NO_3^- , thereby restricting its availability for Anammox or denitrification for the production of N_2 , and removal of this residual O_2 may result in an abrupt shift in the biogeochemistry of the Bay of Bengal OMZ. The O_2 change referred to above seems to indicate that the Bay of Bengal is on the verge of such a shift (Bristow et al., 2017). The vertically-integrated O_2 inventory in the upper 1 km was computed to have decreased from 33.77 ± 4.5 to 28.38 M m^{-2} between 1963 and 2007. However, this decrease was mostly caused by a change in the thickness of the mixed, oxygenated surface layer, which was lower in 2017 compared to 1963; by contrast, the lower OMZ appears to have remained remarkably stable for over four decades (Figure 2.3.8). Should the OMZ of the Bay of Bengal cross the tipping point which it seems to be at right now, the loss of reactive nitrogen to N_2 is expected to increase, throwing the nitrogen budget further off balance (Codispoti et al., 2001). Moreover, production of N_2O may also be enhanced, providing positive feedback to global warming.

2.3.2.2 Red Sea and Persian Gulf

A unique feature of the OMZ of the north-western Indian Ocean is that it is ventilated by freshly formed water masses in the two Mediterranean-type marginal seas (Red Sea and Persian Gulf). Both of these seas are located in highly arid zones, experiencing excessive evaporation and receiving little river runoff. Cooling of consequently high salinity waters in winter elevates densities of these waters, causing them to sink and fill deeper parts of the two seas. While in the Red Sea such deep water formation occurs in the extreme northern parts, particularly in the Gulfs of Suez and Aqaba (Morcos, 1970), in the Persian Gulf it takes place off the coasts of the United Arab Emirates (UAE) and Kuwait (Reynolds, 1993; Swift & Bower, 2003). The Red Sea is much deeper (average depth 491 m, maximum depth $>2500 \text{ m}$ - Morcos, 1970) than the Persian Gulf (average depth 36 m, maximum depth $\sim 90 \text{ m}$ - Al-Said et al., 2018). The Red Sea is separated from the Gulf of Aden by a shallow sill (depth 137 m) at the Bab-el-Mandeb Strait - Naqvi & Fairbanks, 1996). The Hormuz Strait, which separates the Persian Gulf from the Gulf of

Oman, does not have a similar sill. Both basins receive less saline waters from the Indian Ocean, transported by near-surface currents to make up for the excessive water loss through evaporation. However, in order to maintain the salt balance these semi-enclosed seas also export dense waters to the north-western Indian Ocean through the Gulfs of Oman and Aden as near-bottom outflows over the two straits. These water masses, called the Persian Gulf Water (PGW) and Red Sea Water (RSW), easily identifiable by their high salinities, are found at depths of $\sim 200\text{-}350 \text{ m}$ and $\sim 500\text{-}800 \text{ m}$, respectively, in the Arabian Sea (Wyrki, 1971). Because of greater depth, volume and presence of a sill at its entrance, the ventilation time of the Red Sea is much longer ($\sim 36 \text{ yr}$ - Naqvi & Fairbanks, 1996) than that of the Persian Gulf (1.2 yr - Al-Said et al., 2018), and the patterns of O_2 distribution are quite different. The Red Sea water column is remarkably homogenous in terms of temperature and salinity below the sill depth. However, chemical data do not show such homogeneity (Morcos, 1970), with the O_2 profiles showing a pronounced mid-depth minimum that generally intensifies toward the south with values going down to $\sim 0.2 \text{ ml L}^{-1}$ (Figure 2.3.9). The low- O_2 concentrations are associated with relatively high temperature ($\sim 22 \text{ }^\circ\text{C}$) which is an important determinant of hypoxia tolerance to marine organisms (Seibel et al., 2016). Natural O_2 depletion in the Persian Gulf is more modest, restricted only to the central and southern parts and largely to the summer season where/when the water column is stratified (Al-Yamani & Naqvi, 2018). Because both PGW and RSW contribute significantly to water mass composition of the OMZ of the north-western Indian Ocean, changes in the amounts of O_2 carried by these water masses are important.

Ongoing deoxygenation trends in the Red Sea have not been documented so far, and there is a dearth of recent O_2 data in the publicly available data bases to investigate such trends. Fortunately, two Argo floats generated O_2 profiles in the northern Red Sea (north of $\sim 23^\circ\text{N}$) - one from 29.09.2015 to 19.02.2017 and the other from 30.09.2015 to 29.12.2016. The data from these floats are compared with measurements made during a cruise of R.V. *Sagar Kanya* in the same region in May 1983 (Naqvi et al., 1986) (Figure 2.3.9). While it would be hazardous to draw definite conclusions based on just two sets of measurements, O_2 values recorded by the floats during 2015-2017 are generally and quite substantially lower than those obtained during the *Sagar Kanya* survey. Also included in Figure 2.3.9A is an O_2 profile from the GEOSECS Sta. 407 (Lat. 19.92°N , Long.

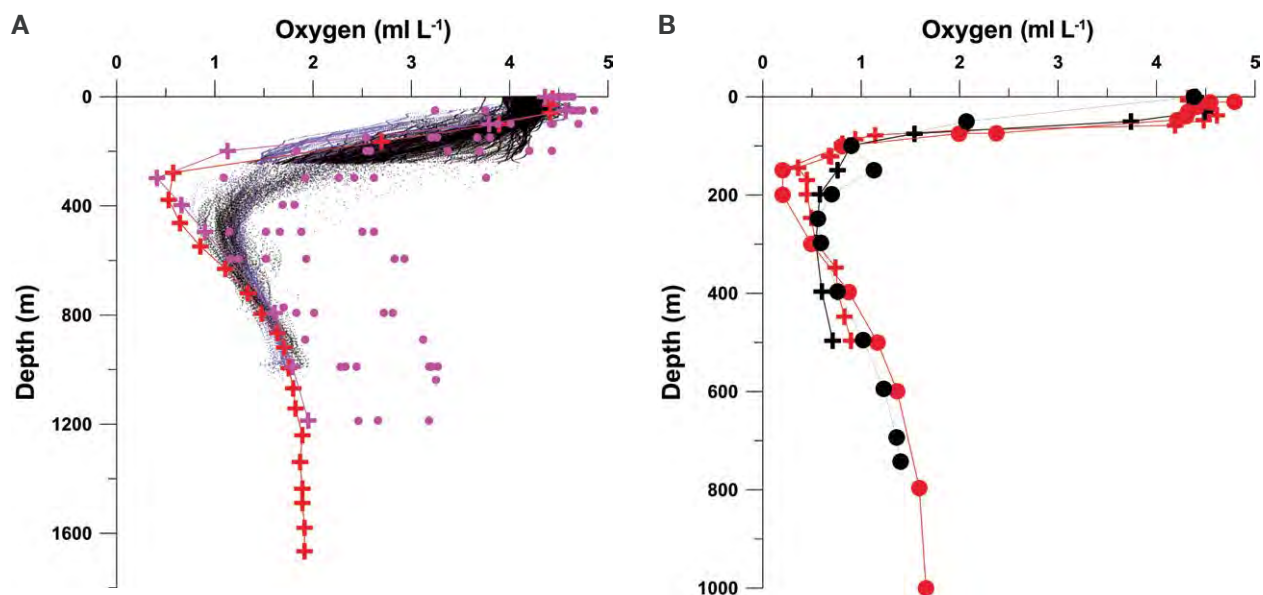


Figure 2.3.9 (A) Comparison of O_2 profiles from two Argos floats deployed in the Red Sea north of $\sim 23^\circ N$ latitude: #146, from 29.09.2015 to 19.02.2017 (black symbols) and #147, from 30.09.2015 to 29.12.2016 (blue symbols) with Winkler O_2 measurements (magenta unconnected circles) made by the author in the same area in May 1983 on board R.V. *Sagar Kanya*. O_2 profiles at a site in the central Red Sea obtained during the GEOSECS Expedition (Sta. 407 - Lat. $19.92^\circ N$, Long. $38.48^\circ E$, sampled on 22.12.1977) and at a nearby *Sagar Kanya* station (Sta. 40 sampled on 24.05.1983) are shown by red and magenta crosses, respectively. (B) Comparison of O_2 profiles at two *Sagar Kanya* stations (Sta. 70 - $16.03^\circ N$, $41.39^\circ E$ - black circles, and Sta. 74 - $14.78^\circ N$, $42.12^\circ E$ - black crosses) with O_2 profiles from two closely located stations sampled during cruises of R.V. *Tyro* on 27.05.1992 (Cast 7168075 - red circles) and 03.02.1993 (cast 7160570 - red crosses). These data were obtained from the National Oceanographic Data Center, USA.

$38.48^\circ E$) taken on 22.12.1977 and another from the closely located Sta. 40 sampled on 24.05.1983 on the same *Sagar Kanya* cruise. The GEOSECS and *Sagar Kanya* data match very well with each other, as do O_2 profiles from two other *Sagar Kanya* stations (Sta. 70 - Lat. $16.03^\circ N$, Long. $41.39^\circ E$, and Sta. 74 - Lat. $14.78^\circ N$, Long. $42.12^\circ E$) with the profiles from two closely located stations sampled during cruises of R.V. *Tyro* on 03.02.1993 and 27.05.1992, respectively. This shows that the *Sagar Kanya* observations were not abnormal. Thus, it appears that substantial deoxygenation has already occurred in deep waters of the Red Sea over the past three decades. However, this trend needs to be confirmed by recent data from the southern Red Sea where seasonality is smaller and the O_2 minimum is more pronounced. The very low O_2 values measured on the *Tyro* cruises, incidentally the most recent bottle data in the database of the National Oceanographic Data Center (NODC), underline the potential vulnerability of the Red Sea to anthropogenic deoxygenation.

The RSW undergoes substantial modification through mixing as it descends from the Bab-el-Mandeb Strait and finds its density level in the Gulf of Aden (Grasshoff, 1969; Morcos & AbdAllah, 2012). With an initial O_2 content of $\sim 1.5 \text{ ml L}^{-1}$ (Morcos & AbdAllah, 2012), the RSW is a source of O_2 to the O_2 -depleted ($< 0.5 \text{ ml L}^{-1}$)

waters it mixes with in the Gulf of Aden. Deoxygenation within the Red Sea is thus expected to affect O_2 distribution in the Gulf of Aden and the adjacent Arabian Sea where RSW spreads horizontally. Trends of any deoxygenation in the Gulf of Aden are not yet known but are expected to be similar to those described above for the western Arabian Sea.

Flowing directly into the core of the OMZ where denitrification is most intense, PGW is perhaps more important than RSW in regulating biogeochemical cycling in the Arabian Sea. Although O_2 supply from this watermass is small, it is nevertheless enough to prevent the onset of denitrification in the north-western Arabian Sea. The PGW also has a relatively elevated concentration of total organic carbon (TOC) compared to the water it mixes with (Hansell & Peltzer, 1998). Changes in the initial concentrations of both TOC and O_2 in this watermass have the potential to alter the extent and intensity of the OMZ. There is compelling evidence to suggest that such changes are already occurring. Emergence of summertime hypoxia in the central Persian Gulf has been reported by Al-Ansari et al. (2015) who observed an O_2 decrease by as much as 1 ml L^{-1} relative to the historical data. More recently, high TOC concentrations (up to $543 \mu M$) have been observed in the northern Gulf (Al-Said et al., 2018). Significantly,

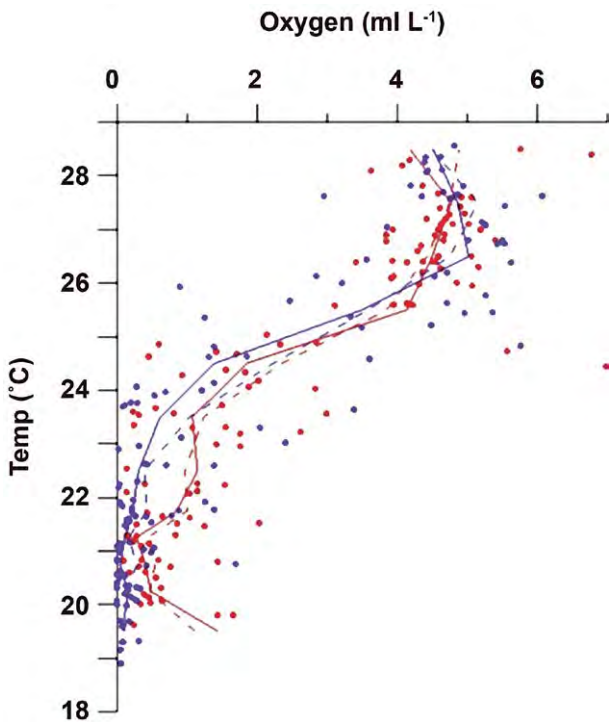


Figure 2.3.10 Comparison of O_2 concentrations with reference to temperatures over the inner and mid-shelf regions (depths < 60 m) off Karwar (see Figure 2.3.1), central west coast of India, during the upwelling period in 1971–1975 (red symbols) and 1997–2004 (blue symbols). Mean and median values for 1 °C-bins are shown by the dashed and solid curves, respectively (modified from Naqvi et al., 2006c).

a reduction in runoff from the Shatt al-Arab river has made surface waters in the region seasonally (in winter) the densest found anywhere in the Gulf implying that the organic matter derived from sewage or produced by phytoplankton in the northern Gulf would be quickly injected into Gulf Deep Water, to be eventually flushed into the core of the OMZ of the Indian Ocean (Al-Said et al., 2018). In addition, model simulations show that the size and intensity of this OMZ are very sensitive to warming of waters in the Persian Gulf and Red Sea (Lachkar et al., 2019). Thus, the ongoing physico-chemical changes in the marginal seas are likely to lead to expansion and intensification of the Arabian Sea OMZ.

2.3.2.3 Coastal waters

The available information suggests that O_2 concentrations in bottom waters over the Omani shelf might have decreased in recent decades (Piontkovski & Al-Oufi, 2015). This is also supported by data presented by Naqvi et al. (2010). However, there is a dearth of recent O_2 measurements from this region. In contrast to this, the seasonal low O_2 zone over the western Indian shelf, the largest of its kind in the world (Figure 2.3.3), has been fairly well studied. Although O_2 deficiency off India has

been known since the 1950s (Banse, 1959; Carruthers et al., 1959), its regular monitoring was initiated by the National Institute of Oceanography (NIO), Goa, only in the 1990s. A number of cruises were undertaken during which multi-disciplinary observations were made along transects running perpendicular to the coast. In 1997 a time series station, the Candolim Time Series (CaTS), was also established off Goa at a depth of ~28 m. The CaTS data show marked interannual changes in the duration as well as intensity of O_2 deficiency but no clear long-term trend (Naqvi et al., 2009). The most intense anoxic conditions were recorded in the early 2000s (especially in 2001) when high hydrogen sulphide (H_2S) concentrations were recorded over large parts of the shelf at depths as shallow as 5 m and as deep as 65 m. This was attributed to an intensification of O_2 deficiency over the western Indian shelf due to enhanced anthropogenic nutrient loading (Naqvi et al., 2006c). Although anoxic events of comparable magnitude have not occurred since, current conditions are still more severe than those indicated by the historical data. The most extensive of such data, although restricted only to salinity, temperature and O_2 , were obtained under the UNDP/FAO-sponsored Integrated Fisheries Project (IFP). Repeat observations were made under this programme from 1971 to 1975 along a number of coast-perpendicular transects, including one off Karwar, just south of Goa. A comparison of the O_2 data generated during the IFP with those collected by NIO for the same shelf segment (depth < 60 m) and the same season (August–September) between 1997 and 2004 (Figure 2.3.10) shows considerable scatter. However, the means and medians of subsurface concentrations are significantly lower for 1997–2004 than for 1971–1975. Significantly, zero O_2 concentrations, characteristic of sulphidic waters, were never recorded on the IFP cruises, implying the absence of H_2S . Other data subsequently collected by NIO (Naqvi et al., 2000 - Supplementary Information) also show that the subsurface environment was denitrifying but not sulphate reducing at least until the 1980s. It is still not clear what caused a shift to sulphidic conditions that have persisted but have not intensified steadily since the monitoring began at the CaTS site. It has been suggested that the intensity of anoxia may be modulated by basin scale events especially the Indian Ocean Dipole (IOD) (Vallivattathillam et al., 2017). The IOD is the Indian Ocean counterpart of the El Niño and La Niña events that are well known to occur in the Pacific Ocean (Saji et al., 1999). Positive IOD years, of which 1997 is an extreme example, are distinguished by anomalously low sea surface temperatures (SSTs) in the

eastern equatorial Indian Ocean and high SSTs in the western Indian Ocean, a reversal of the normal trend, accompanied by wind and precipitation anomalies. Isolation of human-induced environmental changes including changes in O_2 distribution from those resulting from irregular but naturally caused climate modes, like IOD, continues to be a major challenge.

Further south along the same coast, monthly observations for one year in 2012 at a station located over the mid-shelf (Lat. 9.969°N, Long. 75.831°E, depth 52 m) off Kochi, which was also sampled on a monthly basis by Banse (1959) from July 1958 to January 1960, revealed remarkably little change in O_2 concentrations over the intervening period (Gupta et al., 2016). However, 2012 was an IOD year when upwelling was weaker, and so the prevalence of lower O_2 concentrations during a normal year cannot be ruled out.

High population density and rapid industrialization have led to large increases in waste discharges, often untreated, into most Indian rivers, resulting in the development of low O_2 conditions in several estuaries, creeks, bays and fishing harbours such as Ratnagiri, Veraval and Porbandar Harbours; Mahim Bay and Versova Creek (Mumbai); and the estuaries of rivers Ulhas (near Mumbai), Kolak (near Daman), Tapi (near Surat) and Sabarmati (at the head of the Gulf of Cambay) along the north-west coast of India (Figure 2.3.1), with the O_2 concentration sometimes falling below 0.15 ml L^{-1} . For example, measurements in the Tapi Estuary from 1983 to 2011 revealed a change from normoxic to hypoxic conditions (Ram et al., 2014). The estuary remains hypoxic/anoxic during all seasons, but anoxia is more pronounced during the summer and at low tide. The environmental condition of the Tapi Estuary has impacted coastal waters, resulting in fish kills (Ram et al., 2014). Development of anoxia has also been observed in the bottom layers of Kochi Backwaters along the south-west coast of India (Martin et al., 2010). Like most estuaries along the Indian west coast, the intrusion of O_2 -poor upwelled water also occurs in this estuarine system. High O_2 demand in bottom waters arising from eutrophication maintains anoxic (including sulphidic) conditions up to 6 km upstream from the bar mouth of the estuary.

Despite immense runoff from numerous major rivers that are believed to bring large quantities of nutrients into the Bay of Bengal (Seitzinger et al., 2002), O_2 deficiency in shallow waters over the continental shelf is not as

intense in the Bay of Bengal as in the Arabian Sea. Even though as stated above the OMZ in the Bay of Bengal is almost as intense as that in the Arabian Sea, it is located offshore at depths exceeding ~100 m. Unlike the Arabian Sea, it does not come up over the continental shelf close to the surface because of the lack of large-scale upwelling along the Indian east coast, except locally in some areas such as the Andhra coast where some intensification of low O_2 conditions has been reported (Sarma et al., 2013). A more severe event was observed off the south-east coast of India in 2010 leading to prevalence of hypoxic conditions even in shallow waters with O_2 concentrations going down to 0.1 ml L^{-1} at 59 m depth (Satpathy et al., 2013). Although this event was attributed to land-based pollution, the data presented point to an offshore origin of nearly-anoxic waters, possibly associated with an eddy. While O_2 deficiency may develop to a very limited extent close to points of sewage discharge from large population centres, the absence of big hypoxic (dead) zones, like the one in the Gulf of Mexico (<https://gulfhypoxia.net/>), off the mouths of major rivers such as the Ganges-Brahmaputra (Mitra et al., 2018) in the Bay of Bengal is counter-intuitive. This supports the view (Naqvi, 2008) that nutrient runoff by rivers flowing into the Bay of Bengal is not as large as predicted (Seitzinger et al., 2002). Unfortunately, reliable recent O_2 data are nearly non-existent to assess the extent of O_2 change along the coasts of all other countries (Bangladesh, Myanmar, Malaysia, Thailand and Indonesia).

Some estuaries in western Australia near Perth (e.g. Swan-Canning Estuary and Peel-Harvey Estuary), have been impacted by eutrophication and, at some times of the year have O_2 levels below hypoxia threshold (1.4 ml L^{-1}) (Hipsey et al., 2014; Thomson et al., 2017; Tweedley et al., 2015). However, the scale of the problem is far smaller than in other major hypoxic estuarine systems such as the Chesapeake Bay along the US east coast (Officer et al., 1984).

2.3.4 Ecosystem consequences

Oxygen depletion in sea water has a wide variety of impacts on marine biogeochemistry and ecosystems (Briertburg et al., 2018, and references therein), all of which are seen in the low O_2 waters of the Indian Ocean as well. Benthic ecosystems in the Indian Ocean are worst affected by this phenomenon because of the unusually large area of continental margins exposed to hypoxic/anoxic waters (Helly & Levin, 2004).

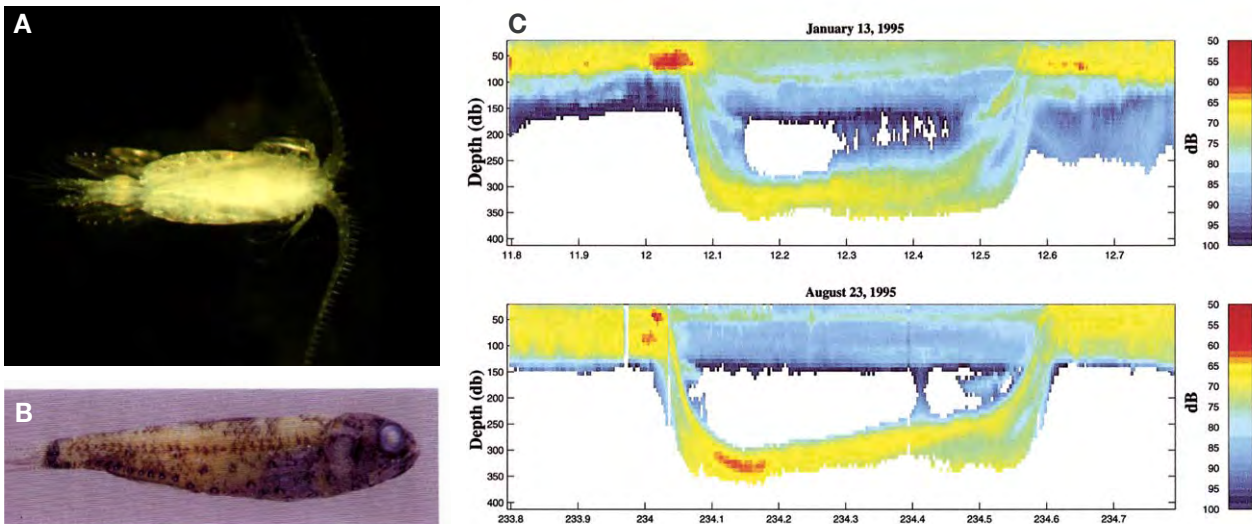


Figure 2.3.11 Life in anoxic environments is dominated by bacteria that are able to utilize chemical species such as nitrate and sulphate to decompose organic matter and gain energy. However, a few multi-cellular organisms are capable of tolerating low O_2 concentrations by suppressing their metabolism (Seibel et al., 2016). Examples from the Arabian Sea include (A) the copepod *Pleuromamma indica* (Saraswathy & Iyer, 1986) (from http://www.mmcer.ynu.ac.jp/shimo/my_site/photos1/peji/Planktonic_copepods.html#70) and several species of myctophids (lanternfish), of which (B) *Benthosema pterotum* (image courtesy P.K. Karuppasamy) is most abundant (Gjosaeter, 1984). Estimated stocks of myctophids in the Arabian Sea (~100 million tonne) slightly exceed total annual global marine fish catch. This huge biomass undergoes spectacular diurnal migration to the functionally anoxic core of the OMZ to escape from predators during the day as shown by the Acoustic Doppler Current Profiler (ADCP) back-scatter records (C) at a location near the heart of the denitrification zone for 24 hours on 13/01/95 and 23/08/95 (after Morrison et al., 1999).

Oxygen deficiency greatly reduces benthic biodiversity, promoting dominance of hypoxia-tolerant groups like polychaetes (Ingole et al., 2010; Levin et al., 2009; Raman et al., 2015). Where O_2 -depleted waters reach the sun-lit zone, they strongly impact phytoplankton community structure. A dramatic shift in phytoplankton composition, with massive blooms of *Noctiluca scintillans* replacing diatoms thereby altering the trophic structure, has been ascribed to the emergence of hypoxic conditions close to the surface during winter in the northern Arabian Sea (Figure 2.3.7) (Gomes et al., 2014). As in other areas, O_2 depletion also affects vertical distribution and diurnal migration of zooplankton in the open ocean (Morrison et al., 1999; Wishner et al., 1998) and in coastal waters (Madhupratap et al., 1996) of the Indian Ocean. At the higher trophic level, while most fishes are excluded from O_2 deficient waters, some species of myctophids (lanternfish) are adapted to live in the functionally anoxic core of the OMZ to which they migrate during the day to avoid predation (Figure 2.3.11; Morrison et al., 1999). The total biomass of myctophids in the Arabian Sea is incredibly high (~100 million tonne; Gjosaeter, 1984). Diurnal migration of such a huge biomass up and down the water column is of great ecological and biogeochemical relevance.

Complete loss of O_2 from the water column favours the development of diverse microbial populations that

utilize anaerobic pathways to derive energy, mediating elemental transformations that are of immense geochemical significance (Wright et al., 2012). For example, denitrification is by far the most important sink term in the reactive nitrogen budget (Codispoti et al., 2001), producing N_2 , the most abundant gas in the atmosphere, thereby countering biotic and abiotic N_2 fixation. The OMZs that support anaerobic respiration pathways are distinguished by an increase in total bacterial numbers to the extent that it causes a significant increase in water turbidity (Naqvi et al., 1993). These bacteria evidently support unusual food chains that are yet to be fully explored.

2.3.5 Societal consequences

The most important consequence of deoxygenation is its adverse effect on biodiversity and living resources. Unfortunately, published information available on this important aspect from the Indian Ocean is scarce. However, several instances of fish kills (Figure 2.3.12) suspected to be caused by hypoxia often associated with algal blooms have been documented (e.g. Naqvi et al., 1998; Piontkovski et al., 2012; Ram et al., 2014). Along the west coast of India, demersal fish landings appear to be strongly linked with the intensity of seasonal anoxia, showing pronounced declines during strong anoxic events, for example in 2001 when sulphidic conditions



Figure 2.3.12 An incident of severe fish mortality observed on Caranzalem Beach (Goa, west coast of India) on 24th August, 2019. Such fish kills are commonly caused by the upwelling of low-oxygen subsurface water from offshore during late summer/early autumn. © D.M. Shenoy, National Institute of Oceanography.

prevailed on a large scale over the western Indian shelf (Naqvi et al., 2009). The recently reported dominance of dinoflagellates over diatoms in the northern Arabian Sea in the winter, attributed by Gomes et al. (2014) to expansion of hypoxia in the upper water column, may potentially affect fisheries, since diatoms have been the principal primary producers, forming the base of food chains leading to commercially important species (Figure 2.3.7). Potential socio-economic impacts of such ecosystem shifts remain to be evaluated. Another notable effect of deoxygenation is its positive feedback to climate change through enhanced production of greenhouse gases, especially N_2O . The Indian continental shelf is an especially important hotspot of N_2O production during seasonal anoxia (Figure 2.3.3; Naqvi et al., 2000) implying that an expansion of the OMZs may substantially increase oceanic N_2O emissions. On a longer timescale, enhanced loss of reactive nitrogen as N_2 from the expanded/intensified oceanic OMZs and in sediments would affect biological productivity, and therefore ocean's capacity to sequester atmospheric CO_2 , thereby affecting climate; this has been hypothesized to have happened in the geological past (Altabet et al., 2002).

2.3.6 Implications of continuing ocean deoxygenation

The Indian Ocean contains a very large volume of water that has extremely low O_2 concentrations but is still not

functionally anoxic (i.e. it does not support anaerobic processes such as denitrification). Even though rate of O_2 loss appears to be generally slower in the region than, for example, in the North Pacific, with continuing deoxygenation and expected decrease in O_2 supply from the south as well as increase in productivity, an expansion of the volume of anoxic water seems inevitable. If and when that happens, it will greatly impact biogeochemical fluxes such as a substantial increase in oceanic nitrogen loss (Bristow et al., 2017). Expansion/intensification of the existing coastal hypoxic/anoxic (dead) zones and the emergence of new ones as a consequence of enhanced nutrient loadings are, in all likelihood, also going to happen, if they are not already happening, given the large population density in countries surrounding the North Indian Ocean. South Asia is a hot spot of nutrient export to the ocean, accounting for 28% of the global total nitrogen (TN) and total phosphorus (TP) exports, the majority (>60%) of which is received by the Bay of Bengal (Figure 2.3.13) (Mayorga et al., 2010). It is estimated that the TN runoff to the Bay of Bengal alone will increase from 7.1 million tonne in 2000 to 8.6 million tonne in 2050, whereas TP export may remain unchanged at ~1.5 million tonne (Pedde et al., 2017). Coastal areas adjacent to river mouths in the north-eastern Indian Ocean (e.g. off Bangladesh and Myanmar) are particularly vulnerable to eutrophication and consequent deoxygenation resulting from riverine inputs of nutrients. Emergence of hypoxia here will have far reaching impacts on fisheries and associated livelihoods of a large number

of people. Finally, the ongoing rapid deterioration of the marine environment of the two marginal seas (Persian Gulf and Red Sea), especially through eutrophication and deoxygenation (Al-Ansari et al., 2015; Sheppard et al., 2010) and warming (Lachkar et al., 2019) will have a potentially large impact on the extent and intensity of the mid-water O₂ deficiency in the north-western Indian Ocean.

2.3.7 Conclusions / Recommendations

The information presented above does not show as consistent and as large a trend of deoxygenation in the upper water column in the Indian Ocean as in other oceanic areas, perhaps reflecting differences in ventilation of subsurface waters arising from the unusual geographical setting of the Indian Ocean. However, the geographical setting and associated unique climatic conditions in conjunction with high population density of the surrounding landmasses also make biogeochemistry and ecosystems in the region more vulnerable to human-induced deoxygenation. The unique impact of ongoing changes in the two marginal seas on the open-ocean OMZs needs to be evaluated in detail. Also, of particular interest is how conditions in the large volume of water

presently on verge of turning fully anoxic, especially in the Bay of Bengal, will evolve in future in response to changes in physics as well as nutrient loading from land.

A severe lack of information on the health of coastal waters of a majority of countries bordering the Indian Ocean, including potential hotspots off major river mouths (e.g. Indus in Pakistan, Ganges-Brahmaputra in Bangladesh and Irrawaddy in Myanmar), presently limits our ability to evaluate effects of human activities including deoxygenation. As enhanced nutrient loading will eventually lead to development/intensification/expansion of dead zones at the mouths of these rivers, and remedial measures will have to be initiated to contain this problem, capacity building in these countries for sustained observations and development of regional observational networks must be given a high priority. In addition to ocean deoxygenation, such a monitoring programme should also cover other related changes such as warming, eutrophication and acidification arising from human activities. Understanding how these multiple stressors may act in concert is necessary for predicting the impact on the marine environment and ecosystems and their socio-economic ramifications.



Figure 2.3.13 The estuary of River Hooghly, a distributary of the Ganges. The Ganges-Brahmaputra River System, along with several other rivers, brings very large quantities of fresh water and dissolved & suspended matter to the Bay of Bengal. These rivers form extensive deltas that house some of the world's largest mangrove ecosystems. Increases in organic matter and fertilizer loadings to estuarine and coastal water are expected to lead to development of hypoxic zones in coastal Bay of Bengal in the future. © Dr. Sandip Mukhopadhyay, University of Calcutta.

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2.4 Evidence for ocean deoxygenation and its patterns: Eastern Boundary Upwelling Systems

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Summary

- Eastern boundary upwelling systems (EBUS) are one of the ocean's most productive biomes, supporting one-fifth of the world's wild marine fish harvest. These ecosystems are defined by ocean currents that bring nutrient-rich but oxygen-poor water to coasts that line the eastern edges of the world's ocean basins. As naturally oxygen-poor systems, EBUS are especially vulnerable to global ocean deoxygenation.
- The dynamics of EBUS are intimately linked to global alterations in ocean chemistry and circulation from climate change. Upwelling currents connect the vast region of the subsurface open ocean that is experiencing declines in dissolved oxygen with the productive coastal waters of EBUS. The strength and location of upwelling currents depend on wind fields that are also affected by climate change. For some systems, this combination of changes will result in an intensification and expansion of coastal low oxygen zones.
- In comparison to the open ocean, long-term changes in dissolved oxygen availability in dynamic EBUS are much more challenging to resolve. Nonetheless, important trends have started to emerge. In a number of systems, dissolved oxygen (DO) has declined by approximately $10 \mu\text{mol kg}^{-1}$ per decade. This is of great concern because many EBUS locales already sit near if not pass the canonical threshold for hypoxia of $60 \mu\text{mol kg}^{-1}$. Observations of strengthening in winds that drive the upwelling delivery of low-oxygen and nutrient-rich waters in some systems portend heightened risks of ecosystem changes that outpace those expected from ocean deoxygenation alone.
- Because many EBUS are already exposed to low-oxygen conditions, the risk of crossing important biological thresholds that regulate the distribution and productivity of fishery-dependent stocks, and ecosystem functioning are heightened. Shallow water anoxia has already resulted in mass die-offs of fish and shellfish in some systems. Expansion of low oxygen zones have led to rapid, transient invasion of hypoxia-tolerant jumbo squid in others. Movement of fish away from low oxygen zones have also affected the accuracy of fishery-independent surveys even as the needs for tools for managing in the face of climate change grows.
- The intensification and expansion of low oxygen zones can have further ecosystem consequences as oxygen-dependent cycling of elements by microbes alter the supply of nutrients or in extreme cases, lead to increased production of toxic hydrogen sulphide gas (H_2S). Low oxygen EBUS are also regions of CO_2 enrichment as the loss of DO is coupled to the production of CO_2 . In combination with ocean uptake of human CO_2 emissions, CO_2 levels in some EBUS have already reached levels where the calcium carbonate shells of marine life are now being readily dissolved. Eastern boundary upwelling systems thus represent hotspots for both hypoxia and ocean acidification where development of mitigation and adaptation solutions are urgently warranted.

Ocean hypoxia effect	Potential consequences
Oxygen declines induces species range shifts, changes to vertical and across-shelf movement patterns, and losses in spawning habitats.	<ul style="list-style-type: none"> Altered ecological interaction rates among consumers and prey, and species that compete for resources. Altered ecological interactions as invasive hypoxia-tolerant species increase in abundance. Reduced fishery productivity as population replenishment declines for benthic spawning species and those that have strong habitat dependence for growth. Increased fishery conflicts as multiple targeted species are compressed into narrow oxygen refuges. Increased management uncertainty as fishery-independent surveys are compromised by reduced accessibility of fish to survey methodology.
Spatial and / or temporal expansion of areas currently affected by suboxia or anoxia as well as novel development of suboxic habitats in regions where they have previously been absent.	<ul style="list-style-type: none"> Increased loss of nitrogen nutrients as denitrification intensifies. Increased risk of water column hydrogen sulphide accumulation effects as sulphate reduction intensifies. Altered ratios of nutrient availability as the flux of iron and phosphorus from sediment increases.
Intensification of ocean acidification in conjunction with coastal hypoxia.	<ul style="list-style-type: none"> A wider array of taxa is affected and/or the effects of hypoxia are amplified if hypoxia and ocean acidification act as compounding or interactive stressors on organisms. More rapid shift to no-analogue state where multiple aspects of coastal ocean environment move away from natural ranges in exposure.

2.4.1 Introduction

Eastern boundary upwelling systems (EBUS) represent one of the ocean's most productive biomes. Even though EBUS comprise some 1% of the area of the ocean, the productivity of these coastal ecosystems supports one-fifth of the world's ocean wild fish harvests (Pauly & Christensen, 1995) and gives rise to important habitats for highly migratory seabirds, marine mammals and pelagic fishes (Block et al., 2011). Eastern boundary current upwelling systems can be readily identified from satellite maps of sea surface temperature (Figure 2.4.1A) as coastal regions that are colder than expected for their latitude. Ocean water gets colder with depth. The presence of cold water signals wind-driven ocean currents that transport or upwell cold, nutrient-rich waters from deeper layers of the ocean. Once upwelled nutrients reach the sunlight surface, they fuel dense blooms of phytoplankton (Figure 2.4.1B) that serve as the base of ocean food webs.

The dissolved oxygen (DO) content of ocean water also declines with depth. This reflects the loss of DO from

the respiration of microbes and other marine life as they consume the rain of organic matter that sinks down from the productive ocean surface. In fact, the high level of nutrients found in upwelled waters is a direct product of this process of organic matter remineralization. The surface ocean also acts as an insulating layer that keeps the waters below from replenishing lost DO with oxygen from the atmosphere (Figure 2.4.2). The atmosphere does have a central role to play, however, in structuring EBUS through the actions of coastal winds. Equatorward winds are common to coastlines that lie on the eastern edge of ocean basins. These winds serve as engines that move the surface ocean. These surface currents do not simply flow in the same direction as the equatorward winds, however. Known as the Coriolis effect, currents in motion on a rotating planet are deflected to the right in the Northern Hemisphere and to the left in the Southern Hemisphere. The movement of surface waters away from the coastline lies at the heart of upwelling as seaward surface flows (known as the Ekman layer) must be counterbalanced by deep waters that rise and move toward the coast. As a consequence of coastal winds, eastern boundary current upwelling systems are one

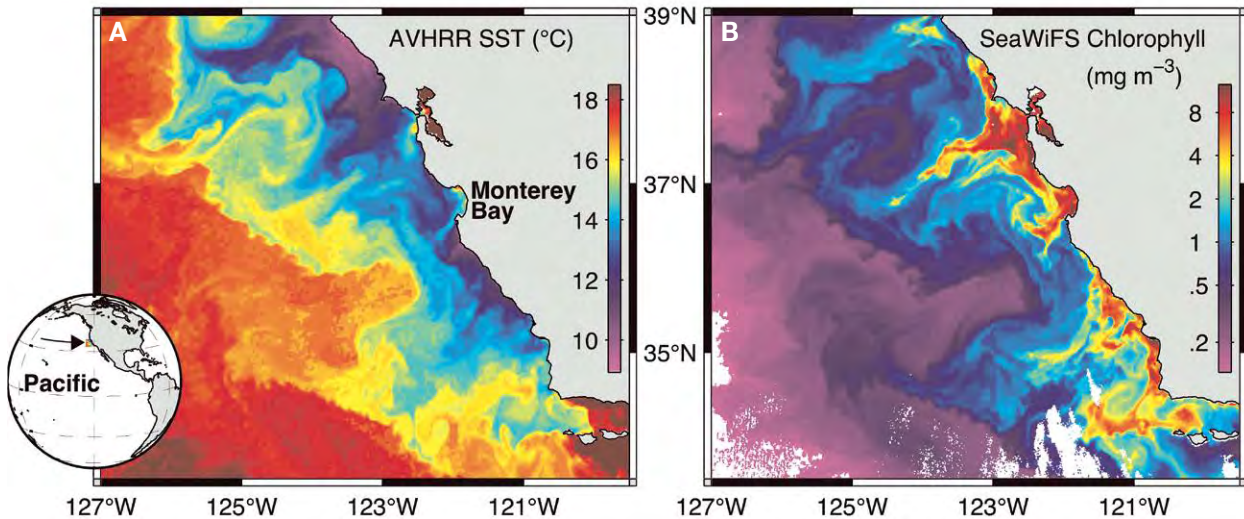


Figure 2.4.1 Satellite remote sensing imagery of Central California Current upwelling: A) Sea surface temperature (AVHRR), B) Surface chlorophyll (SeaWiFS) August 2000. © John P Ryan Monterey Bay Aquarium Research Institute.

of the few places in the ocean where nutrient-rich but oxygen-poor deep waters are transported to relatively shallow depths. Once upwelled, oxygen-poor waters can be further robbed of oxygen as the exceptional productivity of EBUS accelerates the rain of organic matter that fuels oxygen consumption above and in the sea floor (Adams et al., 2013).

As inherently oxygen-poor and in many instances, oxygen-deficient systems, it is not surprising that EBUS represent hot spots for ocean deoxygenation concern, particularly as relatively small DO declines can push systems past thresholds for hypoxia ($DO \leq 60 \mu\text{mol kg}^{-1}$) or suboxia ($DO \leq 5 \mu\text{mol kg}^{-1}$) (Deutsch et al., 2011). However, the sensitivity of EBUS to ocean deoxygenation is further compounded by strong climate-dependence in the very factors that give rise to low oxygen baseline conditions in EBUS. As systems that receive oxygen-poor oceanic waters, the global reductions in oxygen solubility from a warming ocean and slowing exchange of oxygen between the atmosphere and the deep ocean from a more strongly stratified sea can directly impact EBUS (Breitburg et al., 2018). In particular, because oceanic DO declines are not distributed evenly but can be most strongly focused at depth layers where upwelling currents are often drawn from (Ito et al., 2017), EBUS face disproportionate impacts from oceanic deoxygenation. The sensitivity of EBUS is also structured by the effects of climate change on coastal upwelling (Bakun et al., 2010). Winds are generated by spatial differences in atmospheric pressure, and coastal upwelling winds arise from pressure differences between a cool ocean and a warm continental land mass. As

land masses are projected to warm more quickly than the ocean, a long-standing hypothesis posits that atmospheric pressure differences are expected to intensify and/or shift spatially to alter upwelling winds (Bakun, 1990). For systems where upwelling winds intensify or lengthen seasonally, increased flux of low DO, high nutrient waters can directly and indirectly strengthen local deoxygenation (Bakun, 2017).

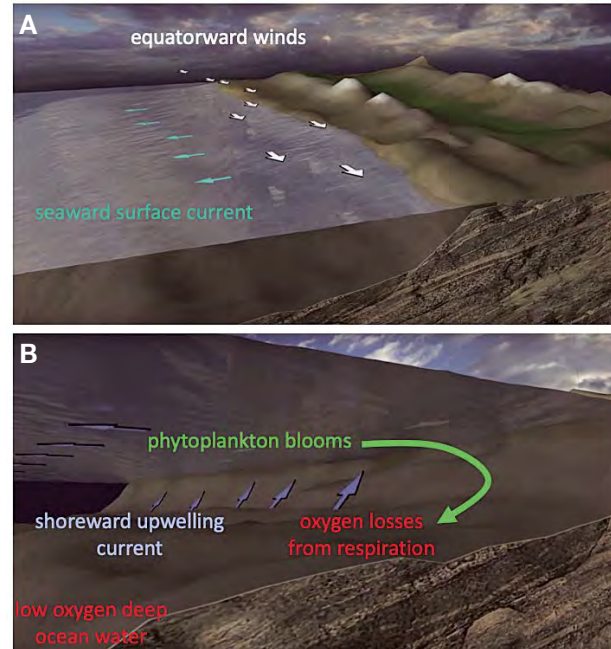


Figure 2.4.2 A) Equatorward coastal winds drives the flow of surface water away from the coast. B) Seaward surface flows are compensated by the upwelling of deep ocean water across the continental shelf. This deep water is deficient in dissolved oxygen and enriched in nutrients that promotes phytoplankton blooms. Low DO ocean water can experience further losses of DO as sinking phytoplankton cells are respired by microbes. © College of Earth, Ocean and Atmospheric Sciences - Oregon State University.

2.4.2 Geographic definition

As their name indicates, EBUS are located at the eastern margins of ocean basins where equatorward winds give rise to coastal upwelling currents (Figure 2.4.3). There are four major EBUS. In the Eastern Pacific Basin, the Humboldt or Peru-Chile Current System (HCS) lies off the coasts of Peru and Chile, while the California Current System (CCS) stretches from British Columbia, Canada to Baja, Mexico. In the Eastern Atlantic, the Benguela Current System (BCS) is situated along the coasts of Angola, Namibia and South Africa while the Canary Current System (CaCS) extends along the coasts of the Iberian Peninsula into North-west Africa.

Although the four major EBUS share broad commonalities in physical and ecological structures their locations give rise to notable differences in their present, as well as future, exposure to low-oxygen conditions (Chavez & Messie, 2009). One important factor is the location of EBUS relative to oceanic oxygen minimum zones (OMZ) (Figure 4.2.3) (Monteiro et al., 2011). In the eastern Pacific Ocean, broad expanses of the ocean interior are marked by vertical profiles where the DO-rich surface waters give way to a DO minimum layer that can reach anoxia ($\text{DO} = 0 \mu\text{mol kg}^{-1}$) (Thamdrup et al., 2012). Where the OMZ is particularly shallow such as along reaches of the HCS, coastward upwelling flows can directly draw suboxic

or even anoxic water to compensate for the seaward movement of the surface Ekman layer. In the Northern Pacific, OMZ is typically found too deep to serve as the source water for upwelled water (Connolly et al., 2010). Instead, upwelled water is drawn from the top of the OMZ where DO concentrations often range near hypoxic levels (Adams et al., 2013). In contrast, DO levels in the OMZ of the Atlantic Ocean do not reach the extremely low values found in Pacific Ocean OMZ. This does not mean that low DO and deoxygenation are less of a concern in the Atlantic systems. The development of anoxia in portions of the Benguela Current System highlight the importance of coastal biogeochemical processes in driving DO loss (Pitcher et al., 2014).

2.4.3 Trends and impacts

Future changes in oxygen dynamics in EBUS can be thought of as the product of global-scale decline in oceanic oxygen content, and system-scale alterations in upwelling-favourable winds that affect the delivery of oxygen-poor water to the coast and the supply of nutrients that fuel further local drawdown of DO. To understand the likely scope for future changes, we can consider the observed changes in oceanic and atmospheric forcings. The ability to resolve trends in DO is strongly dependent on the background variability of a given system (Long et al., 2016). Thus, it is not surprising that considerable attention has been paid

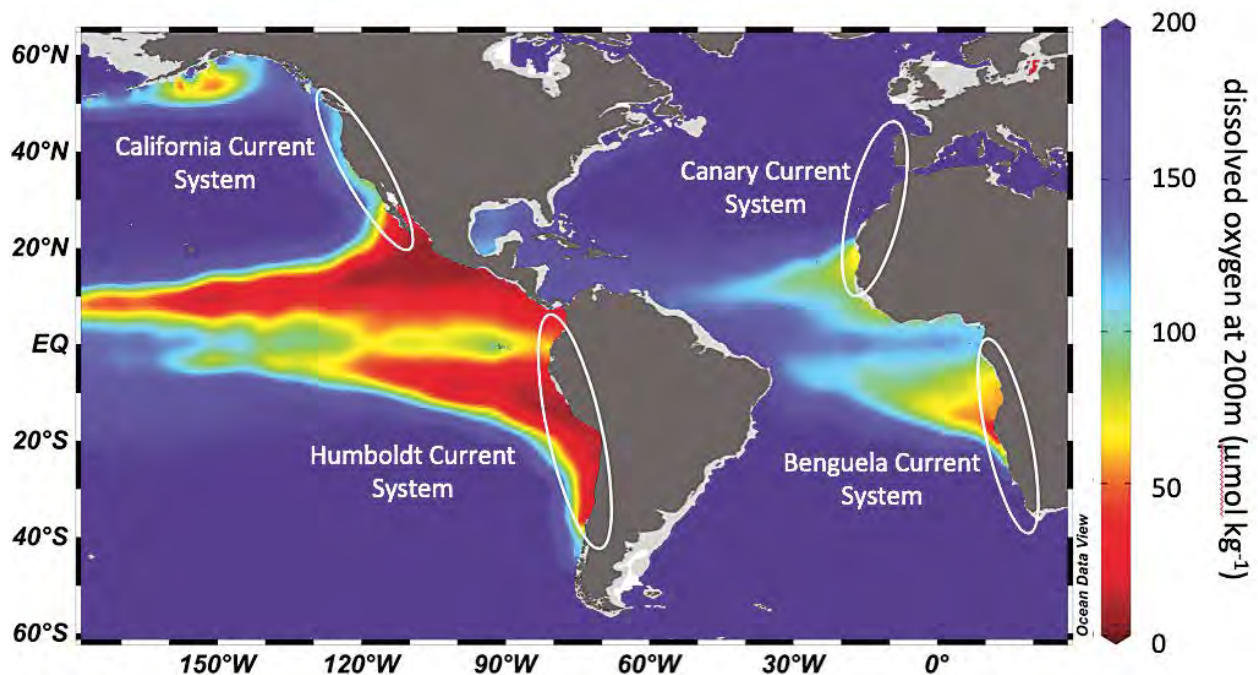


Figure 2.4.3 Location of the four major eastern boundary upwelling systems and dissolved oxygen values at 200m depth illustrating the location of each system relative to oceanic oxygen minimum zones. Data from World Ocean Atlas 2013.

to time trends of DO change in the global open ocean (Stramma et al., 2008). Analyses of the past five decades of available data point to a globally averaged DO loss rate of 0.4% per decade (Schmidtko et al., 2017). At first glance, this appears to be a minor rate of loss but because DO declines are not distributed evenly across the ocean, certain regions experience rates of loss that are considerably higher. In particular, areas near OMZ exhibit DO loss rates in excess of 4% per decade (Schmidtko et al., 2017). The volume of suboxic waters in OMZ increases non-linearly with DO decline, doubling in size with a 1% drop in mean DO (Ito & Deutsch, 2013). This expansion of oceanic suboxia has immediate consequences for the Humboldt Current System as it draws upwelled water directly from the Eastern Tropical Pacific OMZ. In absolute terms, DO losses in the upper 300m of the ocean (the range of depth from where upwelling water is typically drawn from) range upwards of $5 \mu\text{mol kg}^{-1}$ per decade (Stramma et al., 2012). This is notable as oceanic source waters that arrive in the CCS may hold only $90 \mu\text{mol kg}^{-1}$ of DO, already close to the canonical hypoxia threshold of $60 \mu\text{mol kg}^{-1}$ (Adams et al., 2013).

Model simulations of the impacts of climate change on ocean oxygen inventory point to the need for long, five decades plus records for deoxygenation trends to emerge from background natural variability (Long et al., 2016). This imposes important constraints on our ability to resolve deoxygenation trends in temporally-dynamic coastal EBUS where requirements for time series lengths can be even greater. Nevertheless, for the CCS, where long-term observations have been the most extensive, multi-decadal declines in DO (Pierce et al., 2012) and shoaling of hypoxia horizons (Bograd et al., 2008) have been reported. Declines in DO in recent decades (past 20-30 years) have been the strongest on record, with rates in the order of $10 \mu\text{mol kg}^{-1}$ per decade (Crawford & Pena, 2013). It is noteworthy that long-term measurements from multiple independent programmes have reported rates of DO decline that have been quite uniform across the CCS. Oxygen loss trends from Vancouver Island to Southern California range narrowly between 8 to $13 \mu\text{mol kg}^{-1}$ per decade (Crawford & Pena, 2013). We have fewer long-term records of DO from other EBUS. In the Benguela Current System, Moloney et al. (2013) report a decline of $9 \mu\text{mol kg}^{-1}$ per decade between 1957 and 2007 for St. Helena Bay, - a large productive bay that has been subject to episodic anoxia events (Pitcher & Probyn, 2017). For EBUS, changes can also manifest as increases in the

frequency or severity of oxygen-deficiency events. In the CCS, nearshore suboxia and anoxia events have occurred in the past decade that have no precedence in the observational record that extends back to the 1960s (Chan et al., 2008).

Insights from time-series analyses also highlight the climate sensitivity of oxygen dynamics in EBUS across inter-annual to inter-decadal time scales (Buil & Di Lorenzo, 2017). The impacts of ENSO variability on ecosystem dynamics in the HCS has been particularly well characterized where strong El Niño events results in a marked rise in oxygen levels that reorganizes the structures of benthic and pelagic communities (Bertrand et al., 2011; Escribano et al., 2004; Gutiérrez et al., 2008). In the southern CCS, decrease and subsequent increase in the volume of suboxic water between 1960 and 2005 were found to be well correlated with shifts in the phases of the Pacific Decadal Oscillation (PDO) index (Deutsch et al., 2011). During cool PDO periods, the thermocline and OMZ shoals increasing the supply of nutrients and resultant rain of organic materials that drive respiratory losses of DO. A larger fraction of this respiration also takes place within shallower OMZ reinforcing the tendency toward suboxia expansion. In the North Atlantic, declines in DO have been linked to weakening of trade winds associated shifts in the Atlantic Multidecadal Oscillation index (AMO) that are important to the ventilation of subsurface water masses (Montes et al., 2016). Anomalous events detected from long-term time series have also provided insights into the linkages between basin-scale changes in ocean conditions. In 2002, increased supply of nutrients from the Gulf of Alaska heightened coastal productivity, oxygen demand and the eventual emergence of nearshore hypoxia in the northern CCS (Grantham et al., 2004). These observations highlight the sensitivity of EBUS oxygen to climate through changes in winds, stratification and circulation that takes place over local to basin scales.

Because oxygen dynamics in EBUS are the product of complex interplay of physical and biogeochemical factors, future changes are unlikely to simply follow mean ocean trends in deoxygenation. Indeed, model projections suggest that DO in the tropical ocean may rise in the future if warming slackens trade winds that drive equatorial upwelling (Bianchi et al., 2018). In contrast, coastal upwelling as first proposed by Bakun (1990) is projected to increase as enhanced continental warming strengthens low-pressure systems on land

relative to high-pressure systems in the sea. The growth of modelling and observational studies stimulated by Bakun (1990) has provided general support for increased upwelling in recent decades (Sydeman et al., 2014; Varela et al., 2015; Wang et al., 2015). The deepening of this literature has also revealed important differences in how different EBUS and regions within EBUS are changing (Aravena et al., 2014). Support for upwelling increases are strongest for the HCS, CCS, and BCS (Sydeman et al., 2014). Within systems, evidence of upwelling increases is strongest for poleward regions of individual EBUS (Garcia-Reyes et al., 2015). Our understanding of the potential mechanisms behind upwelling intensification has similarly diversified. Recent work has emphasized the importance of poleward movement and expansion of oceanic high-pressure systems from climate change in structuring upwelling winds (Garcia-Reyes et al., 2015; Rykaczewski et al., 2015).

Eastern boundary upwelling systems are oceanic in their nature and discussions of future trends have most often focused on offshore and wind-forced changes. However, studies illustrating the effects of terrestrial nitrogen inputs on the nitrogen budget (Howard et al., 2014) and phytoplankton bloom formation (Beman et al., 2005) in coastal upwelling systems, as well as the effects of atmospheric iron deposition in enhancing primary production that contribute to DO losses in OMZ (Ito et al., 2016) suggests that projections of future oxygen trends in EBUS will need to consider the role of pollution from human activities across a variety of scales. As the ocean warms, increasing stratification will inhibit the resupply of oxygen into the ocean but this change can also reduce primary production that fuels oxygen loss, and suppress the upwelling of oxygen-poor waters to the coast. In addition, increased upwelling may lead to greater flushing of nearshore waters so that local development of hypoxia may be moderated in intensity and/or location. These are important factors that can serve to offset deoxygenation trends faced by EBUS. At the moment, their influence is poorly resolved and contributes to real uncertainties in the projections of future conditions in EBUS.

2.4.4 Ecosystem consequences

Oxygen availability is a major environmental gradient that organizes the structure and functioning of marine ecosystems. The effects of oxygen change also tends to be highly non-linear with declines when DO is

already low, soliciting disproportionately large biological responses (Pörtner, 2010). As a result, the expression of ocean deoxygenation in EBUS is expected to bring about important changes in ecosystem dynamics. The potential ecosystem consequences of future ocean deoxygenation can be illustrated by how marine ecological communities and biogeochemical cycles shift in response to currently observed gradients in DO.

Oceanic microbes play a dominant role in elemental cycles that govern the supply of nutrients, availability of trace elements, DO levels, and seawater pH. The metabolic processes of microbes can exhibit sharp thresholds in activity as DO declines from hypoxic to suboxic and anoxic conditions (Ulloa et al., 2012). One particularly important suite of processes is the cycling of nitrogen – a fundamental nutrient that limits ocean productivity. The natural decay of organic matter releases nitrogen compounds that are readily used by phytoplankton to fuel their growth. In DO-deficient waters, however, microbes that transform biologically-available nitrogen compounds into inert N_2 gas become active (Wright et al., 2012). This important loss of nutrients only occurs when DO drops below $5 \mu\text{mol kg}^{-1}$ (Babbin et al., 2014) or less (Bristow et al., 2017) and the expansion of anoxic water in the eastern tropical North Pacific OMZ has been linked to increasing loss of nitrogen between 1972 and 2012 (Horak et al., 2016). The onset of suboxia can also have global consequences for the climate system. Nitrous oxide (N_2O) is an important greenhouse gas with 298 times the heat trapping capacity of CO_2 and oxygen-deficient waters are a major oceanic source of N_2O to the atmosphere. This greenhouse gas is produced by microbes as a byproduct of nitrogen metabolism and its production is accentuated as DO levels decline. Because low DO and active nitrogen cycling converge in productive EBUS, resulting in exceptional hotspots for N_2O emissions (Arevalo-Martínez et al., 2015), it has been postulated that the ocean deoxygenation and upwelling intensification will strengthen this positive feedback in the climate system (Codispoti, 2010). For EBUS, local feedbacks will also be important to consider. The production of hydrogen sulphide by microbes is an active process in oxygen-poor environments particularly in sediments. In the HCS and the BCS, transient water column accumulation of hydrogen sulphide, a compound toxic to wide suites of marine fish and invertebrates, have been observed (Schunck et al., 2013) and enhancement of coastal upwelling by climate change has been postulated to increase

the likelihood of such events (Bakun, 2017). Concerns for potential cascading ecosystem consequences of expanding hypoxia also arise from the supply of iron and phosphorus from sediments (Capone & Hutchins, 2013). The fluxes of these elements are tightly linked to oxygen concentration and can be instrumental in regulating productivity directly or indirectly through controls on nitrogen fixation (Moore et al., 2013).

The sensitivity of microbial communities to DO declines is mirrored by the sensitivities exhibited by the broader suite of marine animals that also make up the water column and seafloor ecological communities of EBUS. Compilations of laboratory studies on marine life from around the world highlight the potential for lethal and sub-lethal effects of low DO to occur well above the canonical threshold of $60 \mu\text{mol kg}^{-1}$ (Vaquer-Sunyer & Duarte, 2008). This holds particular concerns for EBUS as DO levels readily range below $60 \mu\text{mol kg}^{-1}$ in the HCS, CCS, BCS (Helly & Levin, 2004). Considerable details are lost of course when the DO sensitivities of many species are aggregated into global mean values, and myriad of life history adaptations that are known from inhabitants of OMZ (Gibson & Atkinson, 2003) might suggest the potential for reduced biological vulnerability to future oxygen declines in systems where exposure to low oxygen conditions is already common. While some taxa that inhabit such systems can exhibit dampened sensitivity to oxygen declines, this sensitivity is by no means universal (Chu & Gale, 2017; Seibel et al., 2016). Across oxygen-deficient water column and seafloor habitats in EBUS, episodes of DO decline are often accompanied by community changes. For example, seasonal formation of hypoxia in Saanich Inlet in British Columbia results in rapid reorganization of fish and crustacean communities as more oxygen sensitive species are displaced from zones of hypoxia (Chu & Tunnicliffe, 2017). In the central CCS, ENSO-driven changes in DO are propagated into estuaries and can drive population level changes in fishes that rely on estuarine nursery habitats (Hughes et al., 2015). To the south, long-term observations that began in 1951 have revealed that abundance of deep-water fishes is reduced by 63% as the system transitions into periods of relatively low DO levels (Koslow et al., 2011). The authors speculated that the decline reflects the loss of refuge from visual predators as oxygen-loss makes deeper habitats become in accessible to prey fishes. This habitat compression effect has also been proposed as a contributor to the opposing fluctuations in the abundance of sardines and anchovies in the HCS

where the avoidance of oxygen-poor waters by sardines represent a loss of foraging habitat that can be utilized by more hypoxia-tolerant anchovies (Bertrand et al., 2011).

2.4.5 Societal consequences and implications of continuing ocean deoxygenation

Eastern Boundary Upwelling Systems link oxygen changes that are taking place in the global ocean with impacts to some of the world's most productive coastal ecosystems. While this represents one of the most direct connections between ocean deoxygenation and society, considerable uncertainties remain. In fact, one immediate societal consequence of ocean deoxygenation may be increasing uncertainty in our ability to rely on the productivity of coastal ecosystems or in the efficacy of management approaches that have been employed to date.

In the CCS, coast-wide fishery-independent surveys of groundfish stocks used to inform stock assessments have revealed a strong influence of DO on where fish are distributed, their condition and catch per unit effort—a key metric used to estimate abundance (Keller et al., 2010, 2015). Expansion and intensification of low oxygen zones can thus not only influence where fish will be caught but also how managers estimate population size and management targets. In the BCS, episodic hypoxia events that drive mass strandings of the rock lobsters (*Jasus lalandii*) results in destabilization of catch and mortality rates that challenges the management of a commercially important fishery that is already under pressure from over-exploitation (Branch & Clark, 2006; Cockcroft, 2001). Continuing ocean deoxygenation can also bring ecological surprises, whose occurrence and consequence may be difficult to forecast. Recent rapid poleward range expansion by the hypoxia-tolerant jumbo (Humboldt) squid (*Dosidicus gigas*) (Figure 2.4.4) in the California and Humboldt Current Systems have been putatively linked to expansion of low oxygen zones (Gilly et al., 2013; Stewart et al., 2014). While the expansion appears to be have abated at the moment, the sudden introduction of a large, highly active predator presented considerable challenges to projections of ecosystem changes in EBUS.

The uncertainty imposed by continued ocean deoxygenation will amplify and be amplified by challenges from future ocean warming and the progression of ocean acidification (Breitbart et al., 2015). The former

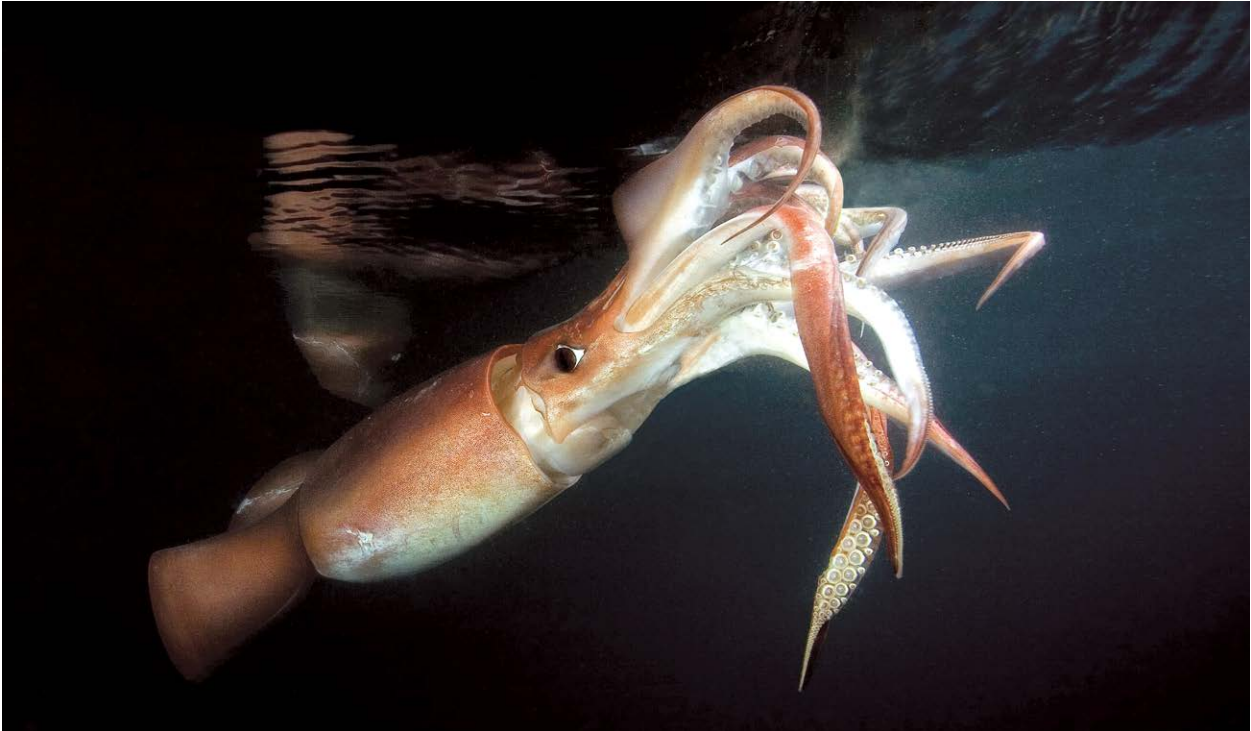


Figure 2.4.4 Jumbo (Humboldt) squid *Dosidicus gigas* in Sea of Cortez, Baja, California © Waterframe / Alamy stock photo.

reflects the effects of greenhouse gases on the earth's heat balance and the latter reflects the impacts of CO₂ emissions and its storage in the ocean on seawater pH and associated chemistry. Termed “hot, breathless, and sour,” these multiple stressors can act synergistically to impact marine life (Gruber, 2011). For example, ocean warming accentuates the impacts of hypoxia in part by increasing organismal demand for oxygen (Pörtner & Knust, 2007; Vaquer-Sunyer & Duarte, 2011). The effects of ocean acidification are similarly magnified when organisms are also challenged by the stress of hypoxia (Gobler & Baumann, 2016; Miller et al., 2016).

Although ocean acidification is a globally pervasive problem, the interaction between ocean acidification and ocean deoxygenation represent particularly acute coupled stressors for EBUS. Low DO levels common to EBUS ultimately reflect the cumulative breakdown of organic matter which consumes oxygen and releases CO₂. As a result, some of the highest levels of pCO₂ measured in surface ocean waters can be found in EBUS (Emeis et al., 2017; Feely et al., 2016; González-Dávila et al., 2017; Shen et al., 2017), reaching levels not expected for the mean global ocean until the middle of the 21st century. As a result, EBUS represent hotspots for both ocean deoxygenation and ocean acidification (Chan et al., 2017; Reum et al., 2015), where the addition of CO₂ from society's emissions to an already

elevated background level of CO₂ puts systems close to, and in many instances past, thresholds for biological impacts (Bednaršek et al., 2017).

2.4.6 Conclusions / Recommendations

The impacts of ocean deoxygenation will not be evenly felt across ecosystems. For EBUS where DO values already centre near thresholds for biological impacts, the confluence of future OMZ expansion and climate modulation of coastal upwelling and local productivity point to their risk as early impact systems to global deoxygenation. The true scope of ocean deoxygenation's impacts, however, will be dependent on the realized rate and scale of oxygen changes, and the capacity of natural and human systems to mitigate and adapt to a more hypoxia- or anoxia-prone ocean. Thus, even as global greenhouse gas emissions lie at the heart of ocean deoxygenation, recent assessments have highlighted the importance of local to regional-scale actions in fostering global-change readiness in EBUS (Chavez et al., 2017). Actions include sustaining and growing integrated ocean observing capacity to detect and track the progression of hypoxia and covarying ocean acidification and warming stressors. Integration in observing reflects the need for not only physical and biogeochemical measurements but also those for physiological, population, and ecological metrics. In turn,

the ability to identify and provide early warning of which species or parts of the system are most vulnerable can guide priorities in protection. There is also a premium need for research and partnerships that will grow new local mitigation and adaptation solutions that decision-makers can draw on to ostensibly buy time until the root causes of ocean deoxygenation are addressed (Klinger et al., 2017).

While the challenges are great, efforts are underway to enhance monitoring and research to support ocean deoxygenation actions. For example, because of the strong covariation between carbonate and oxygen chemistry and the utility of combined measurements in assessing data accuracy, the growth of ocean acidification observing networks regionally (e.g. OA-Africa, California Current Acidification Network, etc.) and globally (i.e. Global Ocean Acidification Observing Network) is also leading to enhanced observing capacity, intellectual exchanges and partnerships for ocean oxygen monitoring. Recognition of coastal vulnerability to ocean acidification and oxygen deoxygenation has also stimulated new research into the use of green infrastructure in the form of seagrass and kelp beds to locally mitigate oxygen and pH declines (Duarte et al., 2017). Equally important are efforts to identify and promote sources of biological and ecological resilience to ocean chemistry changes. Examples of local adaptation to ocean acidification highlight the potential for evolutionary rescue (Munday et al., 2013) in conferring some level of resilience to ocean deoxygenation. The use of available management tools such as marine protected areas to support climate change adaptation is another arena of active research (Roberts et al., 2017). In Baja California, marine reserves supported larger and more demographically-diverse populations of pink abalone (*Haliotis corrugate*) that were better able to withstand and recover from hypoxia events relative to unprotected areas (Micheli et al., 2012). Ocean deoxygenation has quickly emerged as a leading pathway for climate change impacts. Monitoring and research efforts that identify what's most at risk and grows our portfolio of mitigation and adaptation solutions will play a disproportionate role in preparing coastal EBUS communities and nations for the changes ahead.

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2.5 Hypoxia in estuaries and semi-enclosed seas

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Summary

- In the last 65 years, over-enrichment of waters with nutrients or organic matter (eutrophication), has emerged as a problem that threatens and degrades coastal ecosystems, alters fisheries, and impacts human health in many areas around the world. Hypoxia is one of the most acute symptoms of this eutrophication and harmful algal blooms another.
- The global extent of eutrophication-driven hypoxia and its threats to ecosystem services are well documented, but much remains unknown relative to human health, social, and economic consequences.
- The importance of maintaining adequate levels of oxygen in coastal systems is best summarized by the motto of the American Lung Association: “if you can’t breathe nothing else matters”.
- Over 900 areas around the world have been identified as experiencing the effects of eutrophication. Of these, over 700 have problems with hypoxia, but through nutrient and organic loading management about 70 (10%) of them can now be classified as recovering.
- There is no other environmental variable of such ecological importance to coastal ecosystems that has changed so drastically in such a short period of time as a result of human activities as dissolved oxygen.

Coastal hypoxia effect	Potential consequences
Loss of biomass.	<ul style="list-style-type: none"> • Direct mortality of fisheries species. • Direct mortality of prey species. • Reduced growth and production. • Reduced recruitment.
Loss of biodiversity.	<ul style="list-style-type: none"> • Elimination of sensitive species. • Reduced diversity. • Increased susceptibility to disease and other stressors. • Lower food web complexity.
Loss of habitat.	<ul style="list-style-type: none"> • Crowding of organisms into suboptimal habitats. • Increased predation risks from both natural and fishing pressure. • Forced departure from preferred habitat. • Altered or blocked migration routes.
Altered energy and biogeochemical cycling.	<ul style="list-style-type: none"> • Increased energy flow through microbes. • Production of toxic hydrogen sulphide. • Release of phosphorus and other nutrients from sediments that fuels algal blooms. • Loss of denitrification.

2.5.1 Introduction

The human population is rapidly expanding, recently passing 7 billion and will likely exceed 10 to 12 billion by the year 2100 (Gerland et al., 2014). This expansion has led to extensive modification of landscapes at the expense of ecosystem function and services, including pervasive effects on coastal primary production from excess nutrients to overfishing (Ripple et al., 2017). Long-term records of nutrient discharges provide compelling evidence of a rapid increase in the fertility of many coastal ecosystems starting in the 1960s. On a global basis, by 2050, coastal marine systems are expected to experience at least a doubling in both nitrogen and phosphorus loading compared to current levels, with serious consequences to ecosystem structure and function (Foley, 2017; Foley et al., 2005).

The question asked by Foley et al. (2005) is: 'Are land use activities degrading the global environment in ways that undermine ecosystem services, which in turn undermine human welfare?' When it comes to dissolved oxygen the answer is yes. In marine ecosystems, oxygen depletion has become a major structuring force for communities and energy flows at global scales.

Eutrophication can be defined as an increasing rate of primary production and organic carbon accumulation in

excess of what an ecosystem is normally adapted to processing (Nixon, 1995). It is one part of a complex of stressors that interact to shape and direct ecosystem processes. The most obvious ecosystem response to eutrophication is the excessive greening of the water column and overgrowth of algae and vegetation in coastal areas, a direct response to nutrient enrichment. The unseen response to eutrophication is the decrease in dissolved oxygen in bottom waters created by decomposition of the excess organic matter delivered to the sea bed, which can lead to hypoxia or dead zones (i.e. areas where dissolved oxygen levels drop to 2.8 mg O₂ L⁻¹ or lower). In the past this eutrophication-induced low oxygen or hypoxia was mostly associated with rivers, estuaries, and bays. But dead zones now develop in continental seas, such as the Baltic Sea, Kattegat, Black Sea, Gulf of Mexico, and East China Sea.

Much of the sensitivity of organisms to low oxygen is related to the fact that oxygen is not very soluble in water and that small changes in oxygen concentration lead to large percentage differences. For fresh water at 20 °C, 9.1 mg of oxygen (O₂) will dissolve in a litre of water. This would be 100% saturation. A 1 mg O₂ L⁻¹ drop is about a 11% decline in saturation. In addition, oxygen solubility is strongly dependent on temperature and the amount of salt dissolved in the water. Saturation declines about

1 mg O₂ L⁻¹ from 20 to 26 °C and about 2 mg O₂ L⁻¹ from fresh water to sea water at similar temperatures (Benson & Krausse, 1984). So, depending on temperature and salinity, water contains 20-40 times less oxygen by volume and diffuses about ten thousand times more slowly through water than air (Graham, 1990).

Thus, what appear to be small changes in oxygen can have major consequences for animals living

in an oxygen-limited milieu. Physiologically, higher temperatures also increase metabolic requirements for oxygen and increase rates of microbial respiration and, therefore, oxygen consumption. For salmonid fishes, oxygen can become limiting at higher temperatures when oxygen solubility declines (Fry, 1971). Concentrations of dissolved oxygen below 2 to 3 mg O₂ L⁻¹ are a general threshold value for hypoxia for marine and estuarine organisms, and 5 to 6 mg O₂ L⁻¹ in fresh water. However,

Table 2.5.1 Planetary boundary processes (Rockström et al., 2009) and how exceeding them will affect dissolved oxygen.

Earth-System Process	Parameters (units)	Proposed Boundary	Current Status	Pre-Industrial Value	Consequences for oxygen
Climate change	(i) Atmospheric carbon dioxide concentration (parts per million by volume)	350	387	280	More carbon dioxide in water reduces oxygen concentration
	(ii) Change in radiative forcing (watts per metre squared)	1	1.5	0	Warmer water holds less oxygen
Rate of biodiversity loss	Extinction rate (number of species per million species per year)	10	>100	0.1-1	Lower oxygen will stress more species
Nitrogen and Phosphorus Cycles	(i) Amount of N ₂ removed from the atmosphere for human use (millions of tonnes per year)	35	121	0	More N and P entering coastal systems will increase primary production, which will in turn decompose and lower oxygen increasing hypoxia
	(ii) Quantity of P flowing into the ocean (millions of tonnes per year)	11	8.5-9.5	~1	
Stratospheric ozone depletion	Concentration of ozone (Dobson unit)	276	283	290	Unknown
Ocean acidification	Global mean saturation state of aragonite in surface sea water (Ω)	2.75	2.9	3.44	More acidic waters contain less oxygen
Global freshwater use	Consumption of freshwater by humans (km ³ per year)	4,000	2,600	415	Reduced river flow would improve low oxygen conditions
Change in land use	Percentage of global land cover converted to cropland (%)	15	11.7	Low	More cropland leads to more nutrient runoff, see Nitrogen and Phosphorus Cycles
Atmospheric aerosol loading	Overall particulate concentration in the atmosphere on a regional basis		To be determined		Unknown
Chemical pollution	Amount emitted or concentration of persistent organic pollutants, plastics, endocrine disrupters, heavy metals and nuclear waste in the global environment, or the effects on ecosystem and functioning of Earth systems		To be determined		Unknown

species and life stages differ greatly in their basic oxygen requirements and tolerances (Vaquer-Sonyer & Duarte, 2008).

The relatively low solubility of oxygen in water combined with two principal factors lead to the development of hypoxia and at times anoxia. These factors are water column stratification that isolates the bottom water from exchange with oxygen rich surface water and decomposition of organic matter in the isolated bottom water that reduces oxygen levels. Both factors must be at work for hypoxia to develop and persist in bottom waters.

2.5.2 Geographic definition

Hypoxia caused by human activities occurs on every continent, including Antarctica (Conlan et al., 2004). Over the last 60 to 70 years alarming global trends of declining oxygen concentrations have emerged both in coastal areas and in the open oceans (Gilbert et al., 2009; Ito et al., 2017; Schmidtko et al., 2017). Similar trends have been documented for lakes, starting over 100 years ago, some 70 years prior to the spread of hypoxia in coastal regions (Jenny et al., 2016). Many of these declining oxygen trends have been linked to human activities directly or indirectly. Rockström et al. (2009) proposed that there are boundaries which if exceeded will negatively impact global ecosystems including humanity. While oxygen was not one of the nine boundaries discussed, it is influenced by many of the processes discussed (Table 2.5.1). The expanding size of the human population has led to three of the boundaries being crossed, which are climate change, rate of biodiversity loss, and the nitrogen cycle. Of these, alterations to the nitrogen cycle have the most direct consequences for dissolved oxygen, followed by climate change. The more nutrients added to the sea the more organic matter will be produced, which will create a greater oxygen demand when it is decomposed, potentially leading to more hypoxia.

Since the 1960s, the global number of hypoxic systems has about doubled every ten years up to 2000 (Figure 2.5.1). Prior to 1960, there were about 45 systems with reports of eutrophication-related hypoxia. During the 1960s, another 60 systems were added. The 1970s saw estuarine and coastal ecosystems around the world becoming over-enriched with organic matter from expanding eutrophication and the number of oxygen-depleted ecosystems jumped from about 100 to 180. In

the 1980s many more systems reported hypoxia for the first time bringing the total to about 330. More hypoxic areas were reported in the 1990s than any other decade and the total rose to about 500 systems. By the end of the 20th century the total was about 500 and hypoxia had become a major, worldwide environmental problem. About 15% of these hypoxic systems (70) are now showing signs of improvement (Conley et al., 2011; Diaz et al., 2010). At the end of the first decade of the 21st century another 140 sites reported hypoxia, bringing the total to about 640. This total of 640 does not include about 65 sites that Conley et al. (2011) identified from the Baltic region. When these are added the total number of dead zones jumps to about 700. An additional 230 coastal sites were identified as areas of concern that currently exhibit signs of eutrophication and are at risk of developing hypoxia (Diaz et al., 2010).

2.5.3 Trends and impacts

The past 65 years have witnessed a ten-fold increase in the number of eutrophication-driven hypoxic areas. There are signs of a slowing in the growth of the number of hypoxic systems, mostly because North America and Europe are well studied and almost completely reported. Altieri et al. (2017) examined latitudinal trends in the number of known dead zones and research effort and concluded that there are hundreds of tropical dead zones yet to be identified, particularly in Asia, the Indo-Pacific, and oceanic islands. It is highly likely that globally there are over 1,000 dead zones based on the very strong correlation between human population centres and the presence of hypoxia, and the under-reported ecosystems in those locations. The distribution of coastal oxygen depletion is either centred on major population concentrations, or closely associated with developed watersheds that deliver large quantities of nutrients. The distribution of dead zones closely matches the deposition of nitrogen from human activities in North America, Europe, and South America (Figure 2.5.2). While some of the highest deposition rates are in India and China, there is little information on water quality to assess oxygen conditions.

Since the early 2000s many assessments of global environmental and resource health identify hypoxia as one of the factors threatening coastal and ocean life, for example the Millennium Ecosystem Assessment (2005). In addition, climate model predictions and observations reveal regional declines in oceanic dissolved oxygen linked to global warming (Deutsch et al., 2011; Ito et

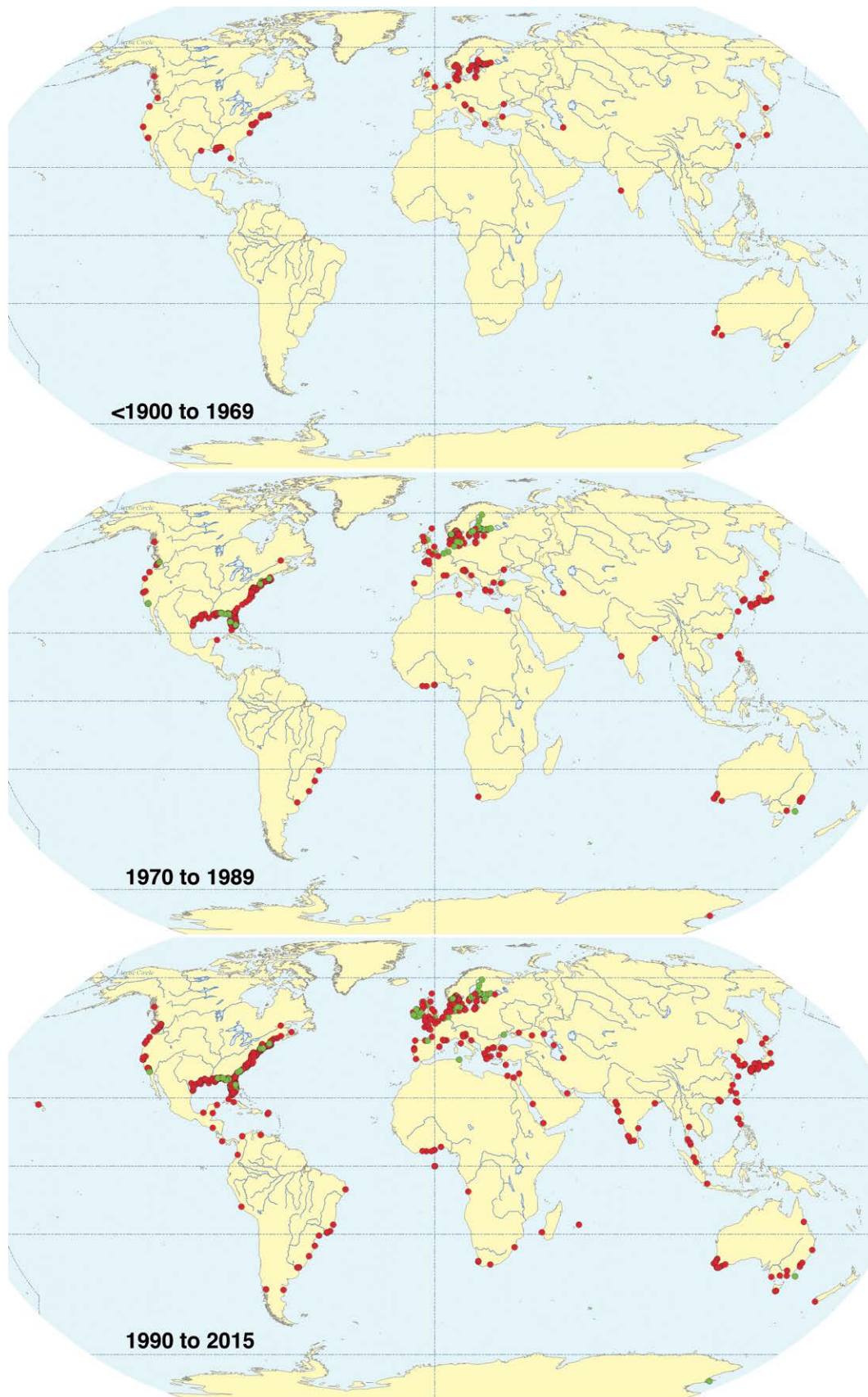


Figure 2.5.1 Global pattern in the cumulative development of coastal hypoxia through time. Each red dot represents a documented case related to human activities. Green dots are sites that have improved. Based on Diaz & Rosenberg (2008), Diaz et al. (2010), and Conley et al. (2011).

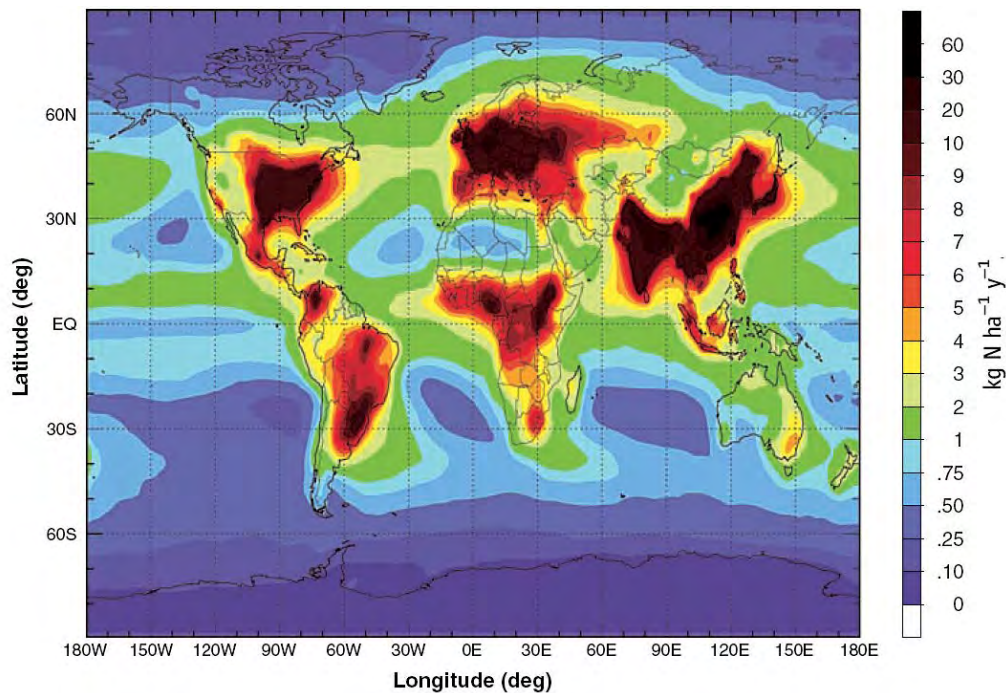


Figure 2.5.2 Global nitrogen deposition estimated from total N (NO_y and NH_x) emissions, 105 Tg N yr^{-1} (Galloway et al., 2008).

al, 2017). To understand hypoxia and its effects on ecosystems requires several perspectives that start at a local level, move to regional, and finally to a global perspective. The most important scale is local for stressors like coastal development, nutrients, pollution, and eutrophication. At local scales (<1 to $1,000 \text{ km}^2$) impacts are most pronounced and where there is most information. At regional scales ($>1,000$ to $1,000,000 \text{ km}^2$) it is a mix of influences from land and sea. This involves local land-based impacts and processes bleeding into regional seas, and large-scale open ocean processes at the boundaries of regions, such as upwelling and water column stratification depth. Much of the problem with hypoxia at local and regional levels can be directly tied to concentrations of human populations and agriculture, both of which have significantly altered the global nitrogen cycle (Gruber & Galloway, 2008; Seitzinger et al., 2010), (Figure 2.5.3). Global scales factors that influence oxygen and hypoxia are changes in circulation patterns, climate, temperature, and pH.

Climate change, whether from global warming or from microclimate variation, will have consequences for eutrophication-related oxygen depletion that will progressively lead to an onset of hypoxia earlier in the season and possibly extending it through time. The influence of multiple climate drivers needs to be considered to understand what future change to expect (Table 2.5.2). Climate change may make systems more susceptible to development of hypoxia through its direct

effects on water column stratification, precipitation patterns, and temperature. These effects will likely occur primarily through warming, which will lead to increased water temperatures and subsequent decreases in oxygen solubility. Warmer surface waters will extend and enhance water column stratification, a key factor in the development of hypoxia (Laurent et al., 2018). Warmer water will increase organism metabolism, which is the key process for lowering oxygen concentrations. In addition to warming, future climate predictions include large changes in precipitation patterns. If changes in precipitation lead to increased runoff to estuarine and coastal ecosystems, stratification and nutrient loads are likely to increase and worsen oxygen depletion (Justic' et al., 2007; Najjar et al., 2010). Conversely, if stratification decreases due to lower runoff or is disrupted by increased storm activity or intensity, the chances for oxygen depletion should decrease (Table 2.5.2).

Much of how climate change will affect hypoxia in the coastal zone will depend on coupled land-sea interactions with climate drivers (Table 2.5.2). But the future pervasiveness of hypoxia will also be linked to land management practices and expansion of agriculture to feed an ever-increasing human population. Land management will affect the nutrient budgets and concentrations of nutrients applied to land through agriculture (Sinha et al., 2017). If in the next 50 years humans continue to modify and degrade coastal systems as in the previous 100 years (Halpern et al.,

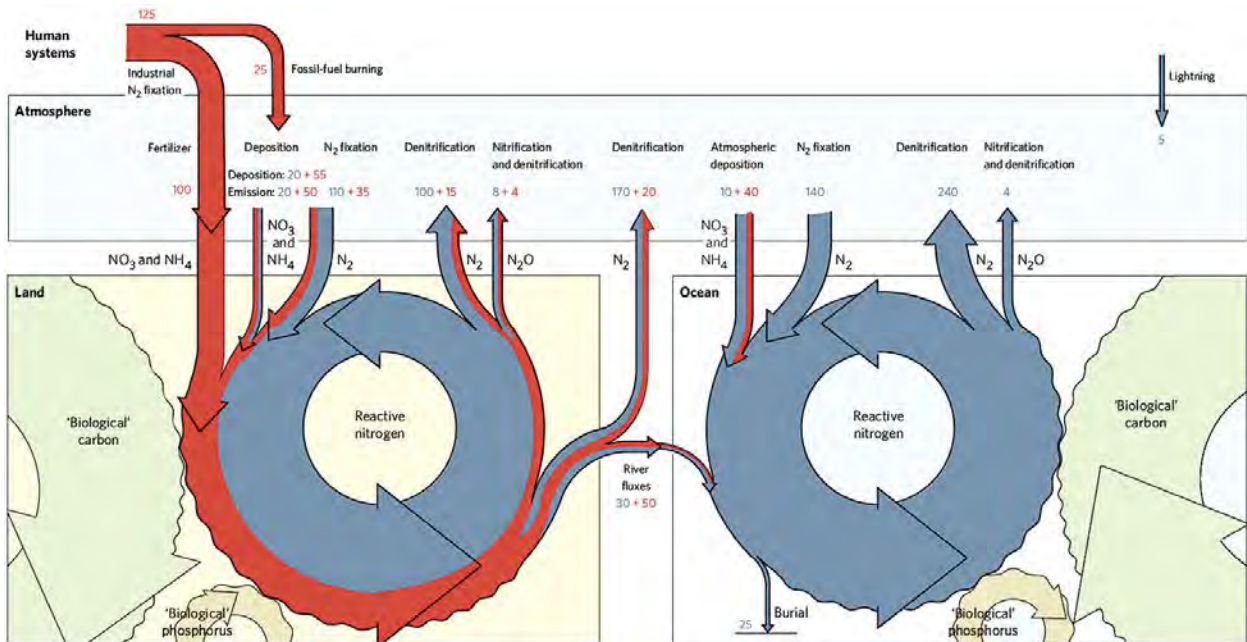


Figure 2.5.3 The global nitrogen cycle on land and in the ocean from Gruber & Galloway (2008). Major processes that transform molecular nitrogen into reactive nitrogen are shown. There is also a tight coupling between the nitrogen cycles on land and in the ocean with those of carbon and phosphorous. Blue fluxes denote 'Natural' (unperturbed) fluxes; orange fluxes denote anthropogenic perturbation. Numbers are in Tg N yr^{-1} and are for the 1990s.

2008), human population pressure will likely continue to be the main driving factor in the persistence and spread of coastal dead zones. Overall, climate drivers will tend to magnify the effects of expanding human population.

Climate related changes in wind patterns are of great concern for coastal systems as wind direction and strength influence the strength of upwelling/downwelling, which in turn affect stratification strength and delivery of deepwater nutrients into shallow coastal areas. Even relatively small changes in wind and current circulations could lead to large changes in the area of coastal sea bed exposed to hypoxia. Changes in the pattern of upwelling on the Pacific coast off Oregon and Washington due to shifts in winds that affected the California Current systems appeared to be responsible for the recent development of severe hypoxia over a large area of the inner continental shelf (Chan et al., 2008; Grantham et al., 2004).

Thus, the future status of hypoxia and its consequences for the environment, society and economies will depend on a combination of climate change (primarily from warming, and altered patterns for wind, currents and precipitation) and land-use change (primarily from an increasing human population, agriculture and nutrient loadings). Expanding energy demands associated with population growth now drive climate change that threatens all ecosystems at all scales from local to global.

2.5.4 Ecosystem consequences

Relative to oxygen, we do not know where the boundaries are for ecosystem catastrophe (Table 2.5.1). The amount, severity, and duration of hypoxia and anoxia must all be factored in. While there are, at times, spectacular events such as mass mortalities of sessile organisms, less is known about population level effects of hypoxia and anoxia. Exposure to hypoxia can reduce reproduction over sufficiently large spatial scales as to affect the dynamics of populations and fisheries production (Bianucci et al., 2016; Breitburg, 2002; Rose et al., 2009), and can even trigger genetic changes in future generations, even if these generations themselves are not exposed to hypoxia (Wang et al., 2016). We also know that when hypoxia develops fish, crabs, shrimp, and other mobile marine life will swim away to areas of higher oxygen concentration, often congregating in dense assemblages right along the boundary of low oxygen zones (Craig & Crowder, 2005). This phenomenon is the origin of the term dead zone, a place where fishermen cannot find anything to catch due to the migration of mobile animals out of the affected area. As a dead zone forms, suitable habitat is compressed and the resulting "escape" by mobile fauna comes at a cost. Individuals suffer lost growth potential (due to a shift to less-suitable habitat and increased competition for resources through crowding), increased vulnerability to predation (as fauna are restricted to

Table 2.5.2 Influence of climate drivers on the extent and severity of hypoxia (Modified from Boesch et al., 2007).

Climate Driver	Direct Effect	Secondary Effect	Influence on Hypoxia
Increased temperature	More evaporation	Decreased stream flow	+
		Land-use & cover changes	-/+
	Less snow cover	More nitrogen retention	-
	Warmer water	Stronger stratification	+
		Higher metabolic rates	+
More precipitation	More stream flow	Stronger stratification	+
		More nutrient loading	+
	More extreme rainfall	Greater erosion of soil P	+
Less precipitation	Less stream flow	Weaker stratification	-
		Less nutrient loading	-
Higher sea level	Greater depth	Stronger stratification	+
		Greater bottom water volume	-
		Less hydraulic mixing	+
	Less tidal marsh	Diminished nutrient trapping	+
Summer winds and storms	Weaker, less water column mixing	More persistent stratification	+
	Stronger, more water column mixing	Less persistent stratification	-
	Shifting wind patterns	Weaker/stronger upwelling potential	-/+

shallower, better-lighted waters), higher susceptibility to fishing (by predictably aggregating individuals at the edge of hypoxic zones), etc. (Table 2.5.3). As a result,

hypoxia indirectly influences harvest, both through effects on processes underlying production such as growth and mortality (including effects on juveniles



Figure 2.5.4 Mersey Estuary © Shutterstock.com.

Table 2.5.3 Generalized response of populations to hypoxia and potential economic effect.

Factor	Result	Potential economic Effect
Mortality	Loss of stock, may take years to recover	Lower landings Increased time fishing
Reduced recruitment	Smaller populations, effect may be long lasting	Lower landings Increased time fishing
Reduced growth	Smaller individuals	Lower individual value
Poor body condition	Weaker individuals	Lower value
Increased migration	Energy resources diverted to movement	Smaller individuals Increased time fishing
Aggregation	Exposure to increased risks of predation and exploitation	Less time fishing Easier to catch
Altered behaviour	More/Less susceptible to fishing gear	Increased or decreased catchability

Direct effects on fisheries stocks related to reduced growth, movement to avoid low oxygen, aggregation and predation pressure.

Direct effects on fishers related to increased time on fishing grounds, cost of searching for stocks, and market forces that control dock side prices.

before they are subject to fishing pressure), and on processes influencing catchability (e.g. emigration, avoidance behaviour).

Mechanistically hypoxia is linked to other stressors, e.g. global warming, ocean acidification, and pollution, and it is often the combined effects of these perturbations that shapes marine ecosystems (Breitburg et al., 2015; Farrell, 2016; Gobler et al., 2016). Because hypoxia limits energy acquisition, it is likely to exacerbate the effects of co-occurring stressors that increase energy demands. Additionally, the development and persistence of ocean dead zones can also create toxic hydrogen sulphide (H_2S) that negatively affects marine life separately from the physiological limitations of a decrease in oxygen.



Figure 2.5.5 Bluefish *Pomatomus saltatrix* © Paolo Oliveira - Alamy stock photo.

All of these factors complicate efforts to identify direct population level responses to hypoxia.

The earliest accounts of hypoxia-stressed systems are from European fjords, such as the Drammensfjord and rivers with population and industrial centres, such as the Mersey Estuary (Figure 2.5.4), where a combination of factors including hypoxia led to the elimination of salmon by the 1850s (Alve, 1995; Jones, 2006). In the USA the earliest account of ecological stress associated with hypoxia come from Mobile Bay, Alabama, where in the 1850s, hypoxic bottom water pushed by tides and wind into shallow water caused mobile organisms to migrate and concentrate at the water's edge. These events became known as "Jubilees" as it was easy for people to pick up the hypoxia stressed fish and crabs that had congregated along the shoreline (May, 1973). In all cases, hypoxia caused the movement of mobile fauna, which has energetic consequences, and reduced or eliminated the trophic base for bottom-feeding species, which has adverse consequences for a system's higher level energy flows (Baird et al., 2004).

If it is important for fish and shrimp to reach critical nursery or feeding areas at certain times in their life cycle, then hypoxia may affect population dynamics by delaying arrival or shortening time spent on spawning or feeding grounds. In such cases, the cost of delayed migration in terms of population mortality and production is not known. For example, in 1976 continental shelf hypoxia in the New York-New Jersey Bight blocked the northward migration of bluefish (*Pomatomus saltatrix*) (Figure 2.5.5). Fish that encountered the hypoxic

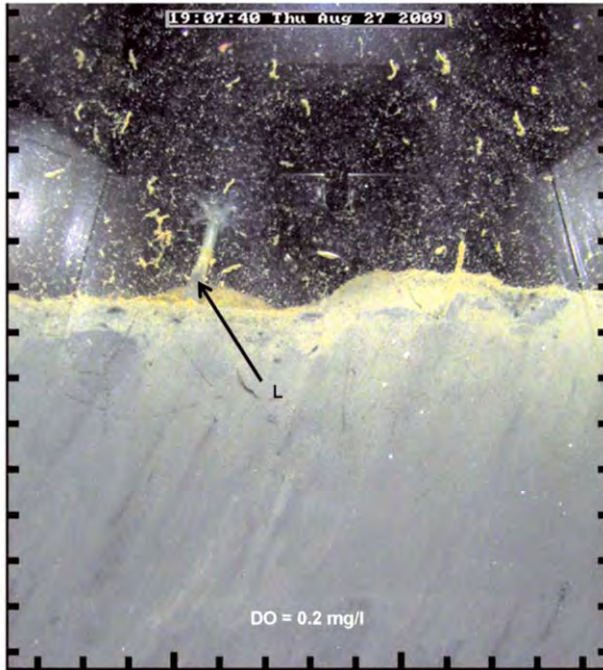


Figure 2.5.6 Hypoxia's impact on infauna behaviour. Sediment profile image of the holothurian, *Leptosynapta tenuis* (L), extending out of the sediment during near-anoxic conditions as it tries to reach water with more dissolved oxygen. Scale around image is in cm units. Light artefacts from reflections are visible on the edge of the image. Modified from Sturdivant et al. (2012).

zone did not pass through or around it but stayed to the south waiting for the hypoxia to dissipate and then continued their migration which was delayed by weeks. On the continental shelf of the northern Gulf of Mexico, hypoxia interfered with the migration of brown shrimp (*Farfantepenaeus aztecus*) from inshore wetland nurseries to offshore feeding and spawning grounds. Juvenile brown shrimp leaving nursery areas migrated farther offshore when hypoxia was not present but were compressed inshore when hypoxia was present. In avoiding hypoxia, brown shrimp aggregated both inshore and offshore of low oxygen areas losing about a quarter of their shelf habitat for as much as six months (Rabalais et al., 2010). The population consequences of this are unknown.

There is a similarity of faunal response across systems to varying types of hypoxia that range from beneficial to mortality (Diaz & Rosenberg, 1995; Vaquer-Sunyer & Duarte, 2008). Consequences of low oxygen are often sublethal and negatively affect growth, immune response, and reproduction (Rabalais et al., 2014). While mobile fauna has to contend with a loss of habitat as they are forced to migrate, and must adjust to changes in prey resources, they are able to at least escape the affected area. Fauna that have limited mobility must

develop physiological and behavioural adaptations (e.g. extract, transport and store sufficient oxygen; maintain aerobic metabolism; reduce energy demand; tolerate H_2S) if they are to survive a declining oxygen environment (Wu, 2002). As hypoxia develops sessile animals initiate a graded series of behaviours to survive (Figure 2.5.6) but will eventually die as oxygen declines or persists through time (Diaz & Rosenberg, 2008). The result is a hypoxia-based habitat compression as hypoxia tends to overlap with essential habitat such as nursery areas, feeding grounds, or deeper, cooler refuge waters during the summer (Craig & Bosman, 2013; Eby & Crowder, 2002).

The development and persistence of dead zones does not have universally negative consequences for ecosystems. Habitat compression from hypoxia may also enhance trophic efficiency contributing to increased fish productivity (Bertrand et al., 2011). We also know that some fauna has adapted to take advantage of oxygen-depleted habitats, utilizing these areas for predator avoidance or feeding on hypoxia-stressed prey. These mobile fauna hover at the edge and migrate into and out of hypoxic zones, using the time out of the dead zone to reoxygenate (Ekau et al., 2010). However, despite documentation of some positive ecosystem responses to deoxygenation, hypoxic habitats are largely lost to the ecosystem for varying lengths of time and have significantly diminished productivity (Sturdivant et al., 2014).

Small and large systems exposed to long periods of hypoxia and anoxia have lower annual secondary production with productivity a function of how quickly benthos can recruit and grow during periods when oxygen is normal (Diaz & Rosenberg, 2008). The extreme case would be the perennial hypoxic/anoxic areas of the Baltic Sea that cover about 70,000 km² where benthic invertebrate production is near zero (Figure 2.5.7). Under normal oxygen conditions this area of the Baltic Sea should be producing about 1.3 million metric tons (mt) wet weight of potential benthic prey for bottom feeding predators (Elmgren, 1984, 1989). In Chesapeake Bay, which has about 3,500 km² of seasonal hypoxia that lasts about three months, about 75,000 mt wet weight of potential prey for fish and crustacean predators is lost (Sturdivant et al., 2014). In the northern Gulf of Mexico severe seasonal hypoxia covers about 20,000 km² and leads to approximately a 210,000 mt wet weight loss of prey from the fisheries forage base. The question remains as to what happens to the "lost" production?



Figure 2.5.7 Dead zone on sea bed in Baltic Sea © Peter Bondo Christensen.

Is it consumed by the microbial community, was it ever produced (benthic production is regulated by growth and recruitment which is stymied during hypoxia), or is it displaced to other areas in the system? If the production isn't displaced but is truly lost, the unknown is whether a system recovers from the secondary production lost to hypoxia during periods of normal oxygen. The Chesapeake Bay has about nine non-hypoxic months to make-up for lost production and the northern Gulf of Mexico six months.

The elimination of benthic prey and hypoxia-based habitat compression can have profound effects on ecosystem functions as organisms die and are decomposed by microbes. Up food chain energy transfer is inhibited in areas where hypoxia is severe as benthic resources are killed directly and mobile predators avoid the area (Figure 2.5.8). As mortality of benthos occurs, microbial activities quickly dominate energy flows (Baird et al., 2004). This energy diversion tends to occur in ecologically important places and at the most inopportune time for predator energy demands (i.e. during the warmer months) and causes an overall reduction in an ecosystem's functional ability to transfer energy to higher trophic levels and renders the ecosystem potentially less resilient to other stressors (Diaz & Rosenberg, 2008). Systems reporting mass mortality provide primary examples of degradation in trophic structure (Oliver et al., 2015).

There is an inherent resiliency to perturbations in marine ecosystems which can make resolving ecosystem level consequences to disturbance difficult (Downing et al., 2012). Hypoxia has clear mortality effects on sessile, and at times mobile, organisms but its population level effects in coastal environments remain uncertain. Much of the evidence supporting negative effects from hypoxia comes from laboratory experiments, localized effects in nature, fish kills, and our intuition that a lack of oxygen can lead to dire consequences (Rose et al., 2009). Scaling to predict effects on food webs and fisheries production is confounded by compensatory mechanisms such as increased production of planktonic prey, increased encounter rates between predators and prey compressed into smaller oxygenated habitat space, and co-occurring stressors that have similar ecosystem responses (Breitburg et al., 2009b; De Mutsert et al., 2016; Rose et al., 2009). As a result, conclusive evidence of wide-spread population level response to hypoxia is lacking. Quantifying the effects of hypoxia on fish populations, whether large or small, is critical for effective management of coastal ecosystems and for cost-effective and efficient design of remediation actions. The potential for interaction of direct and indirect effects, and subtle changes in vital rates (such as reproduction and recruitment) leading to population responses complicates field studies and management but does not excuse us from quantifying the population losses due to hypoxia. As coastal ecosystems continue to decline their capacity to deliver ecosystem services will also decline providing a level of urgency to resolving this question to better enhance future conservation efforts.

2.5.5 Societal consequences

As climate and land-use continue to change, the future forecast is that coastal hypoxia will worsen, with increased occurrence, frequency, intensity, and duration (Diaz & Rosenberg, 2011). The ecological impacts of hypoxia have been assessed (Diaz & Rosenberg, 2008; Levin et al., 2009; Vaquer-Sunyer & Duarte, 2008), but how these ecological effects translate into societal costs is unknown. Human population distribution is increasingly skewed, with the overwhelming bulk of humanity concentrated along or near the coast on just 10% of the earth's land surface. Thus, it is logical that anthropogenic disturbances to coastal ecology will feedback to socio-economics. An economic valuation of hypoxia involves multiple academic fields and the responses can be subtle and difficult to quantify, even when mass mortality



Figure 2.5.8 Range of behaviour and ecological impacts as dissolved oxygen levels drop from saturation to anoxia.

events occur, making quantification difficult (Smith & Crowder, 2011). However, from assessing ecological effects of hypoxia it is known that populations can experience a range of problems that at some point will negatively affect economic interests (Table 2.5.3). Much of the problem in assessing economic consequences is related to the multiple stressors acting on targeted commercial populations (habitat degradation, over-exploitation, pollution) and also factors that stress fisher's economics (aquaculture, imports, economic costs of fishing, fisheries regulations). Hypoxia is not priced in the market, but fish are, and provide a useful measure to quantify economic impact.

Because of their devastating effects on stocks and fishermen, hypoxia-induced mass mortality events are a logical place to begin any assessment. Losses from hypoxia-related mortality of oysters in Mobile Bay, USA, in the early 1970s was estimated at the time to be US\$500,000, but greater economic losses were associated with the declining stocks and poor recruitment of oysters (*Crassostrea virginica*) associated with recurring severe hypoxia (May, 1973). Estimated losses to marine related industries from the New York Bight hypoxic event in the summer of 1976 were over US\$570 million (Figley et al., 1979). Much of this loss was in surf clams that accounted for >US\$430 million. Factored by the area of hypoxia (987 km²) the 1976 event cost about US\$580,000 km⁻² for resources and fisheries related activities and US\$165,000 km⁻² for just the resources lost.

Lack of identifiable economic effects in fisheries landing data does not imply that declines would not occur should conditions worsen. In the northern Gulf of Mexico brown shrimp landings appear to be inversely related to the area of hypoxia (O'Connor & Whittall, 2007). Whether this relationship will remain linear or transform into a catastrophe function (Jones & Walters, 1976) at some critical point is not known. Other large systems have suffered serious ecological and economic consequences from seasonal hypoxia; most notable are the Kattegat with localized loss of catch and recruitment failures of Norway lobsters (*Nephrops norvegicus*) (Figure 2.5.9) in the late 1980s, and the north-west continental shelf of the Black Sea which suffered regional loss of bottom fishery species also in the 1980s (Karlsen et al., 2002; Mee, 1992, 2006).

Economic valuation of losses from hypoxia seem small relative to the total value of fisheries, but the key point is that losses from hypoxia are measurable in economic terms (Huang & Smith, 2011). For example, the valuation of recreational fishing relative to hypoxia in the Patuxent River, a tributary in Chesapeake Bay, showed that as oxygen declined to mild hypoxic levels total losses for striped bass (*Morone saxatilis*) fishing was about US\$10,000 for the annual hypoxic event with a net present value of about US\$200,000. If the same water quality was allowed to occur in the entire Chesapeake Bay, the net present value of the losses due to hypoxia would be >US\$145 million annually (Lipton & Hicks, 2003). A similar analysis of recreational fishing in north-east and middle Atlantic regions found that overall as oxygen declined capture rate of fish declined (Bricker et al., 2006). The effects of hypoxia on recreational fishing for one species suggests that similar effects are likely being experienced by commercial fishers. This has been documented for shrimp and crab fisheries in North Carolina. Huang et al. (2010) found that hypoxia may reduce annual shrimp harvest by about 13%, valued at about US\$1.2 million annually, and Smith and Crowder (2011) documented that just a 30% reduction in nutrient loading would abate hypoxia potentially adding US\$2.6 million annually to the crab harvest.

Experience with other hypoxic zones around the globe shows that both ecological and fisheries effects become progressively more severe as hypoxia worsens (Caddy, 1993; Diaz & Rosenberg, 1995), suggesting that at some point economic losses will become more obvious and costly. However, currently the direct connection of hypoxia to fisheries landings at large regional scales

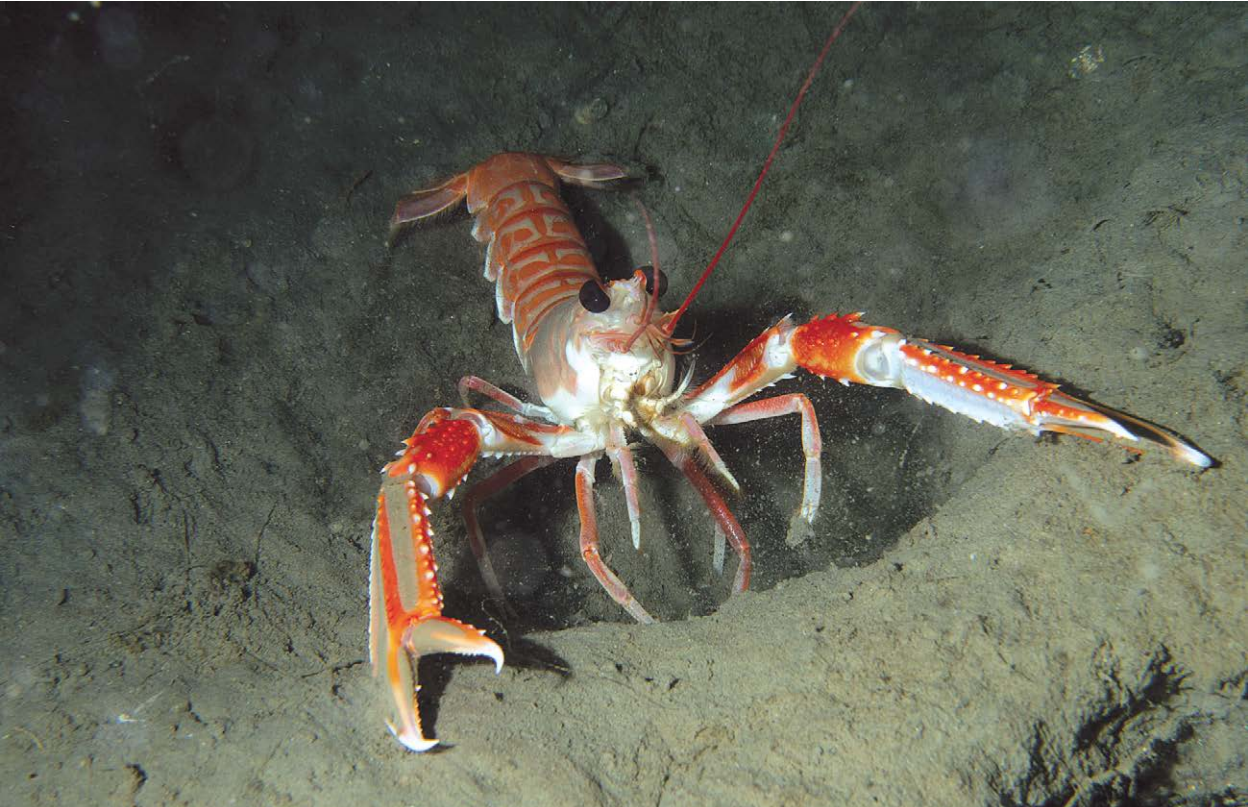


Figure 2.5.9 *Nephrops norvegicus* © Bernard Picton.

is not always clear (Baustian et al., 2009); this is complicated by the fact that many fisheries experience heavy fishing pressure simultaneous with hypoxic zone growth, making it difficult to identify the primary cause of the decline in harvest rates (Breitburg et al., 2009a). There are also a number of factors that include confounding effects of eutrophication, overfishing, and compensatory mechanisms that alter or mask effects of hypoxia on landings. Breitburg et al. (2009b) found a hint of a connection with a possible decline in landings of benthic species in systems where $\geq 40\%$ of bottom area becomes hypoxic. Hypoxia has also been documented to increase the landings of less valuable pelagic fish relative to more valuable bottom-dwelling fish and shellfish (Caddy, 1993; Rabotyagov et al., 2014). Most recently Smith et al. (2017) found the persistence of hypoxia in the Gulf of Mexico can skew a population's size distribution toward smaller individuals reshaping seafood markets; as a result of this population skew, hypoxia increased the relative price of large shrimp compared with small shrimp. These findings translate into tangible responses from the fishing industry in terms of fishing behaviour and effort and are further confounded by other economic considerations (e.g. fuel).

There is a counter-argument that a causality of hypoxia (namely eutrophication) could have positive economic opportunities. Bricker et al. (2014) determined that the nutrient rich Chesapeake Bay could be utilized to productively foster shellfish aquaculture. They suggest that if $\sim 40\%$ of the estuary bottom is cultivated for shellfish aquaculture it would promote growth of a now depleted oyster stock, remove eutrophication impacts directly from the estuary through harvest, and as a consequence remediate hypoxia. Bricker et al. (2014) suggest this approach could be applied to estuaries around the USA, particularly river-dominated low-flow systems with moderate to high levels of nutrient-related degradation, as a means for nutrient remediation, replenishment of diminished bivalve stocks, and enhancement of economic output. The plausibility of this approach would be largely dependent on the rate of return on investment. Would harvest and sales of oysters be sufficient to cover initial capital costs and costs associated with aquaculture management? These are big unknowns that would need to be resolved to address the viability of this approach. As it currently stands, eutrophication and hypoxia are only documented to negatively impact aquaculture practices resulting in large die-offs and economic hardship (San Diego-McGlone et al., 2008).

2.5.6 Implications of continuing ocean deoxygenation

Within the last 60 years over-enrichment of our waters primarily with nutrients from fertilizers has emerged as one of the leading causes of water quality impairment. These nutrients have led to a greening of our seas and are an indirect consequence of agricultural and municipal activities that support a rapidly expanding human population. On a global basis, humans have been adding more nitrogen to land or ocean than is supplied by natural biological nitrogen fixation (Figure 2.5.3). It is estimated that as a result of human activities the flux of nitrogen has more than doubled over natural values while the flux of phosphorus has tripled (Foley et al., 2005; Gruber & Galloway, 2008).

Virtually all the ocean's food provisioning ecosystem services for humans require oxygen to support organism growth and production. Oxygen is just absolutely necessary to sustain the life of all the fishes and invertebrates we have come to depend upon for food and recreation. By the early 1900s dissolved oxygen was a topic of interest in research and management, and by the 1920s it was recognized that a lack of oxygen was a major hazard to fishes. But it was not obvious that dissolved oxygen would become critical in shallow coastal systems until the 1970s and 1980s when large areas of low dissolved oxygen started to appear with associated mass mortalities of invertebrate and fishes. From the middle of the 20th century to today, there have been drastic changes in dissolved oxygen concentrations and dynamics in marine coastal waters. Diaz and Rosenberg (1995) noted that no other environmental variable of such ecological importance to estuarine and coastal marine ecosystems as dissolved oxygen has changed so drastically from human activities, in such a short period of time.

Accounts of environmental problems related to low dissolved oxygen pre-date our ability to measure oxygen concentration in water. For example, the Drammensfjord in Norway appears to have been persistently hypoxic and anoxic since at least the 1700s based on foraminiferan proxies (Alve, 1995). Even in this small fjord with extended residence time of deep water, historical naturally occurring anoxia has been made worse over the last two centuries by eutrophication. Improvements were observed only after reductions in organic loading. Another example would be the Mersey Estuary, England, which had poor water

quality and hypoxia since at least the 1850s but is now recovered through concerted management efforts (Jones, 2006).

2.5.7 Conclusions / Recommendations

Recognizing the negative consequences of coastal eutrophication and related hypoxia, nations have to make socio-economic commitments for reducing nutrient loads to the adjacent estuaries, bays and seas, upon which they depend. Worldwide there are currently over 700 coastal hypoxia systems, about 70 have responded positively to remediation. All but one improved as a result of management of point discharges. The north-west continental shelf of the Black Sea is the only exception, which responded positively to a reduction in nutrient runoff after the collapse of the Soviet Union. Once the second largest anthropogenic hypoxic area on earth, it is now reduced through concerted efforts to reduce point discharges and runoff from agricultural lands (Capet et al., 2013; Langmead et al., 2008; Mee, 2006).

The management and reduction of hypoxia can only be accomplished by reducing the general problem of eutrophication from a combination of sewage/industrial discharge and nutrient runoff. Nutrients generally increase biological production, while hypoxia acts in the opposite direction, reducing biomass and habitat quality. Overall, the combination of stressors associated with eutrophication has and continues to degrade our coastal systems.

The impacts of hypoxia and nutrient enrichment on food webs and fisheries will be strongly influenced by the extent to which they co-occur. Unless the leakage of nutrients from land-based sources to the sea can be reduced, the future for our estuarine and coastal resources looks bleak. Where applied, nutrient management has reversed the effects of hypoxia. But concerted effort in the future will be needed to allow more systems to recover, particularly for those systems affected primarily by land-runoff.

For hypoxia in Europe and North America much is known about its occurrence in coastal areas, including spatial and temporal patterns. Less is known from the other continents, where most of the human population lives, and oceanic islands. For all systems, less is known about long-term trends, factors controlling dissolved oxygen depletion and replenishment, impacts on ecological processes, and economic losses. To

formulate effective strategies for remediating coastal hypoxia it is essential to have an understanding of what the specific drivers are and what responses to expect with various remediation approaches. Some of these drivers are under state or national control, while others lack defined ownership/responsibility. However, management of hypoxia including the control of drivers of eutrophication is often a transboundary issue.

At some point degraded habitat as a result of eutrophication and hypoxia will lead to reduced fisheries landings or possibly collapse of regional stocks. The bad news is that the overall forecast is for all forms of hypoxia to worsen in the future, with increased occurrence, frequency, intensity and duration. The good news is that the consequences of local and regional eutrophication-induced hypoxia can and have been reversed with long-term and persistent efforts to manage and reduce nutrient loads, which in all cases has led to the restoration of ecosystem services.

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Causes of ocean deoxygenation

3

The loss of oxygen in the ocean can broadly be put down to two overlying causes – eutrophication as a result of nutrient run-off from land and deposition of nitrogen from the burning of fossil fuels, and the heating of ocean waters from climate change, primarily causing a change in ventilation with the overlying atmosphere and a reduced ability to hold soluble oxygen. In this chapter these two main drivers of oxygen deoxygenation are explored, along with the relationship between deoxygenation and algal blooms.

Since the middle of the 20th century, the increased river export of nitrogen and phosphorus has resulted in eutrophication in coastal areas world-wide. Climate warming is expected to exacerbate the decrease of oxygen by reducing ventilation and extending the stratification period; in many places, increasing the delivery of nutrients. A combination of eutrophication and low ventilation of ocean water by oxygen, often due to vertical layering or stratification of the water column, can lead to oxygen deficiencies near the sea bed and in the lower water column.

Saline or thermal stratification, or both, dictate the presence of a pycnocline across which dissolved oxygen diffusion is hindered. Increased water residence time also enhances the probability of oxygen depletion occurring in a coastal area. Physical barriers such as sills at depth and advection of offshore waters can also affect the level of deoxygenation, positively or negatively. The enhanced nutrient inputs from fertilizer and wastewater from the land, stimulate phytoplankton blooms which then die and sink to the sea floor where they degrade and thereby remove oxygen.

Ocean deoxygenation strongly impacts the breakdown of organic matter dramatically changing the sources, sinks and cycling of a range of important elements in the environment. This occurs especially for the biologically important elements such as nitrogen, phosphorus and iron, but also for the production of various greenhouse gases such as nitrous oxide and methane. Continued spreading of deoxygenated areas in the world ocean is a most serious environmental problem with enormous potential impacts on biodiversity and human societies.



3.1 Ocean deoxygenation from climate change

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Summary

- According to the most recent observational estimate, the ocean lost 2% of its oxygen inventory between 1960 and 2010.
- About 15% (range 10-30%) of the oxygen loss is attributed to warming-induced decline in solubility (high confidence).
- Less than 15% of the oxygen decline can be attributed to warming-induced changes in respiration of particulate and dissolved organic matter. Enhanced respiration will tend to generate oxygen deficits close to the sea surface. The increased near-surface vertical oxygen gradient may even increase ocean uptake of oxygen from the atmosphere (low confidence).
- The majority of oxygen loss has been caused by changes in ocean circulation and associated ventilation with oxygen from the ocean surface (medium confidence).
- Current state-of-the-art models simulate deoxygenation rates more than 2 times smaller than the most recent data-based global estimate.

Processes	Likely impacts on deoxygenation
Increasing temperatures reduce the solubility of oxygen (and other gases) in water.	<ul style="list-style-type: none"> Explains about 50% of oxygen loss in the upper 1000 m, corresponding to a solubility-driven oxygen loss of about 0.013 Pmol O₂ yr⁻¹. Until now the solubility-driven contribution to oxygen loss below 1000 m depth amounts to about 2% (about 0.001 Pmol O₂ yr⁻¹). According to the most recent estimate of global deoxygenation (0.096 ±0.042 Pmol O₂ yr⁻¹), solubility changes account for 15% (range 10-30%) of the total oxygen loss during 1960-2010.
Warming-driven increase in respiration rates of particulate organic matter.	<ul style="list-style-type: none"> Metabolic rates increase with temperature, so will respiration rates. Remineralization of sinking organic particles will therefore tend to occur at shallower depths, generating oxygen deficits closer to the air-sea interface and tending to increase the oxygen flux from the atmosphere into the ocean. Overall effect computed from model simulations expected to be a small (< 0.005 Pmol O₂ yr⁻¹) oxygen gain.
Reduced burial in the sediments.	<ul style="list-style-type: none"> By enhancing respiration rates in the water column and in the sediment, ocean warming is expected to reduce the amount of organic matter buried in the sediments. Less burial means that more organic matter is respired, generating additional respiratory oxygen loss in the water column. An upper bound is a complete cessation of burial, which would correspond to a pelagic oxygen sink of about 0.002 Pmol O₂ yr⁻¹, i.e. 2% of the total oxygen loss estimated for 1960-2010.
Warming-driven increase in the respiration of dissolved organic matter.	<ul style="list-style-type: none"> Respiration rates of dissolved organic matter (DOM) are expected to increase with temperature. Estimates are difficult because of the poorly known composition and biological accessibility of DOM. Incubation experiments indicate some warming-induced acceleration of respiration, which might explain up to 10% or 0.01 Pmol O₂ yr⁻¹ of the observed oxygen loss. A corresponding decline of the ocean's DOM inventory has not yet been observed.
Respiration of enhanced release of methane from melting gas hydrates.	<ul style="list-style-type: none"> Warming of bottom waters may result in enhanced destabilization of methane gas hydrates, leading to enhanced release of methane from sediments and subsequent aerobic respiration of methane to CO₂. There is little observational evidence for a warming-induced acceleration of methane release taking place already.
Circulation changes in response to global warming.	<ul style="list-style-type: none"> As the ocean warms from the surface, stratification is expected to increase, with a tendency for a slowing down of the ocean circulation. A slowed-down circulation is expected to account for up to 50% of the observed deoxygenation in the upper 1000 m, and for up to 98% in the deep ocean (> 1000 m). Spatial patterns and individual mechanisms are not yet well understood.

3.1.1 Introduction

Ocean deoxygenation is caused by an imbalance of sources and sinks of oxygen dissolved in sea water. This section addresses how individual oxygen sources and sinks can vary in response to climate change. Based on our still immature quantitative understanding of the climate sensitivity of the various processes at play, estimates will be provided, wherever possible, to what extent past and likely future changes in marine dissolved oxygen can be attributed to individual mechanisms and, ultimately, to anthropogenic climate change.

Waters of the surface ocean are essentially in equilibrium with the oxygen partial pressure of the atmosphere that contains more than 99% of the molecular oxygen available on Earth. Burning fossil fuels consumes oxygen, but because of the large atmospheric oxygen inventory, the associated relative decline of atmospheric oxygen (0.001% per year) is about two orders of magnitude smaller than the current rate of ocean deoxygenation. Air-sea gas exchange typically equilibrates tens of metres of surface waters within days (Kihm & Körtzinger, 2010), with warmer waters having a lower solubility and therefore, at the same saturation levels, holding less oxygen than colder waters. Oxygen concentrations in the surface ocean are therefore highest in cold high-latitude waters (Figure 3.1.1) where deep waters form and thereby transport oxygen into the deep ocean interior to depths well exceeding 1000 metres. Waters above the deep waters of polar origin and below the surface mixed layer belong to the stratified thermocline

that is ventilated via a mostly wind-driven circulation that moves water equatorward and westward along isopycnals in large anticyclonic gyres in the subtropical and tropical oceans (Luyten et al., 1993).

Photosynthesis by marine phytoplankton is an oxygen source within the ocean's light-lit surface waters in close contact with the atmosphere. On regional and seasonal scales, photosynthesis typically makes up for a small fraction of the total air-sea oxygen exchange (Garcia & Keeling, 2001). There are no significant oxygen sources in the dark ocean interior. Here, oxygen can be supplied only via physical processes that transport oxygen-rich waters from the surface to depth (Figure 3.1.2).

The main marine oxygen sink is the respiration of organic matter by microbes and multicellular organisms. The total amount of respiration is controlled by the availability of organic matter, which ultimately depends on primary production in the surface ocean, often limited by nutrients, light or both (Arteaga et al., 2014). Changes in surface-ocean environmental conditions can thus cause changes in oxygen consumption in the ocean interior. By forming particles that sink through the water instead of moving with it, the marine biology can lead to relatively fast changes in respiration in ocean-interior water parcels that may have been supplied with oxygen via direct contact with the atmosphere the last time hundreds of years ago. Changes in particle properties and in respiration rates may also affect the amount of organic matter that is buried in the sediments. Since photosynthetic production of organic

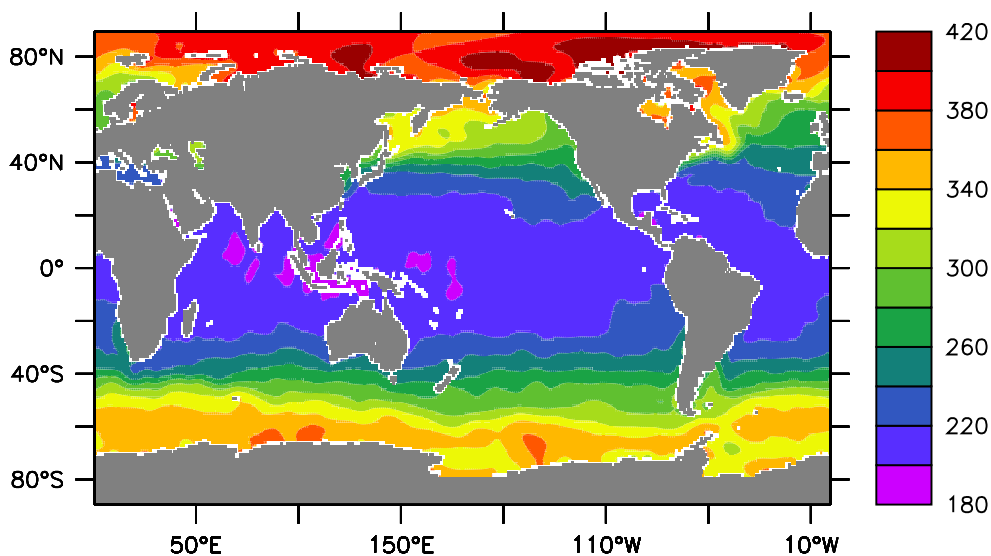


Figure 3.1.1 Global distribution of annual-mean oxygen concentrations in the surface waters compiled from the World Ocean Atlas 2009 (Garcia et al., 2010). Units are $\mu\text{mol kg}^{-1}$.

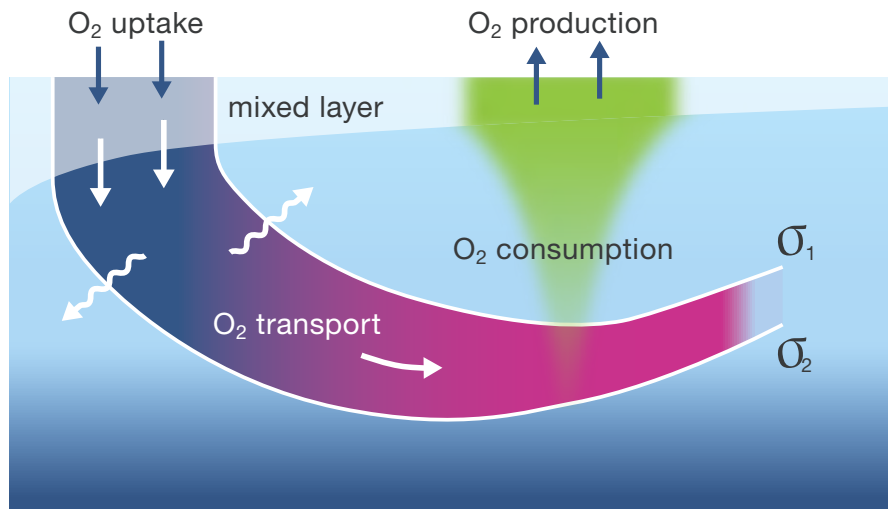


Figure 3.1.2 Schematic representation of oxygen supply to the ocean interior via physical transport that occurs predominantly along isopycnal surfaces (σ) and oxygen consumption by respiration of organic matter exported downward out of the surface ocean.

matter generates oxygen, the subsequent burial and the associated avoidance of respiration constitutes a net oxygen source. Thus, a reduction in burial rates or increase in remobilization from the sediments may contribute to marine deoxygenation. The same holds for a hypothetical reduction in anaerobic remineralization, e.g. by denitrification, at the expense of more aerobic remineralization. However, as denitrification occurs in low-oxygen environments, it is currently estimated to increase rather than decrease. Another biological process that may reduce marine oxygen levels is the microbial oxidation of methane released from gas hydrates found in the sediments at water depths of a few hundred metres and that may destabilize under increasing bottom water temperatures in response to global warming.

The ocean oxygen inventory can thus change via three main pathways:

- i. Changes in initial oxygen concentrations in surface waters in immediate contact with the atmosphere.
- ii. Changes in respiratory oxygen consumption in the ocean interior.
- iii. Changes in ventilation via mixing and circulation that affect the time span, during which respiratory oxygen losses can accumulate in ocean-interior waters since their last contact with the atmosphere.

Since the oxygen content of sea water has been measured accurately for over one hundred years, changes can be derived from compilations of such observations. Schmidtko et al. (2017) estimate a decline

in the ocean's oxygen inventory by about 2% between 1960 and 2010. Current climate-biogeochemistry models, however, do not adequately reproduce observed patterns of oxygen changes and, overall, tend to underestimate oxygen variability and trends (Oschlies et al., 2018). In particular, models simulate a decline in the global ocean's oxygen inventory by typically less than 1% over the past 50 years (Table 3.1.1; Bopp et al., 2013). On average, simulated deoxygenation is more than two times slower than the most recent observational estimate. This discrepancy indicates that an accurate quantitative understanding of ocean deoxygenation is still lacking, and that current estimates of contributions from individual processes and even causes must be regarded with some degree of caution. The following presents observational and theoretical evidence regarding climate-related mechanisms of oxygen changes and discusses the extent to which ocean deoxygenation can be linked to anthropogenic climate change.

3.1.2 Temperature effects on solubility

The solubility of oxygen in sea water determines the concentration of dissolved oxygen in the surface water that is in equilibrium with the overlying atmosphere. It thereby controls the supply of oxygen to the ocean – point (i) above. Oxygen solubility is, like for any gas, a function of temperature and salinity, and decreases with increasing temperature and salinity. For example, oxygen saturation decreases by about 5% for a 2 °C warming from 4 °C to 6 °C. For current climate change, effects of changes in salinity are generally many times

Table 3.1.1 Global ocean oxygen inventory (Pmol), trend (Tmol/decade) and percentage change over the past 50 years as derived from observations (Schmidtko et al., 2017), as simulated by the nine models of the 5th phase of the Climate Model Intercomparison Project (CMIP5) that contain oxygen as tracer (more detailed information about the models is provided in Table 1 of Oschlies et al., 2017), and three simulations of the University of Victoria Earth system climate model of intermediate complexity (UVic 2.9) also described in more detail in Oschlies et al. (2017). Standard deviations as given by Schmidtko et al. (2017) for the observational estimate, and the variance among the 9 CMIP5 models, respectively.

Model	Inventory Pmol	Tmol/decade	% change over 50 yr
CESM1	260,2	-420,6	-0,81
CMCC CESM	271,8	-893,6	-1,64
GFDL ESM2G	275,7	-215,5	-0,39
GFDL ESM2M	244,8	-356,1	-0,73
HadGEM2 ES	192,3	-229,4	-0,60
IPSL CM5A LR	199,3	-529,4	-1,33
MPI ESM LR	255,5	-214,5	-0,42
MRI ESM1	320,4	-30,9	-0,05
NorESM1 ME	342,7	52,4	0,08
UVic 2.9	225,6	-463,2	-1,03
model average	258,8	-330,1	-0,64
Obs. estimate	227,4	-960	-2,11

smaller than the temperature-induced changes (Weiss, 1970). By analysing temporal changes in temperature, one can directly compute the solubility-driven component of oxygen changes. This approach has been used, among others, by Helm et al. (2011) and Schmidtko et al. (2017), who inferred that about half of the oxygen decline measured in the upper 1000m over the past decades could be attributed to temperature-driven changes in solubility (Table 3.1.2). This explains part of the tight relationship between decreasing O_2 inventories and increasing ocean heat content that has been described by Ito et al. (2017) for the upper ocean. Integrated over the entire water column, Schmidtko et al. (2017), however, attribute only 15% of their estimate of oceanic oxygen loss to direct solubility effects. This means that oxygen changes in the deep ocean are, until now, almost independent of solubility changes. This is consistent with the fact that solubility effects originate at the sea surface and have to be transported physically with the circulation into the ocean interior. Water ages in the deep ocean are too old to be substantially affected by anthropogenically driven solubility changes, yet.

3.1.3 Temperature effects on metabolic rates

Chemical rates generally increase with increasing temperature (Arrhenius, 1889). This applies to both primary production (Eppley, 1972) and respiration

(Pomeroy & Wiebe, 2001). Primary production is, in most regions of the world ocean, limited by resources (i.e. nutrients or light) and not temperature (Maranon et al., 2014). Similarly, the total amount of marine respiration is primarily limited by the availability of substrate, i.e. organic matter. In the current ocean, almost all organic matter exported from the ocean's surface layer is respired, except for a very small portion that is buried in the sediments that corresponds to a net oxygen production of $0.002 \text{ Pmol } O_2 \text{ yr}^{-1}$ globally by avoided aerobic respiration (Wallmann, 2010), a rate that is 50 times smaller than the total ocean oxygen loss of $0.096 \text{ Pmol } O_2 \text{ yr}^{-1}$ estimated by Schmidtko et al. (2017).

A likely impact of warming-induced acceleration of metabolic rates is a systematic change in the spatial patterns of respiration and associated oxygen consumption in the water column. The decrease of respiration with depth, z , was first described empirically by an exponential function in the form of $R=R_0 e^{-a/z}$ (Wyrski, 1962) and later replaced by a power law function $R=R_0 (z/z_0)^{b-1}$ (Martin et al., 1987) that was found more appropriate to describe measurements of the downward flux of particulate organic matter over the entire water column. As noted by Brewer and Peltzer (2017), such temperature-independent empirical descriptions, that are still used in a number of conceptual and numerical models of marine biogeochemical

Table 3.1.2 Approximate contribution of individual mechanisms to the observed ocean deoxygenation between 1960 and 2010, referenced to the recent deoxygenation estimate by Schmidtko et al. (2017). Observational evidence is very strong for the solubility driven contribution (+++), positive for ventilation changes (+), plausible for temperature effects on oxidation of dissolved organic matter and methane (o) and absent for temperature effects on remineralization profiles and burial of organic matter (-).

Process	% upper 1000m (0.026 Pmol O ₂ yr ⁻¹)	% below 1000m (0.070 Pmol O ₂ yr ⁻¹)	% total (0.096 Pmol O ₂ yr ⁻¹)	Observational evidence
Solubility	50%	2%	15%	+++
Temperature effects on remineralization profile and air-sea exchange of O ₂			up to -5%	-
Potential warming-induced cessation of burial	< 6%	< 0.3%	< 2%	-
Temperature effects on remineralization of dissolved organic matter			up to 10%	o
Temperature effects on methane oxidation	o	o	o	o
Circulation changes	up to 50%	up to 98%	up to 85%	+

cycles, lead to difficulties in accounting for impacts of warming on respiration and associated effects on tracer distributions. Differences in the consideration of temperature effects can have substantial impacts on projected changes in marine biogeochemical cycles under global warming (Taucher & Oschlies, 2011). In a model study, Segschneider and Bendtsen (2013) applied a temperature perturbation, corresponding to business-as-usual global warming at the end of the 21st century, to remineralization rates. They found that accelerated remineralization of sinking organic matter at higher temperatures made respiration happen at shallower depths. In their model, oxygen concentrations were reduced by a few mM in the upper few hundred metres in the simulation using projected end-of-21st century temperatures based on the RCP 8.5 emissions scenario compared to pre-industrial temperatures. Because organic matter was respired at shallower depths under elevated temperatures, less substrate was exported to greater depth where respiration was reduced and oxygen concentrations were elevated. Assuming that primary production is resource-limited and not temperature-limited and therefore unaffected by warming, Segschneider and Bendtsen (2013) showed that metabolic effects of global warming lead to elevated CO₂ and reduced O₂ concentrations in the near-surface waters resulting from shallower respiration. This leads to a net outgassing of about 0.2 Pg C yr⁻¹, corresponding to a net oceanic oxygen flux into the ocean of 0.02 Pmol O₂ yr⁻¹ in their model study simulating end of 21st century ocean warming. The direct effect of warming on the cycling of freshly produced organic matter is thus

expected to be a net oceanic oxygen gain rather than a loss. Given that less than one quarter of the oceanic heat uptake simulated by the year 2100 has happened before the year 2010, this would compensate for only a small fraction (less than ~0.005 Pmol O₂ yr⁻¹, i.e. about 5%, Table 3.1.2) of the observed estimate of total ocean deoxygenation over the past 50 years.

Since respiration will tend to be faster in a warmer ocean, less organic matter is left over to reach deeper waters and the sea floor. This might affect burial and thereby have a small net effect on total oxygen consumption. However, even if burial of organic matter would cease completely and all organic matter would instead be respired in the water column, this could account for only 2% of the deoxygenation observed over the past 50 years. As only about 10% of the burial occurs in deep waters (Wallmann, 2010), cessation of burial might have largest impact on upper ocean deoxygenation (Table 3.1.2).

Substrate limitation therefore rules out major effects of temperature-driven enhancements of metabolic rates on globally integrated decomposition, and associated oxygen consumption, of freshly produced organic matter. However, enhanced respiration of old and more refractory dissolved organic carbon (DOC), that constitutes a significant oceanic carbon pool of more than 600 Pg C (Hansell et al., 2009), under increased temperatures may lead to a net oxygen decline. While the oceanic DOC pool is composed of a wide spectrum of largely uncharacterized organic compounds, it is still

unclear what limits its consumption and to what extent warming may accelerate the respiration of DOC. If the deoxygenation signal observed between 1960 and 2010 were to be explained solely by respiration of DOC, about 10% of the oceanic DOC pool would have been lost already, for which there is no observational evidence.

From incubation experiments, Bendtsen et al. (2015) inferred that the respiration of the more recalcitrant components of DOC (lifetime of months) increased about twice as fast with increasing temperatures ($Q_{10} > 5$) than respiration of the more labile DOC pool (e-folding lifetime of days, $Q_{10} \sim 2$). Possible effects of a warming-induced acceleration of DOC remineralization in the open ocean are still uncertain. For coastal waters in the Baltic Sea – North Sea transition zone, Bendtsen and Hansen (2015) simulated a decline in oxygen concentrations by 30–40 μM for an assumed 3 $^{\circ}\text{C}$ temperature rise. Assuming this as a globally representative value and relating to the heat required to warm a litre of sea water by 3 $^{\circ}\text{C}$ (11.550 J) yields a deoxygenation rate by enhanced respiration of DOC of about 0.4–0.5 $\text{nmol O}_2 \text{ J}^{-1}$, which is an order of magnitude smaller than the observed relationship between deoxygenation and oceanic heat uptake (2–10 $\text{nmol O}_2 \text{ J}^{-1}$) for an older deoxygenation estimate (Keeling & Garcia, 2002) that approximately doubles for the most recent deoxygenation estimate of Schmidtko et al. (2017) and is consistent with model-derived estimates of $3.7 \pm 0.8 \text{ nmol O}_2 \text{ J}^{-1}$ reported by Resplandy et al. (2018)). If extrapolated to the global ocean, current estimates of local enhancement of DOC respiration by warming may thus explain as much as 10% of the observed ocean deoxygenation. More studies are required to investigate this further.

3.1.4 Oxygen demand of methane oxidation

Oxidation of methane released from sediments at depths of a few hundred metres presents another oxygen sink that may increase when bottom waters warm and thereby destabilize some of the methane hydrates, leading to outgassing of methane from the sea floor, of which most is expected to be oxidized in the water column to CO_2 (Kessler et al., 2011; Mau et al., 2017). Methane hydrate destabilization is expected to begin this century (Biaostoch et al., 2011), but there is no observational evidence for warming having caused, until now, enhanced outgassing of methane from the sea floor (Mau et al., 2017). It is therefore unlikely that enhanced methane release from the sea floor and subsequent oxidation has significantly contributed

to the ocean deoxygenation observed until now. Assuming sustained future warming in 2 x CO_2 and 4 x CO_2 scenarios, however, model simulations predict that warming-induced release of methane and its subsequent oxidation in the water column may lead to substantial oxygen losses, that can amount to 10–30% of solubility driven oxygen losses (see above) on millennial timescales (Yamamoto et al., 2014).

3.1.5 Effects of stratification and circulation changes

As well as the direct effects of warming on marine oxygen sources and sinks, there are indirect effects of warming via changes in transport brought about by changes in ocean stratification and circulation. Climate model simulations show a close correlation between declining oxygen levels and increasing water ages on isopycnal surfaces in the thermocline (Long et al., 2016). Because of the scarcity of abiotic transient tracer observations required to derive water mass ages, this inference is, until now, only based on model simulations. It does, however, suggest that reduced ventilation – point (iii) above – is a dominant driver of upper-ocean deoxygenation. A quantitative and mechanistic understanding of the individual processes is still lacking and attribution to different forcing agents such as anthropogenic warming, internal climate variability or a combination of both (i.e. changing internal variability in a warming world) remains challenging (Andrews et al., 2013).

Ocean ventilation can change as a result of buoyancy forcing in the form of changes in heat and water cycles, and as a result of changes in wind patterns. Changes occur on a multitude of space and time scales and may be linked to anthropogenic climate change and/or natural variability of the climate system, e.g. related to the Pacific Decadal Oscillation (PDO), El Niño–Southern Oscillation (ENSO), North Atlantic Oscillation (NAO) or Atlantic Multidecadal Oscillation (AMO). Up to now, results of numerical models do not generally agree well with observed patterns of oxygen change in the upper ocean (Oschlies et al., 2017), suggesting systematic deficiencies in current models and, presumably, our understanding. The following is an attempt to review what is known about the contribution of individual ventilation mechanisms to ocean deoxygenation.

As the ocean warms from above, stratification tends to increase. At high latitudes, particularly in the northern



Figure 3.1.3 Warming induced glacial melt © Dan Laffoley.

hemisphere, stratification increases also as a result of enhanced freshwater discharge due to warming-induced glacial melting (Figure 3.1.3). Overall, a stronger stratification suppresses downward transport of oxygen-saturated surface waters and upward transport of oxygen-deficient deeper waters to the sea surface. This leads to a net reduction in the air-sea flux of oxygen (Figure 3.1.4) and the transport of newly ventilated oxygen-rich waters into the ocean interior. This is, however, partly compensated by reduced upward transport of nutrients and an associated decline in biological production and the export of organic matter from the productive surface zone to depth (Bopp et al., 2013) and its subsequent remineralization in the ocean interior. Because respiratory oxygen demand depends on the stoichiometric composition of organic matter, as yet uncertain effects of elevated CO_2 concentrations on carbon-to-nutrient ratios in the exported organic matter may have considerable effects on oxygen consumption (Oschlies et al., 2008). As such stoichiometric effects would be related to elevated CO_2 and not to climate change per se, they will not be considered further here.

Besides increasing upper-ocean stratification, surface warming has also been linked to a poleward migration

of isopycnal outcrops (Durack & Wijffels, 2010), which tends to increase the pathways and transit times of waters in the ventilated thermocline. With buoyancy fluxes setting the transformation of water masses in the surface mixed layer, the circulation in the ocean's thermocline is predominantly wind-driven (Luyten et al., 1983). Of prime importance for the ventilation of the thermocline are changes in wind patterns. These are often related to modes of natural climate variability (e.g. PDO, ENSO, NAO, AMO) and the separation from wind changes due to global warming is challenging against the large internal variability of the climate system. A warming-related strengthening has been reported for the Pacific trade winds since the early 1990s (England et al., 2014) and the Southern Ocean westerlies since the 1960s (Marshall, 2003; Thompson & Solomon, 2002).

Regarding the recent strengthening of the Pacific trade winds, Ridder and England (2014) inferred from a model study that the oceanic oxygen content decreases with increasing tropical winds, as a result of enhanced upwelling, enhanced biological production, and enhanced respiration. This interpretation focuses on wind-driven changes in oxygen consumption, in line with a regional study of the subtropical North Pacific

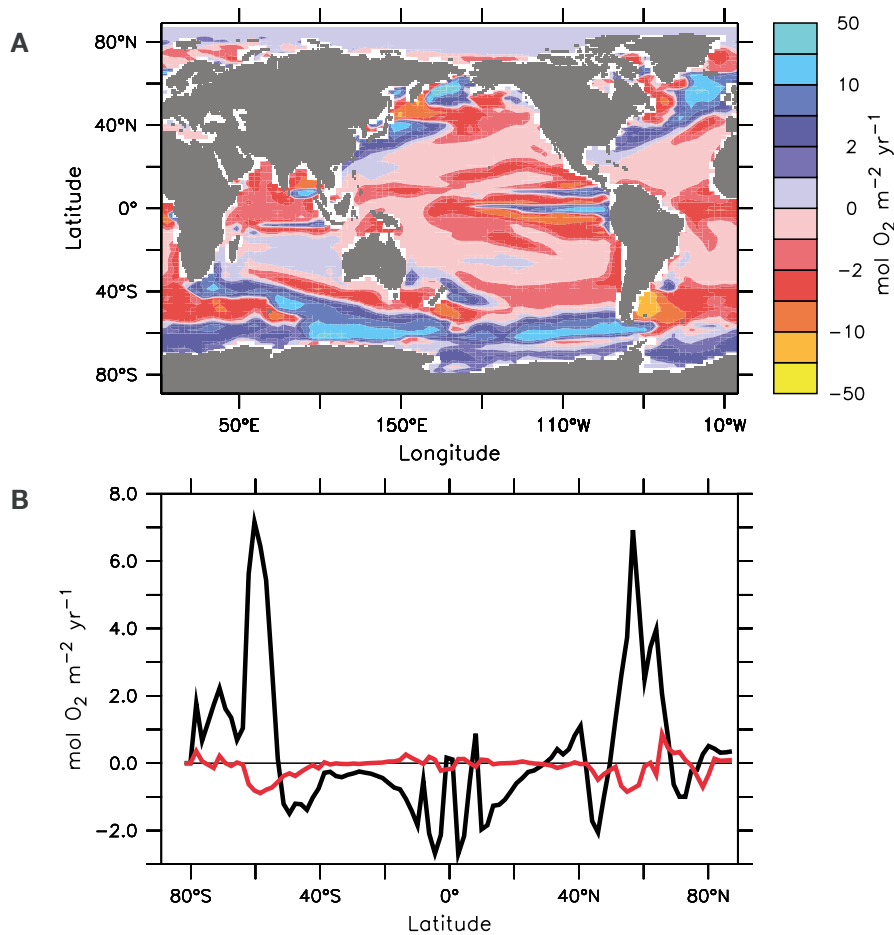


Figure 3.1.4 (A) Annual-mean air-sea oxygen fluxes averaged over the 50-year period 1960–2010 as simulated by the UVic model (reference simulation of Oschlies et al. (2017) using climatological wind forcing). (B) The same air-sea oxygen flux shown in zonally averaged form (black) together with the zonally averaged simulated linear trend in the air-sea oxygen flux integrated over the period 1960–2010 (red).

by Deutsch et al. (2014). Based on observations of sedimentary nitrogen isotopes and a biogeochemical ocean model forced with atmospheric reanalysis fields, they concluded that the volume of low-oxygen waters in the eastern subtropical North Pacific contracted during much of the 20th century and only expanded after about 1990 under strengthening trade winds (with no net change over the past 150 years). In their analysis, the volume of low-oxygen waters was inversely correlated with the depth of the thermocline, with greater depths and smaller low-oxygen volume during warm phases under more sluggish trade winds, and with shallower depths and larger low-oxygen volume during colder phases under stronger trade winds. This interpretation, based solely on changes in oxygen demand, has been challenged by a model study of Duteil et al. (2014) who stressed the importance of changes in the oxygen supply. Besides intensifying upwelling, biological production and respiratory oxygen consumption, stronger trade winds also lead to an intensified wind-driven shallow overturning circulation

and enhanced supply of waters that are relatively rich in oxygen to the tropical thermocline. Changes in wind-driven tropical ocean oxygen supply and demand thus tend to counteract. Yang et al. (2017) demonstrated in their model analysis that impacts of changes in local respiration and oxygen supply via mixing and ventilation tend to have opposing effects on oxygen levels in the eastern tropical Pacific thermocline and also on shorter variations associated with El Niño events.

Regarding the recent and possible future enhancement of Southern Ocean westerlies, a model study by Getzlaff et al. (2016) identified an enhanced ventilation of the thermocline with oxygen-rich southern hemispheric mode waters, leading to a small increase in the global ocean's oxygen content that counteracts up to 10% of the overall warming-induced deoxygenation. The same study also revealed that the observed poleward displacement of the southern hemispheric wind system leads to longer ventilation pathways and regionally lower

oxygen concentrations in the waters arriving from higher southern latitudes in the tropical ocean's thermocline.

According to climate models, enhanced freshwater discharge into the polar oceans results in reduction in the deep ocean overturning circulation (Stouffer et al., 2006). Recent observations indicate some decline of the Atlantic meridional overturning circulation against a background of large intra- and inter-annual variability (Srokosz & Bryden, 2015). The meridional overturning circulation associated with the formation of Antarctic Bottom Water is globally of similar strength compared to the overturning circulation of North Atlantic Deep Water. During recent decades a general warming of these bottom water masses spreading northward into the Pacific, Atlantic and Indian Oceans together with a general reduction in overturning strength has been observed (Johnson et al., 2008; Purkey & Johnson, 2010). This is mirrored by an oxygen decrease by more than $0.012 \text{ Pmol yr}^{-1}$ in the Southern Ocean below 1200 m, i.e. more than 10% of the global ocean oxygen loss (Schmidtko et al., 2017). As deduced from a modelling study by Matear et al. (2000), oxygen changes in the Southern Ocean are predominantly caused by circulation changes, with changes in export production and respiration playing only a minor role. Interestingly, the deoxygenation signal is not apparent in an analysis of oxygen concentrations of retreating Antarctic Bottom Water (Andrie et al., 2003; van Wijk & Rintoul, 2014), limiting the decrease to the deep-water masses above the newly formed bottom water. Both, the replacement of well oxygenated bottom waters by older water masses as well as the accumulating oxygen consumption in these ageing water masses lead to the oxygen decrease observed in the deep waters. According to Schmidtko et al. (2017) almost three quarters of the total oceanic oxygen loss occur in waters deeper than 1200m. With negligible solubility effects at these depths and little direct observational evidence for biological effects, these deep-ocean oxygen changes appear essentially driven by changes in the overturning circulation (Table 3.1.2).

3.1.6 Conclusions

Recent observational estimates indicate that the marine oxygen inventory has decreased by about 2% over the past 50 years, with three quarters of the oxygen loss appearing to be located at depths below 1200 m (Schmidtko et al., 2017). Warming is considered to be a major driver, although direct solubility effects

explain only about 15% of the total changes (50% in the upper 1000 m, Helm et al., 2011; Schmidtko et al., 2017). The remaining part is thought to result from indirect warming effects on stratification and circulation, possibly respiration, changes in marine biology and biogeochemical feedbacks. It is noteworthy that current state-of-the-art models simulate an ocean-wide oxygen decline of only about one third of the observed rate (Table 3.1.1). Agreement is better in the upper ocean with models reaching, on average, 70% of the observed oxygen decline at 300 m depth even though the spatial patterns of oxygen change are not reproduced well (Oschlies et al., 2017). Models also tend to underestimate the interannual to decadal variability of oxygen concentrations at subtropical time-series sites in the Pacific and Atlantic (Long et al., 2016) and of air-sea fluxes inferred from time-series observations in the equatorial Pacific (Edebbbar et al., 2017).

The systematic underestimation of temporal variability and trends in marine oxygen levels by current models is a strong indication of gaps in our understanding of the mechanisms of marine deoxygenation. There may be systematic deficiencies in the models, e.g. too coarse resolution and too diffusive physics, or unaccounted variations in respiratory oxygen demand. Additionally, amplifying feedback processes may not be properly accounted for. These include biogeochemical feedbacks via the release of nutrients, in particular phosphate and iron, from sediments turning anoxic (Niemeyer et al., 2017). Other, impacts not directly related to climate change, such as eutrophication by atmospheric pollutants (Ito et al., 2016), possible stoichiometric effects of elevated CO_2 , or even impacts of industrial fisheries (Getzlaff & Oschlies, 2017) may contribute to ocean deoxygenation. According to current models, we can, until now, attribute at least one third of the observed oxygen loss of about $0.096 \text{ Pmol yr}^{-1}$ to anthropogenic climate change but cannot rule out that climate change explains essentially all of the observed oxygen loss.

3.1.7 References

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3.2 Ocean deoxygenation from eutrophication (human nutrient inputs)

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Summary

- Coastal deoxygenation is driven by excess human inputs of nitrogen and phosphorus that increase the production of carbon and its accumulation in the ecosystem.
- Respiration of the excess carbon by bacteria results in oxygen deficient waters in stratified systems.
- Deoxygenation reduces suitable habitats for many bottom-associated marine organisms and disrupts biogeochemical cycles.
- Climate-driven increases in water temperature and increases in watershed precipitation will likely aggravate estuarine and coastal ocean deoxygenation.
- Mitigation measures require social and political will but can be effective.

Eutrophication-driven low oxygen	Potential consequences
Post-industrial expansion in the 1850s, human alterations to watersheds, and increasing use of artificial fertilizers in the 1950s to present have increased the amount of reactive nitrogen (Nr-N) in the ecosphere by three-fold.	<ul style="list-style-type: none"> Enhanced phytoplankton production in estuaries and coastal waters and accumulation of organic matter in the lower water column and sea bed. Excessive algal biomass, which may be noxious or harmful (toxin-production). Excess carbon reaches the lower water column and sea bed in the form of senescent algal cells, zooplankton faecal pellets, or aggregates.
Physical features of the water column confine the geographic extent of oxygen deficiency in coastal waters; increased nutrients support enriched phytoplankton.	<ul style="list-style-type: none"> Haline or thermal stratification, or both, dictate the presence of a pycnocline (strong density difference in the water column) across which dissolved oxygen diffusion is hindered. Increased water residence time enhances the probability of oxygen depletion occurring in a coastal area. There is an optimal depth at which oxygen deficiency may develop; shallower waters are usually well-mixed and deeper waters do not receive as much fluxed carbon. Physical barriers such as sills at depth, and advection of offshore waters affect the level of deoxygenation, positively or negatively.
Eutrophication-driven deoxygenation affects living resources and coastal ecosystems.	<ul style="list-style-type: none"> Low oxygen decreases suitable habitats for many bottom-dwelling marine organisms. Organisms that can swim away do, but the remaining immobile and burrowing fauna will eventually perish in low oxygen conditions for extended periods. Low oxygen water masses alter migrations, reduce food resources for resident fauna during and after low oxygen events, and affect growth and reproduction.
Reduction of nutrient loads will require social and political will and a reversal of human consumptive habits.	<ul style="list-style-type: none"> Improvements in nutrient management have lessened the negative effects of deoxygenation in multiple areas. Reduction in excess nitrogen requires less use of fossil fuels, implementation of best management practices for agriculture, improved wastewater treatment, and changes in food habits. Anticipated climate changes with warmer waters and increased precipitation will likely aggravate deoxygenation.

3.2.1 Introduction

Human activities alter landscapes and air and water quality in the process of providing food, fuel and fibre to a burgeoning human population. Reactive forms of nitrogen (Nr-N) generated by fossil fuel burning (post 1850s) and industrial production of fertilizers (post 1950s), as opposed to inert N₂ gas generated naturally through lightning and biological nitrogen fixation, enter the environment three times more now than historically (Galloway et al., 2008, 2014; Gruber & Galloway, 2008; Reed & Harrison, 2016; Seitzinger et al., 2010). Mining for phosphorus, since the middle of the 17th century, for use primarily as fertilizer, has resulted in an approximate tripling of the quantities stored in terrestrial and aquatic ecosystems, with a similar three-fold increase in the

flux to the coastal ocean (Bennett et al., 2001). These life-supporting, but in excess, nutrients find their way to estuarine and coastal waters where they support high and often massive production of phytoplankton cascading at times to deoxygenation of the receiving waters. The process of excessive production of carbon, in this case phytoplankton, is known as eutrophication, and usually results from high nutrients loads into aquatic ecosystems. Symptoms of eutrophication in aquatic ecosystems are noxious, and often toxic, harmful algal blooms and the reduction of dissolved oxygen concentrations, i.e. deoxygenation.

The post-industrial revolution increase in the use of fossil fuels, beginning in the 1860s, rose gradually over the next 100 years consistent with population growth

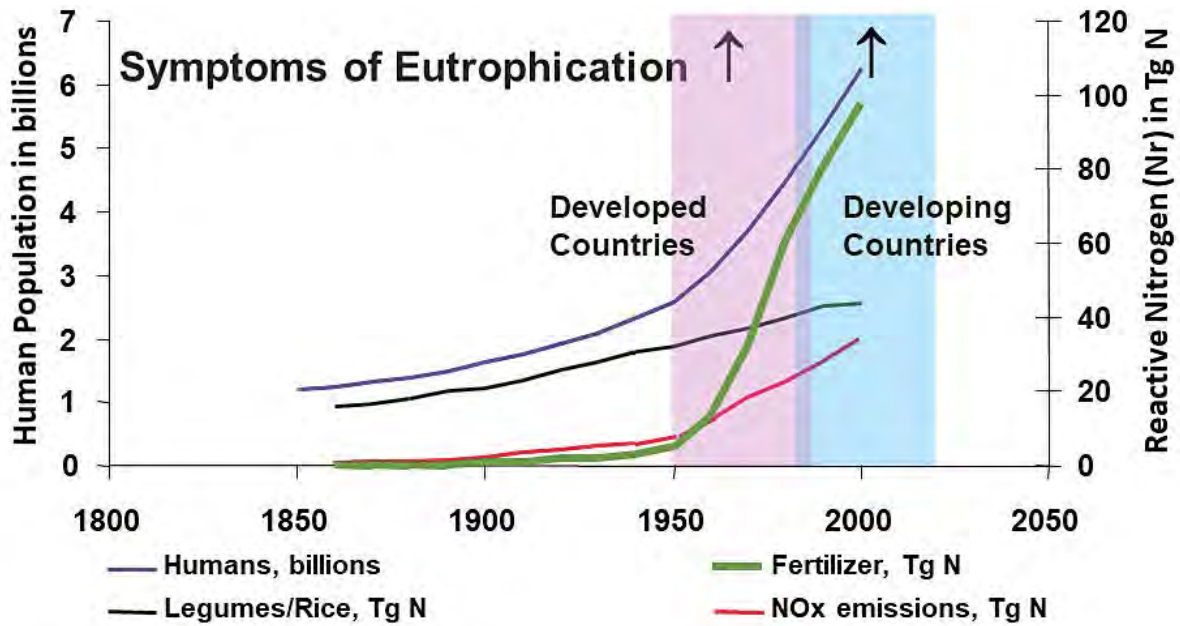


Figure 3.2.1 Period in which the symptoms of eutrophication and hypoxia/anoxia began in developed countries and how the onset of symptoms has shifted in more recent years to developing countries (Rabalais et al. (2014), modified from Galloway and Cowling (2002) and Boesch (2002)).

up to the 1950s (Galloway et al., 2014) (Figure 3.2.1). From then to the 1980s, Nr-N increased linearly by 2.5-fold as fossil fuel use continued to rise with population growth but also as Haber-Boesch production of fertilizer increased along with its increasingly inefficient use in agriculture. Nr-N production has stabilized since the 1980s to ~2010 from off-setting activities, such as reduced NO_x emissions coupled with increased fertilizer use for corn production to support ethanol production and animal production. Along with numerous greenhouse gases that contribute to climate change, nitrous oxides (NO_x) from the burning of fossil fuels are emitted to the atmosphere and return to the landscape in wet and dry deposition. Planting of legumes, such as alfalfa and soybeans, which naturally fix N₂ in root nodules, also increased gradually since the 1860s, as fodder for animals and rotation with other crops, and contribute to excess Nr-N. However, these crops are also fertilized at times. Nitrogen in fertilizers and animal manure is easily turned into gaseous ammonium and returns from the atmosphere to the watershed via precipitation as another reactive N form. As more and more people need food, agricultural expansion continues, and agribusiness and high fertilizer use become part of a global change in landscapes. Other large-scale landscape changes marginalize the ability of natural ecosystems to convert Nr to inert N₂ gas. These include deforestation, loss of wetlands, drainage of croplands via ditches and subsurface tile drains, impervious surfaces, and changes in hydrology, such as

leveeing of rivers that would otherwise allow for natural removal of nitrogen within a flood plain.

The symptoms of eutrophication, including harmful algal blooms and oxygen-deficient bottom-waters, began to occur in parallel with increasing nitrogen loads from the 1950s to 1980s in heavily industrialized watersheds and where artificial fertilizer use steadily increased. These shifts and relationships are consistent in sediment biological and geochemical palaeo-indicators (see Chapter 5). The cohesive temporal patterns of eutrophication and oxygen deficiency are clearer where the number of proxies is higher (Gooday et al., 2009). In regions around the globe where the increase in riverine nutrients was not observed prior to the 1980s (e.g. the lower Changjiang at Datong station; Li & Daler, 2004), nitrate-N rose dramatically up to 2000, when records stopped. Small areas of low oxygen bottom-water (< 1000 km²) were mapped off the Changjiang in the East China Sea in 1988 and 1998. Since then, the presence of large areas of bottom-water oxygen depletion (> 10,000 km²) was first documented in 1999 and again in three additional years through to 2013 (compiled by Zhu et al., 2017) The various areas of bottom-water low oxygen surveyed in the East China Sea did not have similar station grids, nor were the defined levels of “low” dissolved oxygen concentrations the same. Regardless, the timing of increasing river nitrogen levels and occurrence of low oxygen conditions followed the time pattern suggested in Figure 3.2.1 for “developing” nations.

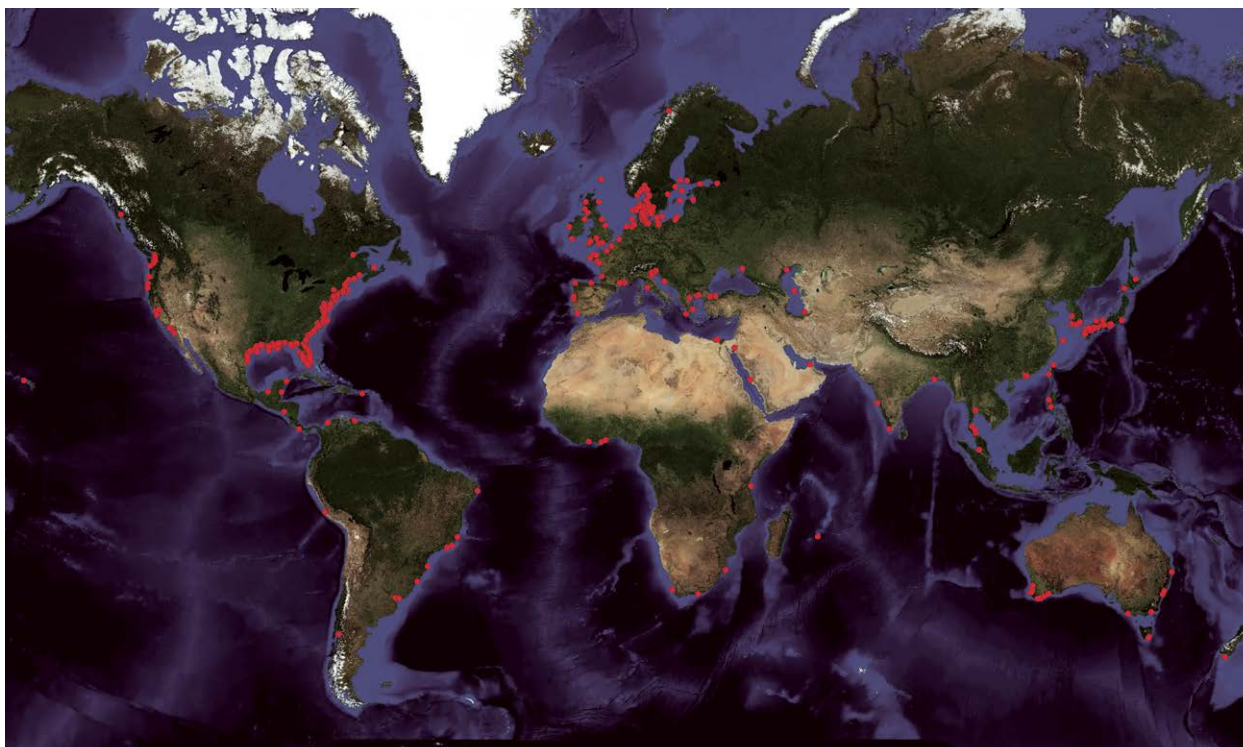


Figure 3.2.2 Distribution of human-caused areas of coastal deoxygenation. A dot represents the first time an area was identified in the scientific literature (as compiled by Diaz and Rosenberg (2008) with some updates). The size of the dot does not correspond to the area or volume of deoxygenated waters. Plotted with data from the World Resources Institute in 2016 (<http://www.wri.org/resource/interactive-map-eutrophication-hypoxia>; accessed November 2017).

The number of human-caused coastal ocean areas of deoxygenation has risen significantly since the 1960s (Diaz & Rosenberg, 2008) (Figure 3.2.2) with an approximate doubling of the number of areas every decade since the 1960s through 2007. Multiple coastal areas in the Baltic Sea were identified more recently from hydrographic data records (Conley et al., 2011). The number of deoxygenated waters in coastal areas is considered to be about 500 (Breitburg et al., 2018; Diaz & Rosenberg, 2008) but reflects different methodologies and approaches to “counting,” grouping or not grouping closely related areas, quality of data, and institutional capacities to conduct the necessary research. For example, Altieri et al. (2017) compiled data on deoxygenation from tropical regions, where the number of low oxygen areas per capita of coastline was much lower than in temperate regions where institutional research capacity is much greater. Furthermore, they concluded that coral reefs are associated with half of the known coastal tropical deoxygenated waters with over 10% of all coral reefs at elevated risk for deoxygenation based on local and global risk factors. There are, however, areas that are no longer oxygen deficient due to management scenarios to reduce excess nutrients (see 3.2.7).

3.2.2. Process of coastal deoxygenation

The physical, chemical and biological processes that lead to deoxygenation differ in magnitude and importance by water body, but there is one basic response (Figure 3.2.3). Deoxygenation occurs when the amount of dissolved oxygen in the water column is decreased by the process of respiration at a faster rate than resupply. Resupply could be through air-sea exchange, photosynthetic production of oxygen, advection of oxygenated waters, or by diffusion of dissolved oxygen across a density barrier. The density barrier, or pycnocline, forms horizontally between two water masses that differ in temperature, salinity or both. The density difference prevents the diffusion of oxygen from a higher concentration layer to a lower concentration layer. In some areas, upwelled waters provide nutrients for the stimulation of primary production, especially Eastern Boundary layers, or bring oxygen-deficient waters from depth onto the continental shelf. These are not features of the Gulf of Mexico shelf adjacent to the Mississippi River, which forms the basis of the Figure 3.2.4.

The carbon source that fuels the respiratory reduction of oxygen most often originates from settled phytoplankton

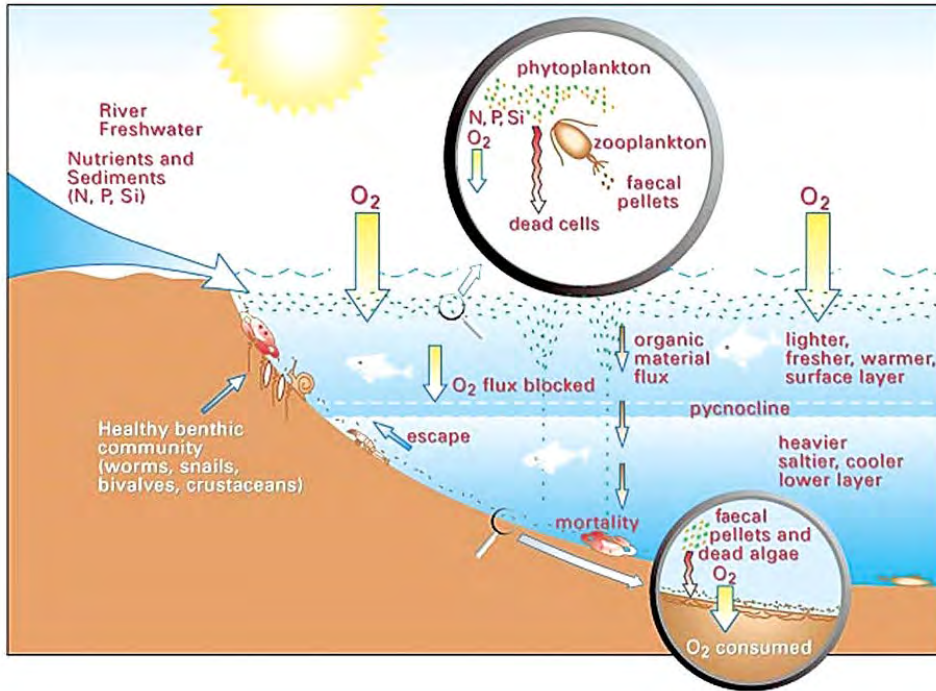


Figure 3.2.3 Biological, chemical and physical processes of eutrophication-driven coastal deoxygenation (modified from Downing et al., 1999).

production in the form of senescent phytoplankton cells, zooplankton faecal pellets, or marine aggregates. The organic matter sinks below the pycnocline to the lower water column or to the sea bed. Aerobic bacteria that utilize the carbon source consume oxygen in the process and deplete the dissolved oxygen in the water column below a strong density gradient. The byproduct,

carbon dioxide, is generated and accumulates in the lower water column, leading to acidification.

The responses of marine organisms range from mortality to shifts in behavioural and reproductive ecology. Organisms that are motile will try to emigrate from the area; others living within the sediments move closer to

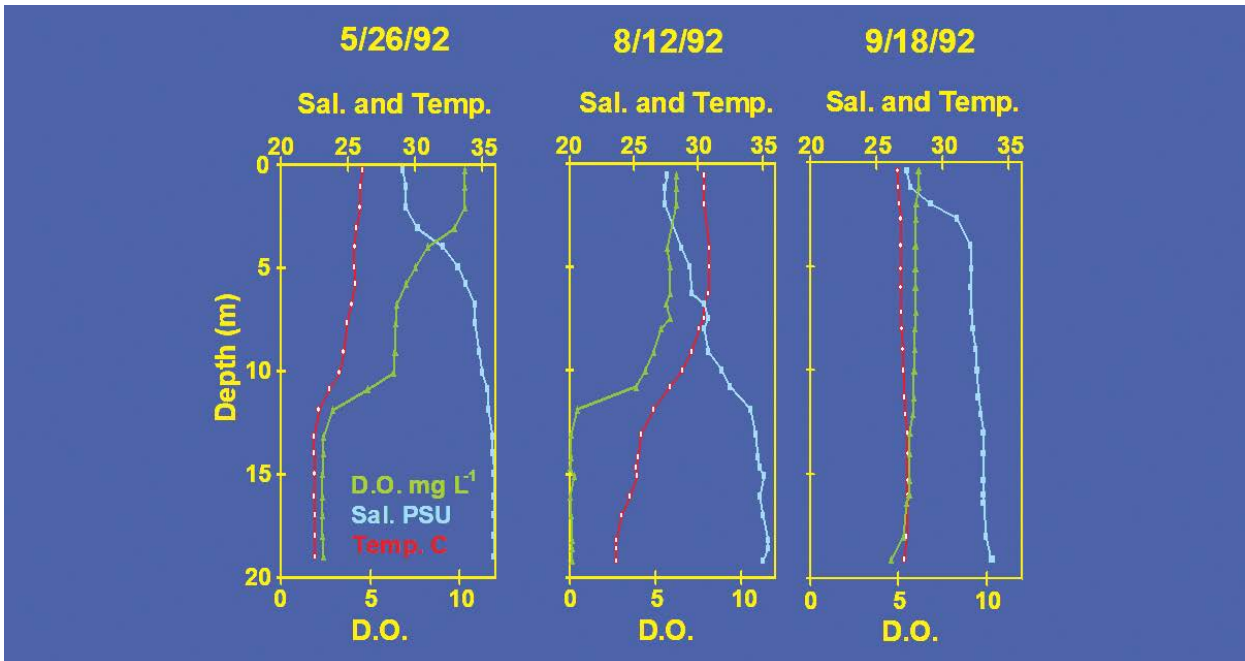


Figure 3.2.4 Development of thermal and haline stratification in spring and summer and mostly destratified water column in autumn, northern Gulf of Mexico continental shelf west of the Mississippi River. Source: N.N. Rabalais.

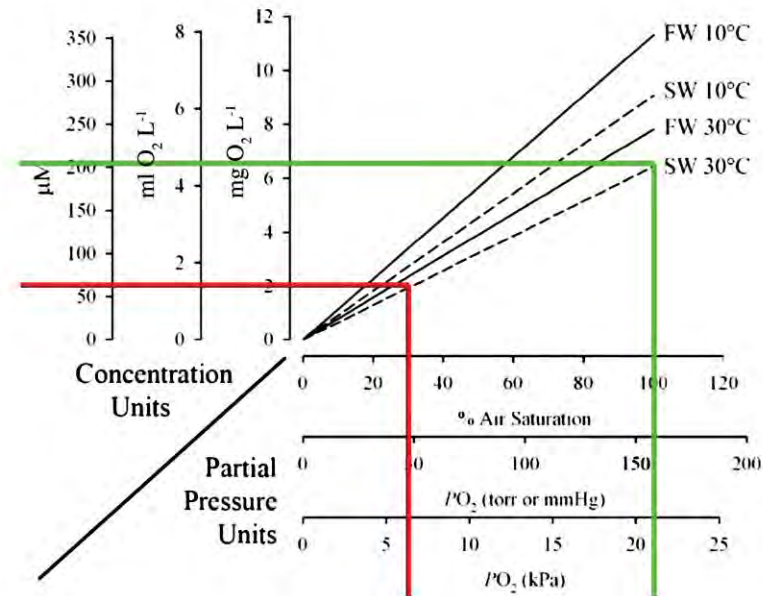


Figure 3.2.5 Nomogram for dissolved oxygen in fresh water (FW) and sea water (SW) at 10 °C and 30 °C (Rabalais et al. (2010), modified from Diaz and Breitburg (2009)). Concentration units are on the Y-axis, and partial pressure units are on the X-axis. Red line is the common definition of “hypoxia” at 2 mg O₂ L⁻¹ dissolved oxygen, or approximately 30% saturation. Green line is 100% saturation in sea water (salinity of 35) at 30 °C.

the sediment-water interface but will eventually die if the dissolved oxygen concentration remains low for long enough. Migration is altered, suitable habitat is reduced, and fish and shellfish landings may be reduced.

3.2.3 Dissolved oxygen levels

There is no agreed definition of what concentration or saturation level equates to deoxygenation. It is the process of loss of dissolved oxygen in a water body over time, in this case through eutrophication-induced oxygen deficiency (Cloern, 2001; Diaz & Rosenberg, 2008; Rabalais et al., 2010). The ability to document change over time is difficult due to a lack of suitable long-term data (Gilbert et al., 2010). Yet, Gilbert et al. (2010) found considerable evidence of decreasing levels in dissolved oxygen concentrations for many areas of the coastal ocean and the open ocean, with the rate of decline an order of magnitude greater in the coastal ocean (within 30 km of the coast) versus the open ocean (> 100 km from the coast).

The solubility of oxygen in coastal waters is determined by a combination of salinity and temperature. Dissolved oxygen saturation decreases with increasing salinity at similar temperatures, and decreases with increasing temperature at similar salinities (Figure 3.2.5). Warming oceans and coastal waters with climate change are expected.

“Hypoxia” is a commonly used term for waters with less than 2 mg O₂ L⁻¹ of dissolved oxygen (equivalent to 1.4 ml L⁻¹, 63 μM, or approximately 30% oxygen saturation). This is the dissolved oxygen concentration where demonstrable behaviour by marine life, such as escape of bottom-dwelling fish and mobile invertebrates out of the area (Figure 3.2.6) or mortality of sedentary crabs, molluscs and worms, occurs. Others, including regulatory agencies, identify a range of physiological or behavioural changes along a continuum of oxygen concentrations (Vaquer-Sunyer & Duarte, 2008).



Figure 3.2.6 Brittlestars and gastropods, normally hidden in cryptic spaces on a coral reef, attempting to flee low-oxygen conditions during a hypoxia event that affected coral reefs on the Caribbean coast of Panama in 2017. Hypoxia resulted in the mass mortality of brittlestars, gastropods, and other motile invertebrates. © Dr Maggie D. Johnson.



Figure 3.2.7 Wilson Inlet, Australia © dpa picture alliance / Alamy stock photo.

3.2.4 Geography

The main features of a coastal area that becomes deoxygenated are: (1) high biological production from over-enrichment by high nitrogen and phosphorus loads; (2) a stratified water column from salinity, temperature or both, mostly in water depths < 100 m; and (3) long water residence time. Longer water residence time allows for development of phytoplankton blooms, containment of fluxed organic matter and the development of stratification.

3.2.4.1 Estuaries

Estuaries vary in physiography, but those most conducive to the formation of hypoxia are characterized by longer water residence times that allow for accumulation of carbon and respiratory depletion of oxygen. Stratification is also a key factor for the development and maintenance of deoxygenation, e.g. Chesapeake Bay, USA (Kemp et al., 2005) and Wilson Inlet, Australia (Brearley, 2005) (Figure 3.2.7).

Deoxygenation is mostly periodic (annually in summer) or, to a lesser extent, episodic (tidal influence) (Rabalais et al., 1994). Seiching of the deoxygenated waters of central Chesapeake Bay from winds forces the water mass into shallow coastal waters for temporary exposure to deoxygenated water (Breitburg, 1992) (Figure 3.2.8). Similar wind-driven deoxygenated water

mass movements occur in Mobile Bay, USA (Schroeder & Wiseman, 1988). Data from two oxygen meters deployed 1 m above the bottom in 20 m water depth within the large area of deoxygenated waters 77 km apart on the Louisiana shelf adjacent to the Mississippi River illustrated: (1) a continuous bottom-water dissolved oxygen concentration at the more western station that was severely oxygen-deficient and often anoxic from mid-June to mid-August, and (2) nearer the Mississippi River delta (Figure 3.2.9), a diurnal signal of values often less than 0.1 mg L^{-1} or as high as $3\text{--}4 \text{ mg L}^{-1}$ (Rabalais et al., 1994). In the case of the former, a temporary increase in dissolved oxygen concentration was caused by advection of deeper more oxygenated water into the deoxygenated water mass (Rabalais et al., 1994).

Stratification, thermally-controlled in the case of Jinhae Bay, South Korea where freshwater input is insignificant (Lee et al., 2017), defines the period of initial deoxygenation, the period of maximal deoxygenation and the increase in bottom dissolved oxygen as it breaks down. Salinity-driven stratification is also involved in many cases. Stretching for 75 km, the uppermost reaches of the Pearl River are permanently deoxygenated (He et al., 2014). Whereas the lower reaches of the Pearl River estuary, while severely deoxygenated in summer, may be re-oxygenated from mixing by typhoons (Su et al., 2017). Similar processes disrupt stratification and re-oxygenate the water column in the low oxygen waters of the northern Gulf of Mexico (Rabalais et al., 2007a). In both instances, re-stratification followed by

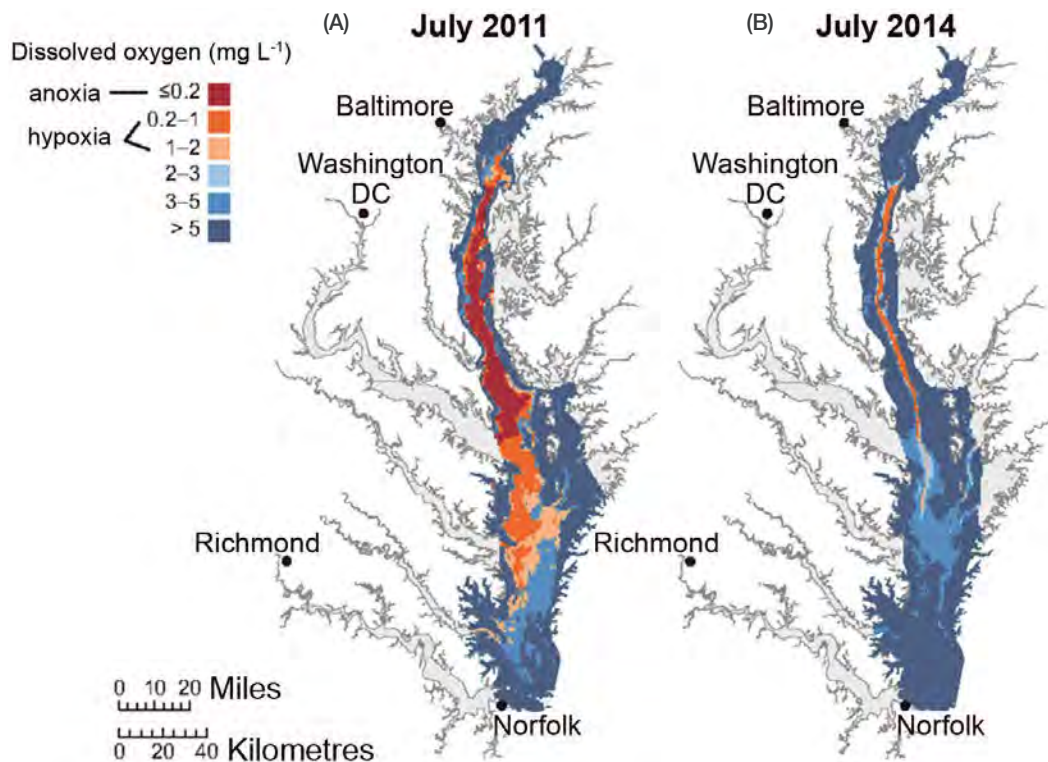


Figure 3.2.8 Distribution of bottom-water dissolved oxygen concentrations in Chesapeake Bay, USA, (A) a near-record high hypoxic volume, and (B) a near-record low hypoxic volume (from Testa et al., 2014).

rapid deoxygenation through respiration of organic matter occurs. The Pearl River estuary organic load is dominated by *in situ* marine phytoplankton biomass (autochthonous) (Su et al., 2017) similar to predominantly marine production in the northern Gulf of Mexico (Nelson et al., 1994; Rabalais et al., 2014; Turner & Rabalais, 1994). The marine source of excess organic matter is a feature of anthropogenic-driven deoxygenation forced by excess nutrient loads from human activities.

3.2.4.2 River-dominated ecosystems

Many river-dominated coastal ecosystems have a large freshwater discharge carrying high nutrient loads (Figure 3.2.10). Thermal warming in the summer strengthens salinity-driven pycnoclines. Examples, not inclusive, are: (1) the northern Gulf of Mexico continental shelf adjacent to the outflow of the Mississippi River (Rabalais et al., 2007a); (2) the northern Adriatic Sea that receives the effluent of the Po River (Justić et al., 1987); (3) Chesapeake Bay where the Susquehanna River provides most of the freshwater inflow (Murphy et al., 2011; Testa et al., 2017); (4) the north-western shelf of the Black Sea with inputs from the Danube, Dneiper and Dneister rivers (Mee et al., 2005, 2006; Zaitsev, 1992); and (5) the oxygen-deficient coastal area in the East China Sea receiving the increasingly nitrogen-laden waters of the

Changjiang (Yangtze River) and atmospheric deposition of Nr-N from a heavily populated region (Yan et al., 2010; Zhu et al., 2017). Deoxygenation is a recurring, seasonal feature of these areas, except for the shelf adjacent to the Danube River, which has seen a reversal of deoxygenation. Earlier reports of deoxygenation under the influence of the Changjiang (Chen et al., 2007) have increased in frequency (Zhang et al., 2010; Zhu et al., 2017).

Initial hydrographic data documenting deoxygenation on the Louisiana continental shelf were few in the 1970s, but systematic surveys beginning in 1985 began to document increasingly larger areas of bottom-water oxygen deficiency (Rabalais et al., 2002) and severity (Rabalais et al., 2007a). Deoxygenation developed on this shelf ca. 1950s and accelerated in severity in the 1970s (Rabalais et al., 2007b) consistent with the increase in nitrogen export from the Mississippi River. Palaeo-indicators (fossilized biological or geochemical indicators of environmental change) also indicate that low oxygen values similar to current conditions were not a feature of this shelf prior to the 1900s (Rabalais et al., 2007b, 2014). The palaeo-indicators are not useful for size of area, but the deoxygenated area on the Louisiana shelf is the second largest coastal region caused by human eutrophication in the coastal ocean,



Figure 3.2.9 Mississippi River Delta © Universal Images Group North America LLC / Alamy stock photo.

averaging 14,000 km² since 1985 and reaching 23,000 km² in 2017.

Much as in the north-western Black Sea, deoxygenation conditions have shifted in the Po River-influenced Adriatic Sea. Justić et al. (1987) documented a decline in the dissolved oxygen content in the northern Adriatic



Figure 3.2.10 Mississippi River plume as it enters the northern Gulf of Mexico. Visible is the high suspended sediment load. Not visible are the high loads of nitrogen and phosphorus that enhance phytoplankton production on the adjacent continental shelf. © N.N. Rabalais.

Sea since the early 1900s. Historical reconstruction of assemblages of the hypoxia-tolerant bivalve *Corbicula gibba* in the Gulf of Trieste (north-east corner of the Adriatic Sea) showed periods of high abundance and organic content versus rare occurrence with implications for eutrophication and deoxygenation dating back 500 years (Tomašových et al., 2017). Associated hypoxia-sensitive foraminifera have declined in abundance and low-oxygen tolerant forms increased since the 1900s indicating a more recent development of deoxygenation similar to the record in Justić et al. (1987). Deoxygenation in the upper portion of the Northern Adriatic Sea opposite Rovinj diminished in presence and geographic extent in the period 1972–2012 with reduced influence of the Istrian Coastal Counter Current (Djakovac et al., 2015). The frequency of events in the western area, which is under a direct influence of the Po River discharges, did not change significantly, although the intensity of deoxygenation events recently were lower than during the 1970s through the early 1990s (Djakovac et al., 2015). Thus, different processes of deoxygenation, geographic area, and methods of determining deoxygenation complicates its occurrence in this broad region.

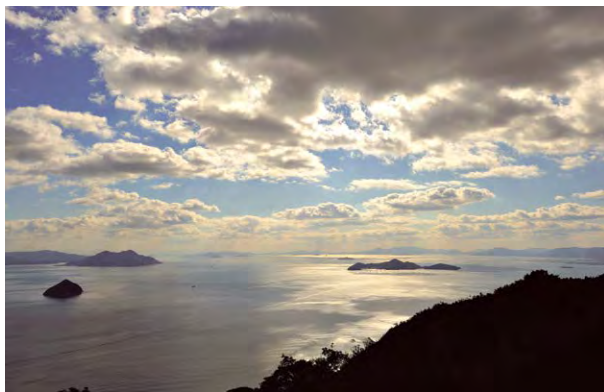


Figure 3.2.11 Seto Inland Sea from the summit of Mt Misen, Japan
© DGP_travel / Alamy stock photo.

3.2.4.3 Semi-enclosed seas

The semi-enclosed Baltic Sea is the largest eutrophication-driven area of deoxygenation in the world's coastal ocean, reaching an area of 25,000 to 60,000 km² in the period 1969–2008 (Conley et al., 2009). Deoxygenation has been a periodic feature of the Baltic Sea for the last 8000 years (Zillén et al., 2008) and is highly dependent on inflow events from the North Sea (Mohrholz, 2018) and high freshwater inflow leading to salinity stratification. Deoxygenation has been aggravated since the 1960s (Conley et al., 2009) by increased nutrient loads from the watershed (Savchuk et al., 2008). The Baltic Sea is composed of connected basins with different depths, but the general situation is for the formation of hypoxic and mostly anoxic conditions on a permanent basis other than during major inflow events. The water column from about 90 m to 130 m in the Eastern Gotland Basin is hypoxic and below 130 m to 250 m is anoxic (Conley et al., 2009).

The Seto Inland Sea (Figure 3.2.11) of Japan has a long history of harmful algal blooms, deoxygenation, and reversal of symptoms of eutrophication resulting from nutrient management (Honjo, 1993). Many of its sub-basins are deoxygenated in summer. There are some regions, including Osaka Bay, Harima-Nada, Hiuchi-Nada, Hiroshima Bay, Suo-Nada and Beppu Bay, where hypoxia occurs every summer (Kasai, 2014). In some sub-areas, e.g. Hiuchi-Nada, deoxygenation is governed more by hydrographic processes than oxygen consumption (Kasai et al., 2007). There remain areas exposed to higher loads of nutrients, especially near population centres.

The Bohai Sea is a semi-enclosed shallow coastal ecosystem on the Chinese mainland with a narrow

connection to the northern East China Sea. The area receives the effluent of the Huanghe and other rivers in an area of rapidly expanding economic developments and associated increases in population. During the past 20 years, increasing eutrophication has led to a high frequency of red tides in the Bohai Sea (Lin et al., 2008), but deoxygenation was not associated with the algal blooms (Zhai et al., 2012). An investigation of scallop aquaculture failure resulted in the documentation of localized deoxygenation in areas of stronger stratification (Zhai et al., 2012). A more recent study in the Bohai Sea (Zhao et al., 2017) clarified Bohai bathymetry and associated features of stratification; deoxygenation was restricted to bathymetrically depressed areas. This differs from the areas studied by Zhai et al. (2012) that were shallower and near sources of fresh water.

3.2.4.4 Fjords and deep waters

Fjords such as Saanich Inlet, British Columbia (Figure 3.2.12), are naturally susceptible to deoxygenation because water residence time is long, sills may prevent exchange with oceanic waters, and thermal stratification



Figure 3.2.12 Saanich Inlet looking towards Mt Baker, Washington State.
© Danita Delimont / Alamy stock photo.



Figure 3.2.13 Extremely low oxygen levels ($< 0.5 \text{ mg L}^{-1}$) near the bottom of a coral reef in Bahia Almirante, Panama killed (A) corals and crabs and (B) affected sponges where low oxygen conditions killed the bottom half of the sponges (Altieri et al., 2017). © Andrew Altieri.

may establish in warmer months (Matabos et al., 2012; Richards, 1965; Tunnicliffe, 1981). Fjords, however, may also be subject to excess nutrients and carbon from human sources, inducing hypoxia, for example Hood Canal in Puget Sound and Puget Sound proper (Brandenberger et al., 2011; Matabos et al., 2012; Parker-Stetter & Horne, 2008) and Himmerfjärden, Sweden (Bonaglia et al., 2014; Savage et al., 2002). The Himmerfjärden, on the other hand, has a long history of deoxygenation. Water sources to the fjord come from land run-off, outflow from Lake Mälaren from the north-west, and discharge from a sewage treatment plant (Bonaglia et al., 2014). The upper part of the estuary experiences regular summer deoxygenation, while the lower part is occasionally oxygen-deficient.

Many areas of Puget Sound experience regular mixing through tidal exchange processes that may reduce the effects of anthropogenic DIN loading, but some are less well mixed and are therefore vulnerable to eutrophication and deoxygenation (Puget Sound Institute, 2012-2015). There is some evidence that DO levels were generally higher in the mid-20th century than they are today (Puget Sound Science Review, 2016) with the latter correlated with increased anthropogenic activity. This conclusion was based on a comparison of historical water quality data to contemporary data (through 2009) (Puget Sound Institute, 2012-2015). The deep waters in the Lower St. Lawrence estuary are presently deoxygenated over a 1,300 km² area owing to a decreasing proportion of oxygen-rich Labrador Current Water in the water mass entering the Gulf of St. Lawrence (Claret et al., 2018; Gilbert et al., 2005). Additionally, the organic carbon content and the



accumulation rates of dinoflagellate cysts and benthic foraminifera have increased from the 1960s to 2000, and a shift in the stable carbon isotope signature of the organic carbon suggests enhanced accumulation of marine organic carbon (Thibodeau et al., 2006).

3.2.4.5 Tropical seas

Deoxygenation events in tropical seas are few compared to higher latitudes but are also less studied or reported (Altieri et al., 2017). Deoxygenation recorded in tropical regions often reflects mostly untreated sewage inputs and agricultural runoff (areas identified in Diaz & Rosenberg, 2008). Seasonal deoxygenation has been observed in the past decade in the Chetumal Bay between northern Belize and eastern Mexico and has affected the health of coral reefs in the area (Herrera et al., 2004). Several estuaries in tropical Brazil are without sufficient oxygen because of untreated sewage from large population centres and pose health hazards (Kozłowski-Suzuki & Bozelli, 2002; Marques et al., 2004; Somerfield et al., 2003; Valentin et al., 1999). Similar areas exist around the globe (République de Côte d'Ivoire, Ukwe et al., 2006; Manila Bay, Philippines, Jacinto et al., 2011; Sotto et al., 2014).

In the Morrocoy National Park, Caribbean coast of Venezuela, changing climate patterns and nutrient

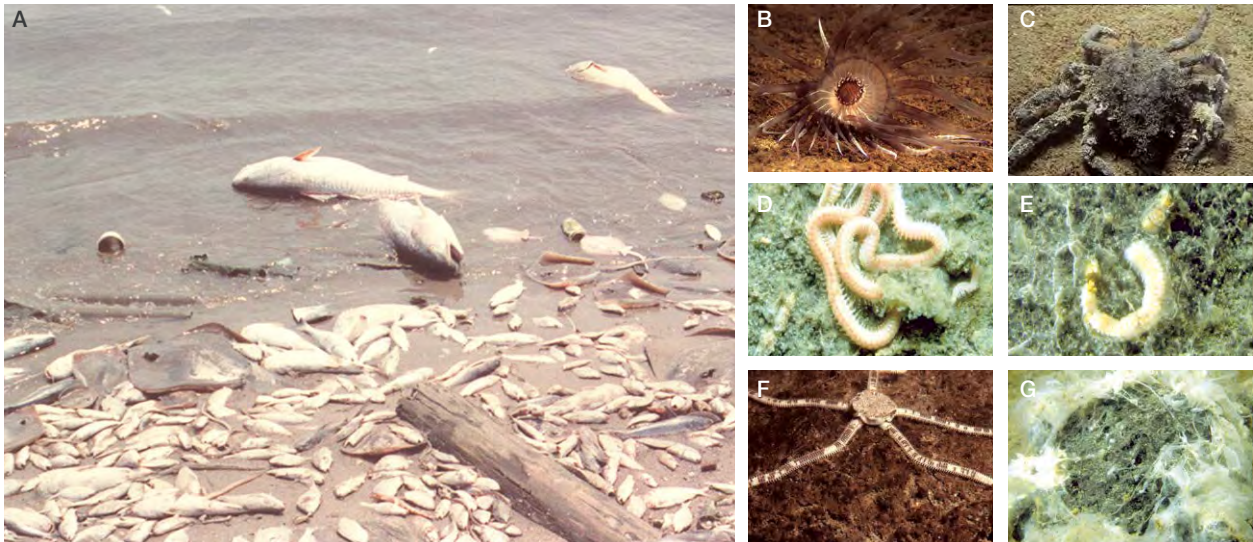


Figure 3.2.14 (A) Fish kill Grande Isle, LA, USA; (B) stressed cerianthid anemone; (C) dead spider crab; (D) stressed polychaete worm; (E) dead polychaete worm; (F) stressed brittlestar, otherwise usually burrowed; (G) anoxic sediments and sulphur oxidizing bacteria. © (A) Kery M. St. Pé; (B), (C), (E), (F), (G) Franklin Viola; (D) Donald E. Harper Jr.

overload has led to algal blooms. Eutrophication led to deoxygenation and contributed to the decline in coral cover, which has fallen from 43% to 5% (Isaza et al., 2006). A massive coral-mortality event caused by deoxygenation affected corals and other reef-associated organisms in Bahía Almirante in the Bocas del Toro region of Panama (Altieri et al., 2017) (Figure 3.2.13). In a well-oxygenated area only $3 \pm 2\%$ of corals were bleached, whereas $76 \pm 11\%$ of the corals were bleached in the severely deoxygenated area. The likelihood of coral reefs being exposed to deoxygenation in the future is high given the trends in resource use by developing countries, many in the tropics, which are copying those of the developed world (Figure 3.2.1).

3.2.5 Ecosystem consequences

Deoxygenation affects coastal ecosystems through a decrease in suitable habitats for many bottom-dwelling marine organisms (many examples in Rabalais & Turner, 2001), and, when severely low in dissolved oxygen, disrupts natural biogeochemical processes, leading in some cases to the generation of greenhouse gases.

The negative effects of coastal deoxygenation include loss of suitable essential habitat for many bottom-dwelling fish and benthic fauna, habitat compression for pelagic fish, direct mortality, increased predation, decreased food resources, altered trophic energy transfer, altered bioenergetics (physiological, development, growth, and reproductive abnormalities), and altered migration (Baird et al., 2004; Eby & Crowder, 2002; Levin et al., 2009; Rabalais & Turner, 2001; Wu, 2002; Wu et al.,

2003) (Figure 3.2.14). There are systematic exclusions of pelagic fish from low oxygen areas depending on their metabolic status and sensitivity to decreasing dissolved oxygen concentration.

Sedentary benthic organisms will try to escape, but are seldom capable of moving very far, and infauna will start to die off as the oxygen continues to decline (Rabalais et al., 2001a). Some benthic infauna are more tolerant to extremely low oxygen and will survive, but in low abundances and low biomass (Rabalais et al., 2001b). Sediment samples are seldom axenic in coastal waters, because some infaunal invertebrates have adaptations to low oxygen, and hydrogen sulphide exposure. The food availability for returning mobile species to previously defaunated sediments is negligible. Loss of biodiversity, abundance and biomass and shifts in benthic community composition are often the harbingers of eutrophication and deoxygenation in many coastal systems (Karlson et al., 2002), and likewise benthic communities are indicators of recovery (Karlsson et al., 2010). Many physiological responses result in altered behaviour or negative impacts (Vaquer-Sonnier & Duarte, 2008), such as reduced growth, loss of reproductive capacity, mortality, and loss of secondary production, including fisheries.

The nitrogen and phosphorus compounds delivered by rivers and streams are of multiple forms and different quantities. During increases in nitrogen and phosphorus from human activities, the ratios of nitrogen-to-phosphorus-to-silica shift and alter the composition of phytoplankton communities, the food

webs they support, and can shift trophic interactions (Turner et al., 1998). Silica is important for the growth of diatoms that are a primary phytoplankton at the base of aquatic food webs. The increased nutrient loads causing deoxygenation may also result in more noxious or harmful phytoplankton blooms, and shift trophic interactions (Davidson et al., 2014; Turner et al., 1998).

The respiration of increased organic matter gives rise to increased $p\text{CO}_2$ levels and lower pH in the bottom waters. The bottom water pH decreases, as dissolved oxygen decreases, and may be aggravated further due to the interaction between open ocean source water acidification and coastal waters (Cai et al., 2011). Lowered pH in coastal waters, in conjunction with weakening sea water buffering capacity and sea water saturation state with respect to aragonite (Cai et al., 2011), remains a serious concern for living resources, especially with regard to shellfish production.

3.2.6 Climate change

Rising air temperatures, as a consequence of human-caused increases in greenhouse gases, is directly correlated with warming ocean waters and deoxygenation in oceanic waters, owing to lower solubility of dissolved oxygen in warmer waters (Breitburg et al., 2018; Keeling et al., 2010). Similar declines in water solubility in warmer waters and other physical factors also apply to coastal areas along with other climate changes that may aggravate symptoms of eutrophication and subsequent deoxygenation in coastal waters (Altieri & Gedan, 2014; Meier et al., 2013; Rabalais et al., 2010, 2014) (Figure 3.2.15). Warming alone will also strengthen the pycnocline and diminish diffusion of surface water dissolved oxygen. Warming waters may change circulation patterns so that advection of deeper oxygen-poor waters move on to continental shelves (Chan et al., 2008; Grantham et al., 2004) or force more wind mixing and reoxygenation (Rabalais et al., 2007a).

Increased precipitation with higher air temperature will result in more water, sediments and nutrients reaching the coastal zone where they are likely to enhance eutrophication through nutrient-enhanced primary production, increased stratification, or both (Baron et al., 2013; Cloern, 2001; Rabalais, 2004; Sinha et al., 2017). Sinha et al. (2017) predicted that eutrophication will worsen in the north-eastern United States and in its mid-west 'Corn Belt,' along with areas

of India, China and south-eastern Asia. There will be, of course, other geographic areas with less precipitation. Excessive reactive nitrogen entering watersheds can be expected to rise with accelerating human population levels, continued reliance on fossil fuels, expanded agriculture and animal husbandry, and increasingly higher application of fertilizers (Reed & Harrison, 2016; Seitzinger et al., 2010) (Figure 3.2.1).

3.2.7 Management of human-caused deoxygenation

The forms of nitrogen and phosphorus, their loads, and their ratios in nutrient-laden waters reaching the coast affect phytoplankton productivity. If a nutrient is limiting to the growth of phytoplankton, increased loads will support increased phytoplankton growth. Most marine waters are considered nitrogen-limited for growth of phytoplankton, and fresh waters are considered to be phosphorus limited. There are multiple examples, however, of this not being the case (Paerl, 2009; Ren et al., 2009; Turner & Rabalais, 2013). For example, Turner and Rabalais (2013) performed a series of nutrient limitation bioassays over a range of distances from the Mississippi and Atchafalaya rivers, and measured light conditions, salinity and water depth for a 30-year period in the area of deoxygenation on the Louisiana shelf. They found that the number of N-limited bioassays was five times greater than the P-limited bioassays. NP synergism occurred where salinity was > 20 and represented 59% of all samples that were not light-limited. The interaction of N and P co-limitation was frequently synergistically additive. The dissolved inorganic nitrogen:phosphate ratio and various concentrations of DIN and inorganic phosphate (Pi) did not offer reliable chemical boundaries describing likely areas of exclusive N or P limitation in these bioassays. Because of these more recent studies, dual control of nitrogen and phosphorus is recommended for eutrophied coastal waters experiencing deoxygenation (EPA Science Advisory Board, 2008; Paerl et al., 2004, 2016).

The ability to develop nutrient management scenarios for nitrogen and phosphorus depends on a knowledge of the sources and amount of nitrogen and phosphorus coming from the watershed. For example, Alexander et al. (2008) used the SPARROW water-quality model that indicated that agricultural sources in the Mississippi River watershed contribute more than 70% of the delivered N and P. Corn and soybean cultivation is the

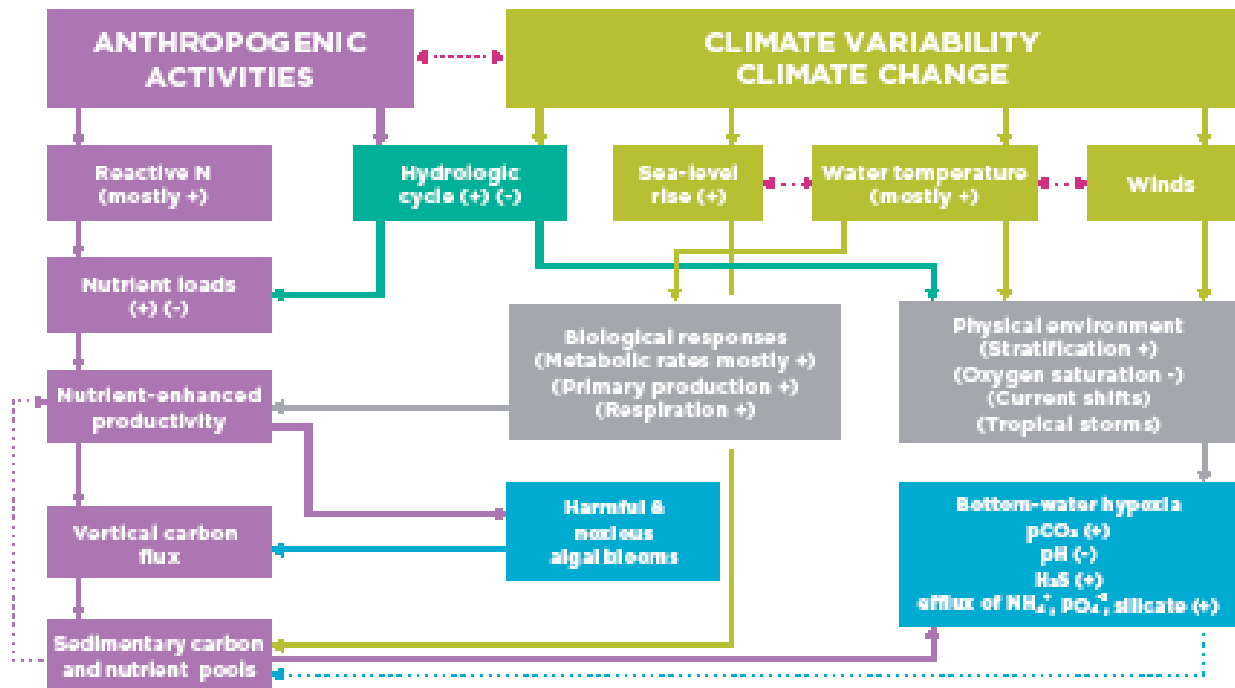


Figure 3.2.15 Conceptual diagram of the impacts of human and climate interactions on nutrient-enhanced productivity, harmful and noxious algal blooms, and hypoxia formation (Rabalais et al. (2014), modified from Rabalais et al. (2010)). Positive (+) interactions designate a worsening of conditions related to algal blooms and hypoxia, and negative (-) interactions designate fewer algal blooms and lessening of hypoxia symptoms. Dashed lines indicate negative feedback processes to nutrient-enhanced production and subsequent hypoxia. The dotted line between “Anthropogenic activities” and “Climate variability/ climate change” indicates that humans largely drive current climate change, but that climate change can certainly affect human activities.

largest contributor of N (52%), followed by atmospheric deposition sources (16%). P originates primarily from animal manure on pasture and rangelands (37%), followed by corn and soybeans (25%), other crops (18%), and urban sources (12%). Other watersheds may have different proportions of sources. For instance, the Chesapeake Bay’s watershed generates similar proportions of non-point source runoff (primarily agriculture), wastewater (urban areas), and atmospheric deposition (burning of fossil fuels); management options may differ from those proposed for the Mississippi River basin.

Solutions do exist. These include modification of agricultural practices, construction and restoration of riparian zones and wetlands as buffers between agricultural lands and waterways, control of urban and suburban non-point sources, use of environmental technologies such as tertiary treatment at point sources, and deployment of controls on atmospheric sources (Mitsch et al., 2001). Many smaller efforts are focusing on sustainable agriculture practices, such as longer-rooted plants, perennial crops, crop rotations, growing of multiple crops in alternating areas, and generating biofuels other than corn-based ethanol.

All the above sounds simple. But, there are multiple obstacles preventing success—lack of regulatory authority, competing interests, political and social impediments, multiple jurisdictions, lobbying interests, environmental organizations, non-supportive farm and energy policies, lack of adequate logistical and financial support, and concern for breaking from traditional practices.

Directed mitigation and management of nutrient sources, however, has led to recovery of eutrophication-driven deoxygenation around the globe. Besides the red dots in Figure 3.2.2, there are areas listed in Diaz and Rosenberg (2008) where there are improvements in dissolved oxygen levels due to management of nutrients. The OSPAR Commission (2017) provides an assessment of environmental health for north-west European maritime areas highlighting where progress in reducing eutrophication under the European Water Framework Directive is being made. The OSPAR Commission (2017) reported, overall, fewer problem areas than the previous report for 2001-2005 and attributed the decline in atmospheric and riverine inputs since 1995 for the improvement.

Benthos and sediment studies of the inner Stockholm archipelago in 2008 indicated a shift from defaunated, reduced laminated sediments, indicative of severely low dissolved oxygen concentrations in the 1990s, to reoxygenated sediments and a healthy benthic community dominated by an invasive polychaete following improved water quality (Karlsson et al., 2010). A comprehensive synthesis of benthic community recovery in Danish waters followed significant reduction of nutrients through directed mitigation measures to reduce non-point and point loads of both nitrogen and phosphorus (Riemann et al., 2016). Several other 'success' stories show that management of nutrient loads can remedy coastal eutrophication, and in many cases (not in the Danish waters example), also reverse deoxygenation. In Danish waters (Riemann et al., 2016), increased stratification occurred over the same years as nutrient load reductions, when there were shifts in vegetated benthic ecosystems and water clarity did not improve much.

3.2.8 Conclusions

There is no doubt that nutrient-driven eutrophication in coastal ecosystems that leads to deoxygenation has increased, especially since the 1950s, accelerated in the 1970s to 1980s, and expanded globally since the 1990s. The worsening of deoxygenation follows an increase in human population, expansion of agriculture and animal husbandry including increased fertilizer use, and increased burning of fossil fuels. These trends will continue unless concerted efforts are taken to slow, or drastically reduce, inputs of nitrogen and phosphorus to watersheds from consumptive human activities. This will require a social and political will that is emerging in some societies and countries but not at the level needed globally to stem and reverse the flow of excess nitrogen and phosphorus to coastal waters.

There are many solutions, including consumer-driven shifts in diet that will result in reduced fertilizer use (Howarth et al., 2002). Personal choices towards a less consumptive life style will not only reduce the carbon footprint but also the nitrogen and phosphorus footprints. Eat less or no meat. Strive for a wheat-based carbohydrate and vegetarian diet and avoid products dependent on corn. Use a non-ethanol gasoline. Drive a fuel-efficient or other energy source vehicle. Be mindful of reversing consumptive habits.

Finally, Levin and Breitburg (2015) called for, and rightfully so, the coupling of currently decoupled realms of research, observations and management for open ocean and coastal deoxygenation. The causes are similar, interactions occur between them, biogeochemical shifts in both affect global processes, management options are similar, and both need an integrated education and awareness emphasis. This integration lags behind where ocean acidification knowledge and awareness has been integrated, but can be addressed and improved.

3.2.9 References

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3.3 Ocean deoxygenation links to harmful algal blooms

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Summary

- The development of hypoxic or anoxic waters is regularly listed as one of the consequences of harmful algal blooms (HABs).
- Events of low oxygen associated with HABs are characterized by high initial oxygen concentrations, exceptional rates of respiration following bloom senescence, and short timescales.
- Coastal environments subject to high biomass HABs and associated events of low oxygen are typified by elevated inorganic nutrients as a consequence of either natural or cultural eutrophication.
- Eastern boundary upwelling systems are highly productive, nutrient-rich environments, prone to high-biomass HABs, and provide some of the earliest accounts of events of anoxia linked to red tides.
- The expansion of HABs is more readily apparent in Asia than in any other part of the world's ocean and it is here that relationships between the increasing prevalence of HABs and aquaculture operations are increasingly reported.
- Several model predictions show the likelihood for increased nutrient pollution and, correspondingly, for continued regional and global expansion of coastal hypoxia and anoxia linked to HABs.

3.3.1 Introduction

Harmful Algal Blooms (HABs) are usually described as proliferations of algae that can cause massive fish kills, can contaminate seafood with toxins, and alter ecosystems in ways that humans perceive as harmful (GEOHAB, 2001). A broad classification of HAB species distinguishes the toxin producers which can contaminate seafood or kill fish, and the high-biomass producers which can cause indiscriminate mortalities of marine life through various means. The development of hypoxic or anoxic waters is regularly listed as one such means and typically follows bloom degradation which fuels microbial respiration and the consumption of oxygen. These blooms are usually ascribed to flagellated species of phytoplankton, notably dinoflagellates, capable of regulating their depth and accumulating near the surface in high densities. In such cases the ocean may become discoloured leading to phenomena referred to as red tides.

Although red tides are often deemed the cause of hypoxia or anoxia with consequent mortalities of marine life, these events are poorly described in the scientific literature. Low oxygen concentrations in the ocean result from an imbalance between air-sea-fluxes, the transport of oxygen by physical means, and the biological production and consumption of oxygen. Events of oxygen deficiency linked to red tides are characterized by the exceptional biomass generated by these blooms, by the inherently high cellular respiration rates of dinoflagellates and by the often abrupt mortality of blooms and consequent elevated consumption of oxygen through aerobic respiration of organic matter by microbes. Events of low oxygen associated with red tides are therefore typically episodic in character and their local and transient properties have contributed to our poor understanding of these events and inadequate assessment of their impacts (Pitcher & Probyn, 2016). Specifically the causes and timing of bloom death leading to the rapid shift from net autotrophy to net heterotrophy are poorly established. In contrast to the efforts to determine the conditions, i.e. mechanisms and strategies that control phytoplankton cell growth and bloom development, considerably less effort has focused explicitly on phytoplankton death. Until recently phytoplankton were considered somewhat immortal unless eaten by predators, but it is now known that phytoplankton die spontaneously under various adverse environmental conditions and various forms of autocatalytic cellular self-destruction have been identified

(Bidle, 2014). Until such mechanisms controlling abrupt termination of blooms in natural systems are better understood events of anoxia and subsequent mortality of marine life will remain unpredictable.

The hydrodynamic properties of coastal systems conducive to bloom development and the formation of red tides are typically inseparable from those physical conditions required for the development of hypoxia or anoxia. While stratification is usually a key requirement in the development of low oxygen in bottom waters, as it provides a barrier to the diffusion of oxygen from surface waters toward the lower regions of the water column, it also promotes the succession of phytoplankton communities to the flagellate taxa so often the cause of red tides (Figueiras et al., 2006). Similarly, areas of the coastal environment that are subject to retentive circulation and are therefore more susceptible to low oxygen, owing to reduced advective exchange, are also subject to a higher incidence of red tides as bloom dispersal by lateral advection is minimized. Once formed, the dynamics of oxygen depletion in red tides may be driven by: (1) the high cellular respiration rates of dinoflagellates which may lead to severe night-time depletion of oxygen, and / or (2) the microbial consumption of oxygen following bloom senescence.

Coastal environments subject to high biomass HABs and associated events of low oxygen are generally typified by an elevated supply of inorganic nutrients as a consequence of either natural or cultural eutrophication. Examples of HABs and consequent anoxia in systems subjected to each of these forms of eutrophication are presented in the following sections. HABs and anoxia in eastern boundary upwelling systems which are considered naturally eutrophic are examined in subsection 3.3.2. This subsection specifically details bloom development, mechanisms of oxygen depletion and the impact on resources in the southern Benguela as a case study. An increasing majority of coastal environments subject to cultural eutrophication, particularly those common to the coasts of USA, Europe and Asia, are characterized by high biomass HABs (Glibert et al., 2018a). Subsection 3.3.3 examines HAB proliferation and oxygen depletion in Asia in response to cultural eutrophication. Unique to Asia is the large scale of aquaculture that characterizes the region and is considered an important source of nutrient pollution, key to HAB development (GEOHAB, 2010). Subsection 3.3.4 takes a look at future trends

in HABs and anoxia and subsection 3.3.5 concludes in outlining the way forward.

3.3.2 HABs, red tides and anoxia in Eastern Boundary Upwelling Systems

Eastern Boundary Upwelling Systems are highly productive, nutrient-rich environments, prone to high-biomass HABs, and provide some of the earliest accounts of events of anoxia linked to red tides. Within these systems episodic events of anoxia are well known in the Humboldt Current system encompassing much of the west coast of South America where they have been linked to red tides since the 1800s. On the Peruvian coast red tides are known locally as “aguajes”, and have for a long time been considered the principal cause of anoxic events and the production of hydrogen sulphide leading to fish mortalities (Rojas de Mendiola, 1979). In the port of Callao, the blackening effects of hydrogen sulphide on the paintwork of ships led it to be known colloquially as “The Callao Painter” (Figure 3.3.1). The dinoflagellate *Gymnodinium splendens* (known now as *Akashiwo sanguinea*) was considered for many years the most common cause of these events (Rojas

de Mendiola, 1979), however, *Prorocentrum micans*, *Prorocentrum gracile*, *Tripos fusus* (formerly *Ceratium fusus*) and *Tripos furca* (formerly *Ceratium furca*) are now also listed as bloom-forming dinoflagellates in this region (Trainer et al., 2010; Figure 3.3.2).

By way of example, in April 2004 a particularly destructive bloom of *A. sanguinea* occurred in Paracas Bay off the central coast of Peru (Kahru et al., 2005). In late March waters of the bay were a brownish-red colour and concentrations of 3.2×10^6 cells L^{-1} were recorded prior to mass fish mortalities. Severely hypoxic conditions were reported following bloom senescence on 12 April at which time fish mortalities were greatest. The local share in the Peruvian anchovy landings decreased from 8.4% in 2003 to 1.7% in 2004. The port was closed for 22 days to reduce effluent discharge into the bay resulting in an estimated loss in revenue of US\$27.5 $\times 10^6$. The local aquaculture sector also reported losses estimated at US\$1 $\times 10^6$ (Kahru et al., 2004).

Of the other major EBUS, the California Current system, encompassing much of the Pacific coast of North America, and the Canary Current system, including the



Figure 3.3.1 Water discolorations in the Humboldt Current area known as ‘aguajes’ have been reported to cause anoxia with the subsequent production of hydrogen sulphide since the late 19th century. The blackening effects of hydrogen sulphide on the paintwork of ships led it to be known colloquially as ‘The Callao Painter’. © Wilder Vargas / Shutterstock.com.

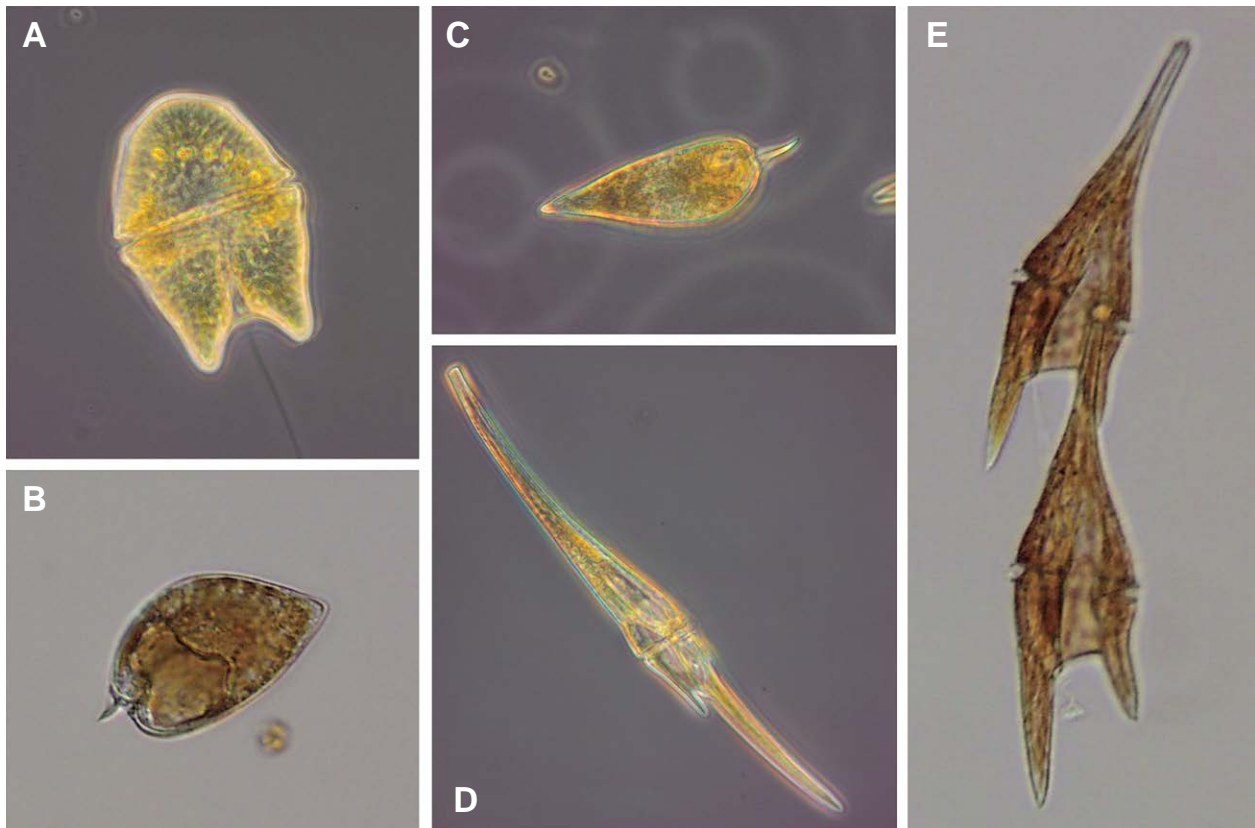


Figure 3.3.2 Aguajes were originally attributed to blooms of the dinoflagellate (A) *Akashiwo sanguinea* (formerly *Gymnodinium splendens*; Rojas de Mendiola, 1979), however, between 1980 and 1995 the dinoflagellates (B) *Prorocentrum micans*, (C) *Prorocentrum gracile*, (D) *Tripos fusus* (formerly *Ceratium fusus*) and (E) *Tripos furca* (formerly *Ceratium furca*) were also reported as the cause of these blooms (Sánchez & Delgado, 1996) © G.C. Pitcher and L.M. Mansfield.

Iberian Peninsula and the north-west African coast, are subject to far fewer events of red tide related anoxia (Trainer et al., 2010). However, the Benguela Current system off the west coast of southern Africa is similar to the Humboldt Current in that events of anoxia linked to red tides are common with reports dating back to the 1800s. Our present knowledge and understanding of these events following scientific investigation over the past 20 years is presented below as a case study of HABs and anoxia in the southern Benguela detailing bloom development, mechanisms of oxygen depletion and the impact on resources.

3.3.2.1 HABs and anoxia in the southern Benguela: A case study

The southern Benguela upwelling system located off the coast of southern Africa has a long history of marine mortalities attributed to red tides and subsequent anoxia (Pitcher & Calder, 2000; Trainer et al., 2010). Here blooms are most often observed in the embayments of St Helena Bay, Saldanha Bay, Table Bay, False Bay and Walker Bay (Figure 3.3.3). Blooms are usually attributed to one or another species of dinoflagellate,

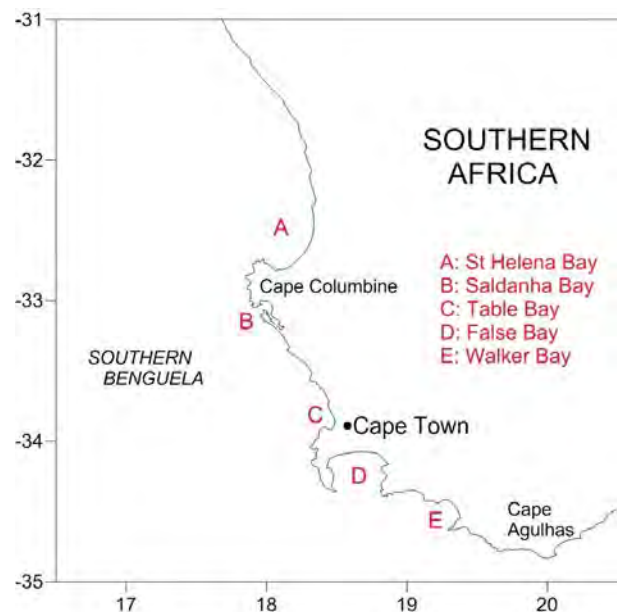


Figure 3.3.3 HAB hotspots in the southern Benguela associated with coastline features ranging from headlands, capes, peninsulas and bays. These mesoscale features interrupt typical upwelling circulation patterns and are more vulnerable to HABs owing to their influence on wind stress and water stratification, and through their retentive circulation that minimizes dispersal by lateral advection. These physical features along with the exceptional productivity of high biomass HABs increase the susceptibility of these areas to oxygen depletion.



Figure 3.3.4 Example red tides in the southern Benguela of (A) the dinoflagellate *Alexandrium catenella* off Elands Bay on 11 April 2012 (© John Foord), (B) a green flagellate of the genus *Tetraselmis* in Saldanha Bay on 15 January 2003 (© Grant Pitcher), (C) *Noctiluca scintillans* on the shoreline of Dassen Island off the west coast of South Africa on 6 October 2006 (© Tony van Dalsen), (D) *Gonyaulax polygramma* in False Bay off the Steenbras River mouth on 25 February 2007 (© Brent Johnson), (E) *Alexandrium minutum* in Cape Town harbour on 26 November 2003 (© Andre du Randt), and (F) the photosynthetic ciliate *Mesodinium rubrum* off Yzerfontein on 10 October 2016 (© Meredith Thornton).

although the photosynthetic ciliate *Mesodinium rubrum*, the raphidophyte *Heterosigma akashiwo*, various coccolithophorids and other flagellates have also been the cause of large blooms and spectacular discoloration of the ocean (Figure 3.3.4, Pitcher et al., 2010).

Some of the earliest accounts of low oxygen events in the southern Benguela that have been attributed to red tides date back to the 1800s (Gilchrist, 1914). In 1869 an incident in Stompneus Bay, a small recess in the south-western corner of St Helena Bay, was described in which fish known locally as geelbek (*Atractoscion aequidens*) were picked up in dark red water, having



Figure 3.3.5 West coast rock lobster (*Jasus lalandii*) © Sabena Jane Blackbird / Alamy stock photo.

been found swimming head above water, apparently in a “stupefied” condition. Another incident in 1907 is described in which Saldanha Bay became filled with red water, known locally as “flower water”, and fish in the bay were seen to be floating belly upwards in a “disabled” condition and were cast ashore in large numbers, apparently on account of the presence of large quantities of decaying matter. The severity of these mortalities led Gilchrist (1914) to list red tides as one of the factors causing fluctuations in fish stocks in the Benguela.

One of the first events to be investigated and documented in the scientific literature was that of a bloom of *Gonyaulax polygramma* in False Bay in March and April 1962 (Grindley & Taylor, 1964). Under westerly winds, the bloom accumulated in the north-eastern corner of False Bay reaching concentrations of approximately 10×10^6 cells L^{-1} ; the sea was reported to have become slimy with rotting plankton and produced an unbearable stench. At this time, dead and dying fish and invertebrates, estimated at over 100 tons, were washed up on the beaches, apparently due to the depletion of oxygen by decaying plankton. Many other accounts of dinoflagellate blooms and events of anoxia in the southern Benguela have followed. However, in April 1978, extensive mortalities in St Helena Bay were for the first time attributed to oxygen depletion following the decay of a bloom of the ciliate *Mesodinium rubrum* (Horstman, 1981). Bloom decay and oxygen depletion followed a dramatic change in colour of the bloom, from the spectacular maroon colour so characteristic of *M. rubrum* blooms, to a rusty-orange discoloration of the ocean.

More recent events of anoxia following dinoflagellate blooms during the 1990s in St Helena Bay have been

associated with some of the largest mortalities recorded within the region. In March 1994 a bloom dominated by the dinoflagellates *Tripos furca* (formerly *Ceratium furca*) and *Prorocentrum micans* (Figure 3.3.2) led ultimately to conditions of anoxia and the production of hydrogen sulphide impacting 30 km of shoreline and causing a mortality of approximately 60 tons of the west coast rock lobster *Jasus lalandii* (Figure 3.3.5) and 1500 tons of fish, primarily the mullet *Liza richardsoni* (Matthews & Pitcher, 1996). This was the first recorded incidence of hydrogen sulphide poisoning in the southern Benguela causing a black discoloration of the sea. In April 1997 the largest ever stranding of 2000 tons of rock lobster followed the decay of a red tide dominated by *T. furca* (Cockcroft et al., 1999). Unprecedented in terms of the magnitude of the loss, which was valued at US\$50x10⁶, the ecological fallout severely impacted the fishing community in the region. The most recent mortality in St Helena Bay occurred in February and March 2015 with the removal of a total of 415 tons of the rock lobster, 21 tons of molluscs, mostly the white mussel *Donax serra*, and 7 tons of various fish species from the beaches. For the first time these mortalities were attributed to blooms of the dinoflagellate *Prorocentrum triestinum* (Ndlovu et al., 2017).

Owing to the severe impacts of red tides on resources in St Helena Bay considerable scientific effort has been directed towards establishing the conditions and processes important to bloom development. Within the inner-shelf environment of upwelling systems, blooms often manifest within embayments where the properties of stratification and retention, which generally favour HABs, tend to be more pronounced (Pitcher et al., 2010). It is for this reason that St Helena Bay, a cape-associated bay, has a particularly high incidence of red tides.

The important role of wind driven circulation in bloom development and transport in St Helena Bay is demonstrated in the conceptual model of Pitcher and Nelson (2006) (Figure 3.3.6 A, B). St Helena Bay is located downstream of Cape Columbine and upwelling-favourable winds result in an upwelling plume off Columbine that tends to isolate the nearshore area in the lee of the cape from the offshore domain, thereby inducing retention on the coastal side of the plume. A positive coupling between upwelling and retention is provided by this structure, with stronger upwelling-favourable winds enhancing retention within the nearshore area, despite the intensification of offshore

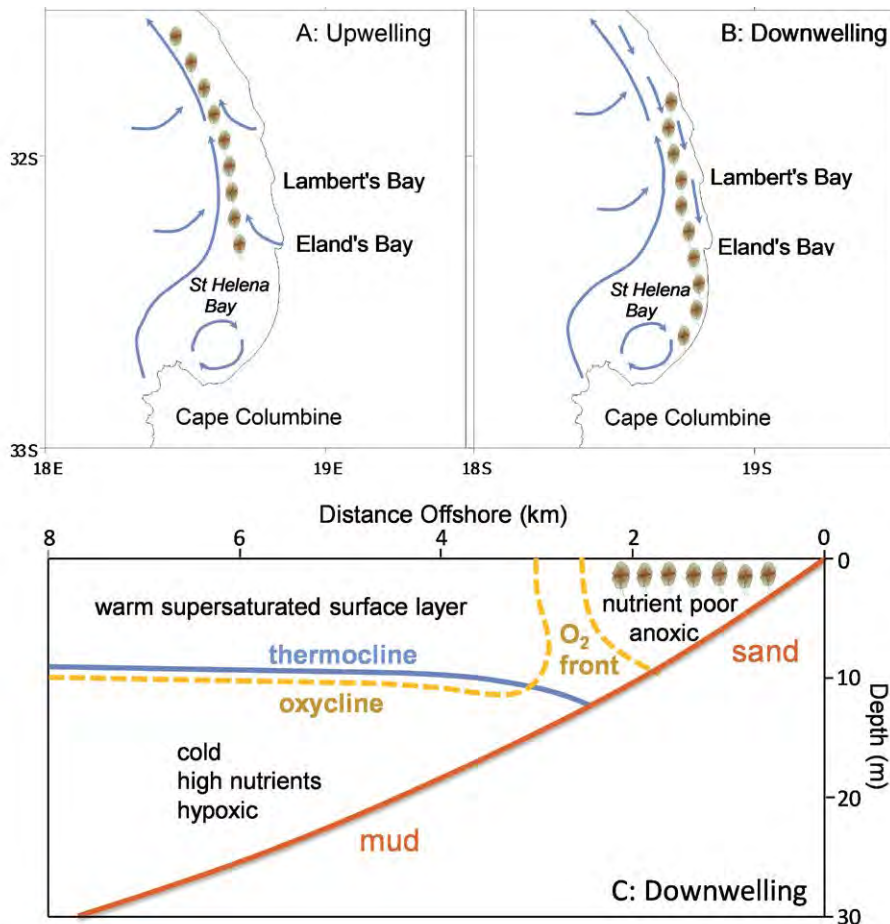


Figure 3.3.6 Conceptualization of harmful bloom events in the greater St Helena Bay region during periods of (A) upwelling and (B) downwelling. Intensified stratification in the lee of Cape Columbine particularly during late summer and autumn favours the seasonal succession and transition to dinoflagellate blooms. Under upwelling conditions dinoflagellates tends to accumulate offshore in a region of convergence, created by a narrow belt of upwelling and the core equatorward flow. Wind relaxation leads to downwelling conditions and the shoreward accumulation of dinoflagellate blooms. Simultaneous development of an inshore counter-current results in the poleward progression of these blooms into the bay. It is at this time that the nearshore regions of the bay are most susceptible to events of anoxia (C). Under conditions of sustained downwelling subthermocline nutrients are inaccessible to these inshore blooms leading to their decay. The exceptional phytodetrital production associated with these blooms and the reduced volume of water within the confines of the shallow nearshore environment result in the depletion of oxygen through the entire water column.

flow associated with upwelling. Intensified stratification in the lee of the Cape particularly during late summer and autumn favours the seasonal succession and transition to dinoflagellate blooms. Under upwelling conditions dinoflagellates tend to accumulate offshore in a region of convergence, created by a narrow belt of upwelling and the core equatorward flow (Figure 3.3.6A). Wind relaxation or reversal is typically associated with the shoreward accumulation of dinoflagellate blooms, and the development of an inshore counter-current results in the general poleward progression of these blooms into the bay (Figure 3.3.6B). It is at this time that the nearshore regions of the bay are most susceptible to events of anoxia.

St Helena Bay is in fact subject to two categories of oxygen deficient waters characterized by different

time scales and mechanisms of depletion (Figure 3.3.6C) (Pitcher & Probyn, 2011; Pitcher et al., 2014). Seasonally recurrent hypoxia is evident in bottom waters as stratification strengthens during the course of the upwelling season, thereby isolating the bottom waters from surface waters, and respiration is fuelled by high bay production and the deposition of increasing amounts of organic matter from the upper water column. Consequently oxygen concentrations in these bottom waters show a seasonal minimum in autumn at which time there is also an expansion in the size of the bottom pool of hypoxic waters. The seasonal expansion of this deep water pool of low oxygen water and inshore incursions of this water, as dictated by the upwelling-downwelling cycle, strongly impact the habitable nearshore zone. Although these hypoxic waters are known to compress the habitat of west coast rock

lobster causing shoreward migrations, which can cause significant stress and overcrowding, these events are not considered the cause of faunal mortalities.

Mass mortalities are rather caused by episodic anoxia following the nearshore accumulation and decay of red tides (Figure 3.3.6C) (Pitcher & Probyn, 2011). These events tend to strip oxygen from the entire water column of shallow nearshore environments and also coincide with corrosive low-pH conditions (Pitcher & Probyn, 2012), and in some cases the production of hydrogen sulphide (H₂S) (Matthews & Pitcher, 1996), which are equally harmful to marine life. Understanding the often rapid transition within these blooms from net autotrophy to net heterotrophy is important in predicting events of anoxia. The development of anoxia overnight has been shown to be achievable owing to the exceptional rates of oxygen utilization at night due to the magnitude of these blooms and the inherently high cellular respiration rates of dinoflagellates (Pitcher & Probyn, 2016). Nutrient stressors are also considered important in driving bloom-to-post-bloom transitions important in determining the biogeochemical fate of the bloom and the onset of anoxia (Pitcher & Probyn, 2016). Concurrent measurements of nutrients and nutrient uptake within blooms in the southern Benguela have shown that nutrient concentrations are unlikely to meet the demands of red tides. The inaccessibility of nutrients particularly during periods of extended downwelling, when subthermocline nutrients are unavailable, is therefore very likely to trigger cell death and bloom mortality further fuelling the microbial foodweb and consumption of oxygen (Figure 3.3.6C) (Pitcher & Probyn, 2011). Such events are regularly responsible for large mortalities of marine life within the St Helena Bay region (Figure 3.3.7), and have severely impacted marine resources in the region (Cockcroft, 2001; Cockcroft et al., 2008).

Oxygen deficient waters in St Helena Bay have specifically impacted the west coast rock lobster which normally dominates faunal mortalities. The west coast rock lobster fishery commenced in the early 1800s and traditionally has been of particular importance to communities on the South African west coast which relied heavily on the seasonal employment it provided (Cockcroft, 2001). Historically fishing has been conducted mainly by traps, deployed from larger vessels in deep water, or by hoopnets in shallow water, operated from dinghies. Lobster mortalities typically occur over a segment of some 80 km of the St Helena

Bay shoreline straddling two fishing zones and have often demonstrated a north-south progression linked to the poleward transport of red tides. A dramatic increase in the number and severity of lobster mortalities attributed to events of anoxia was reported during the 1990s (Cockcroft, 2001). The large mortality in 1994 resulted in a massive 65% decrease in catches in the 1994-95 fishing season. Further mortalities in the late 1990s, including the largest mortality on record in 1997, continued to impact catches. In the fishing seasons of 1998-99 and 1999-2000 catches reached record lows corresponding to 1.3% of the average annual catches made in the 1980s. Lobster mortalities were generally dominated by small females and the recovery of populations following these events was slow particularly in areas where anoxia had severely impacted sessile benthic communities (Cockcroft, 2001). Ultimately the high number of anoxic events during the 1990s is considered to have been an important driver in a major shift of the resource from the traditional fishing grounds on the west coast to more southern fishing grounds. This shift in the resource has led to a decline in the contribution of west coast rock lobster to total lobster landings on the South African coast from about 60% to <10% with major implications for the fishery and fishing community (Cockcroft et al., 2008). The lobster fishery on the west coast has now been reduced to an almost exclusively nearshore hoopnet fishery, and the loss of jobs in lobster processing facilities, coupled with a reduction in the allocation of long-term fishing rights to ensure resource sustainability has resulted in substantial economic hardship for west coast communities.

3.3.3 HABs, red tides and anoxia in Asia

The expansion of HABs is more readily apparent in Asia than in any other part of the world's ocean and it is here that relationships between the increasing prevalence of HABs and aquaculture operations are increasingly reported (GEOHAB, 2010).

3.3.3.1 Japan

Red tides and oxygen deficient waters have for many years posed a significant environmental problem in the coastal waters of Japan owing to increased nutrient loads. The Seto Inland Sea, the largest enclosed coastal sea in Japan, and a major fishing ground and region of intensive aquaculture, was subject to increasing red tides in the 1960s and 1970s in response to eutrophication (Imai et al., 2006). Interestingly, the increase in red

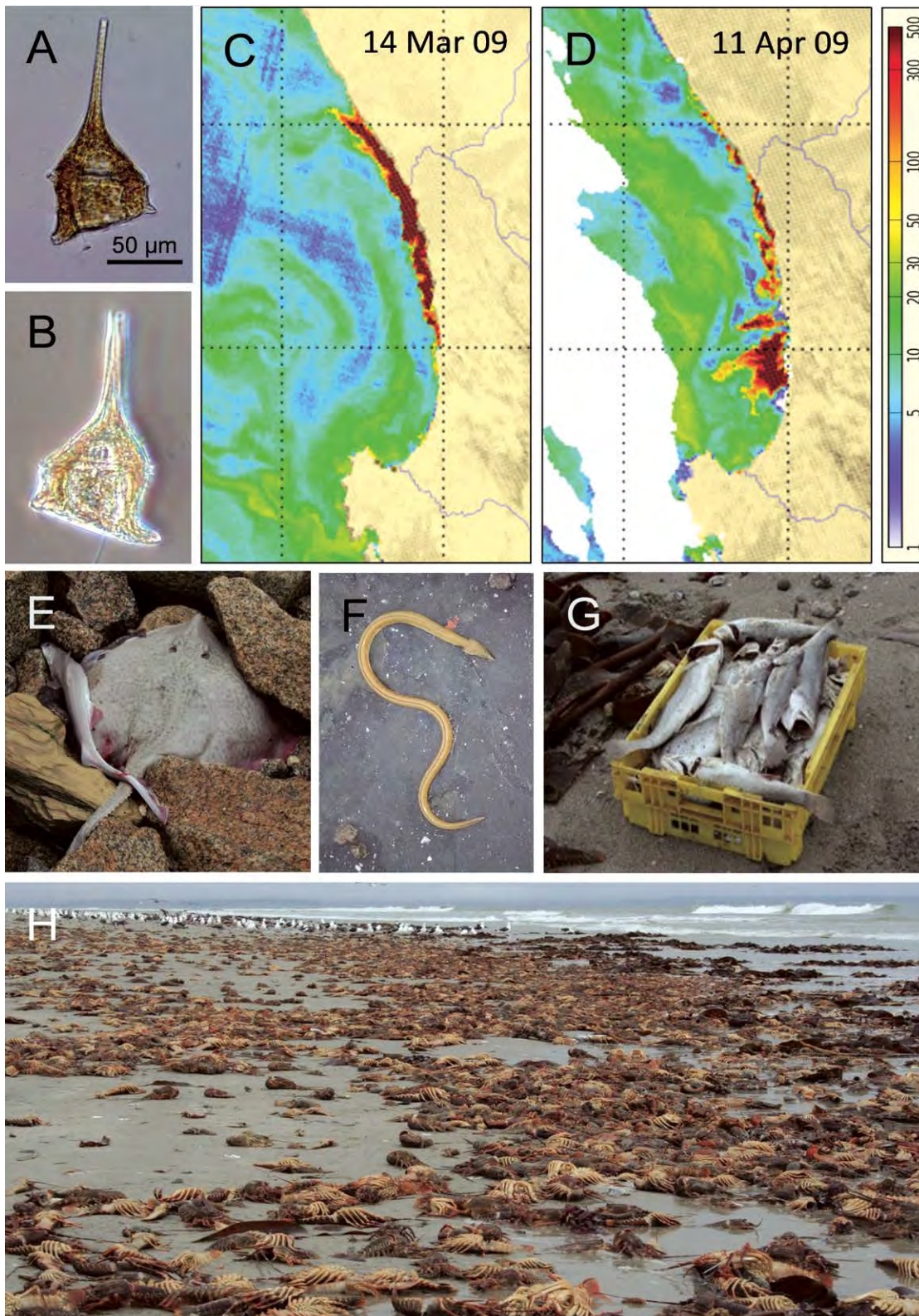


Figure 3.3.7 Light micrographs of the dinoflagellate *Tripes balechii* (formerly *Ceratium balechii*) (A, B) responsible for a red tide in St Helena Bay in 2009. The red tide is effectively tracked by ocean colour data from the MERIS sensor as is evident in images from the 14 March (C) and 11 April 2009 (D) showing bloom development and transport into the bay (Pitcher et al., 2014). Initial build-up of the bloom was observed in February in the northern reaches of the bay. By March blooms were shown to extend in a narrow band over a distance of >100 km. Diminished upwelling and the development of nearshore counter currents in late summer and early autumn resulted in the southward progression of these blooms and their entrainment into the southern reaches of the bay. Here large fish and lobster mortalities resulted from bloom decay and consequent anoxia in early May (E-H; Pitcher & Probyn, 2011). © A, B, E, F, G, H. G.C. Pitcher; C & D from Pitcher et al. (2014).

tide events in the Seto Inland Sea paralleled a rapid rise in the culture of yellowtail (*Seriola quinqueradiata*) (GEOHAB, 2010). Red tide forming species included the dinoflagellates *Gonyaulax polygramma*, *Noctiluca scintillans* and *Scrippsiella trochoidea*, all of which have been associated with indiscriminate fish and invertebrate kills due to oxygen depletion.

While nutrient controls enforced in the Seto Inland Sea in the 1970s led to a reduction in HABs, other bays in western Japan have suffered increased red tides in the 1980s and 1990s, coincident with declining oxygen concentrations and reduced fish and shellfish catches. In 1994 a bloom of *G. polygramma* in and around Uwajima Bay caused mass mortalities of cultured and natural fish and shellfish stocks valued at US\$7x10⁶. The death of fish and shellfish were attributed to anoxic waters and high sulphide concentrations that developed through the whole water column of Uwajima Bay and Hoketsu Bay following decomposition of the bloom (Koizumi et al., 1996). Similarly, the scale of autumn phytoplankton blooms in Ariake Bay has increased markedly and since 1998 red tides have been observed to extend across the entire inner bay (Tsutsumi, 2006). These blooms have markedly impacted nori production with harvests dipping by 35% in some years. Hypoxia in response to the increased prevalence of red tides was first observed in the bottom waters of Isahaya Bay at the head of Ariake Bay in the late 1990s and its spread within the region has coincided with a dramatic decline in the pen shell fishery (*Atrina pectinata*) (Nakata et al., 2010; Tsutsumi, 2006).

3.3.3.2 Korea

Coastal eutrophication caused by industrialization, urbanization and intensive aquaculture, with the consequent development of massive algal blooms has caused severe deoxygenation in Korean coastal regions, particularly on the southern coast (Lee et al., 2018). Here red tides concentrate in embayments such as Jinhae and Gamak Bays leading to enhanced biological consumption of oxygen with negative impacts on benthic ecosystems and aquaculture production. As an example, hypoxia has been known to occur every summer in Jinhae Bay following catastrophic events of mass mortality on oyster farms due to severe hypoxia in 1978 (Lee et al., 2018). Similarly, HABs and the consequent degradation of water quality in Gamak Bay has caused oyster production to decline from 9600 tons in 1991 to 4000 tons in 2008 (Lee & Kim, 2008). These blooms have been attributed

to three phytoplankton species, namely a dinoflagellate belonging to the genus *Prorocentrum*, the raphidophyte *Heterosigma akashiwo* and the diatom *Skeletonema costatum*. Blooms of these species have been shown to be preceded by higher than average precipitation (Lee & Kim, 2008). In some cases artificial structures in the form of dykes have also contributed to hypoxia through the effects of reduced flushing (Lee & Kim, 2008). As an example Shihwa Bay, isolated by means of a dyke as part of a government land reclamation project has subsequently experienced chronic environmental problems relating to red tides and bottom water anoxia leading to massive fish kills (Cho, 2005).

3.3.3.3 China

The number of HABs has increased in all waters of China in the past few decades (Yu et al., 2018). In areas such as the Bohai in north China large volumes of terrestrial pollutants in the form of industrial wastes and domestic sewage drain into the sea from nine rivers adding to bay contamination by intensive shrimp farming. In 1989 the south-west coast of the Bohai was subjected to one of the largest ever red tides in north China dominated by a species of the dinoflagellate *Gymnodinium* (Xu et al., 1993). The bloom seriously impacted 1.5x10⁵ hectares of shrimp ponds with a loss of 1x10⁴ tons of shrimp valued at US\$40x10⁶. Shrimp death was attributed to depleted oxygen concentrations following bloom senescence and a subsequent increase in disease.

One of the most spectacular examples of HAB development in response to eutrophication has been the development of massive blooms of the dinoflagellate *Prorocentrum donghaiense* in the Changjiang Estuary and adjacent East China Sea impacting areas up to 1x10⁴ km² (Gilbert et al., 2018b). Here a 10-fold increase in anthropogenic nutrients exported from the Changjiang stimulated development of these large noxious blooms with corresponding development of hypoxic zones of similar magnitude (Zhu et al., 2011).

Similarly, Tolo Harbour, an enclosed embayment in the north-eastern region of Hong Kong is also subject to severe nutrient pollution linked to increases in the human population. Between 1976 and 1986 the population within the harbour watershed grew 6-fold during which time the number of red tide events increased 8-fold (Lam & Ho, 1989). In 1988 the harbour was subject to a three-month red tide event attributed to the dinoflagellate *Gonyaulax polygramma* (Lam &

Yip, 1990). This was the first reported incidence of a *G. polygramma* dominated bloom in the region with peak concentrations of 23×10^6 cells L^{-1} . Bloom termination coincided with the onset of summer stratification and resulted in anoxia throughout the bay leading to large fish kills and incidents of shellfish mortality. Blooms of *Tripos furca* (formerly *Ceratium furca*) have also been reported to be a common feature of Tolo Harbour with fish kills following night-time depletion of oxygen and bloom die-off (Wong et al., 2010).

3.3.3.4 Philippines

Aquaculture facilities in the Philippines, particularly finfish operations have also been increasingly subject to events of low oxygen attributed to large dinoflagellate blooms. In the northern Philippines, Bolinao Bay in the Lingayen Gulf has been the site of intensive culture of the milk fish *Chanos chanos* since the 1970s. In January and February 2002 fish kills valued at US\$ 9×10^6 followed blooms of the dinoflagellate *Prorocentrum minimum* (Azanza et al., 2005). At the time of bloom senescence oxygen concentrations declined to $1.4 \text{ ml } L^{-1}$ and fish were observed gasping for breath. The intensive nature of fish farming in the region, with a total of 800 fish pens covering an area of 165 ha in 1999, was considered the primary cause of bay enrichment and bloom development (San Diego-McGlone et al., 2008). The presence of fish cages also increases frictional drag thereby reducing currents and flushing rates which further contributes to declining oxygen concentrations.

Fish kills in 2002 were also observed in the southern Philippines in Iligan Bay in March, and were attributed to blooms of the dinoflagellate *Cochlodinium polykrikoides* (Vicente et al., 2002). The presence of dead pelagic and demersal fish coincided with peak dinoflagellate concentrations at which time oxygen concentrations showed dramatic declines particularly with the onset of darkness and night-time respiration. Monitoring within a bloom patch showed afternoon oxygen concentrations in excess of $5 \text{ ml } L^{-1}$ declining to $<0.35 \text{ ml } L^{-1}$ in the early hours of the morning.

Further kills of farmed milk fish occurred in 2010 in the Caquiputan Channel in Anda with an estimated loss of US\$ 1.1×10^6 . This mortality was attributed to oxygen concentrations falling below $0.35 \text{ ml } L^{-1}$ following the decomposition of a massive bloom of the non-toxic diatom, *Skeletonema costatum*, and a toxic

dinoflagellate of the genus *Alexandrium* (Escobar et al., 2013). More recently, in May 2018, a major milkfish kill with an estimated value of US\$ 5×10^5 was reported in Obando, Bulacan, an estuary that empties into Manila Bay (Figure 3.3.8). The Bureau of Fisheries and Aquatic Resources attribute this event to very low oxygen levels and high water temperatures ($34 \text{ }^\circ\text{C}$) evidently preceded by a dinoflagellate bloom.

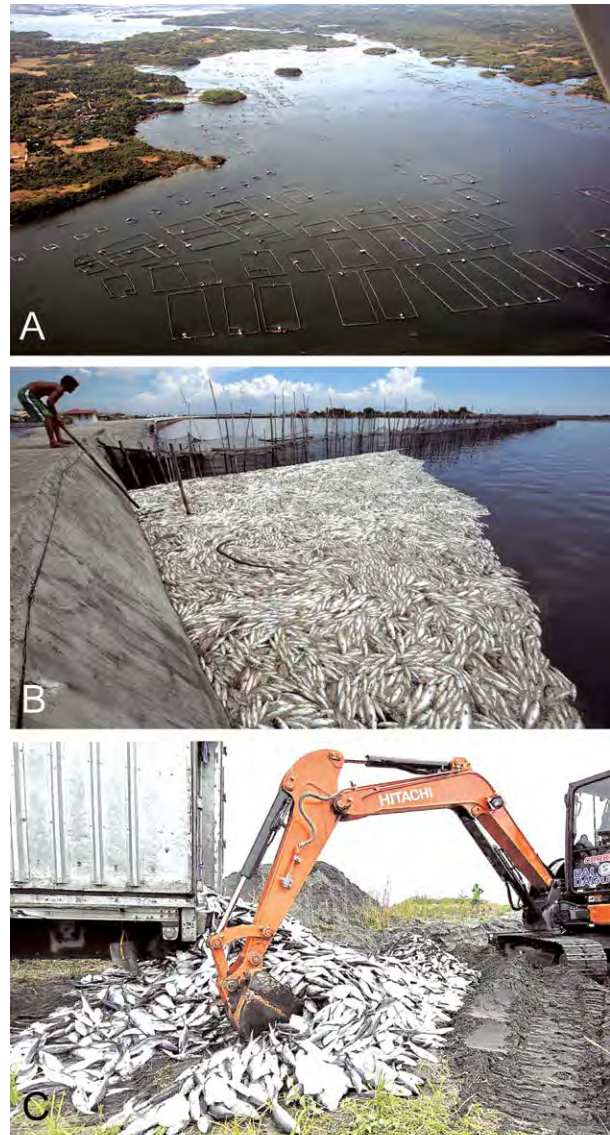


Figure 3.3.8 In Asia an increase in HABS has been observed in response to expanding aquaculture operations. A) As an example a major bloom of *Prorocentrum minimum* is pictured on a fish farm in Pangasinan province in the Philippines in 2013 © Gil Jacinto. B) In May 2018 extensive fish mortalities occurred in response to events of low oxygen following such blooms as depicted by a major mortality of the milkfish *Chanos chanos* in Obando, Bulacan, an estuary leading to Manila Bay as reported by the Bureau of Fisheries and Aquatic Resources, © Michael Varcas of the Philippine Star) and C) in Anda, Pangasinan. © Ray Zambrano of Philippine Daily Inquirer.

3.3.3.5 Malaysia

Malaysia has also experienced considerable growth of the aquaculture sector and finfish farming in particular is considered to pose a significant risk to the environment (Er et al., 2018). Algal blooms associated with massive fish kills have been reported from both the east and west coasts of the Peninsula with aquaculture operations incurring large losses (Teen et al., 2012). In Penang fish kills during 2005-2006 resulted in losses of US\$5x10⁶. These mortalities followed the decomposition of plankton blooms, possibly *Noctiluca scintillans*, and subsequent development of hypoxic and anoxic conditions (Teen et al., 2012). Similarly, Semerak Lagoon, the location of around 1000 fish cages suffered fish mortalities in 2016 following an exceptional bloom of a species of *Skeletonema*. Again low oxygen concentrations of around 2 ml L⁻¹ following bloom decomposition are believed to have been the cause of the mortality (Er et al., 2018).

3.3.3.6 Arabian Sea

Blooms, both red and green, of the dinoflagellate *Noctiluca scintillans* have been associated with events of low oxygen on both the east and west coasts of India (Baliarsingh et al., 2016). Blooms are, however, more frequent in the Arabian Sea where they occur on the south-west coast of India during the monsoon and post-monsoon periods. Here blooms of the red *N. scintillans* have been linked to hypoxic conditions and large mortalities of fish off Cochin in 1998 (Naqvi et al., 1998) while low oxygen conditions following a bloom of the green *N. scintillans* off Mangalore in 2011 were shown to disrupt fishing activities in that fish were observed to avoid low oxygen waters (Sulochanan et al., 2014). In 2008 the south-eastern Arabian Sea was also subjected to large blooms of the dinoflagellate *Gonyaulax polygramma* in the shelf waters off Mangalore (Padmakumar et al., 2018). These blooms were attributed to the large runoff from the Netravathi-Gurpur estuarine system in the post monsoon season and resulted in anoxic conditions with elevated sulphide and ammonia concentrations.

The first ever bloom-associated mass fish mortality in the Arabian Sea was attributed to a bloom of *Prorocentrum minimum* in 1987 in Gwadar Bay, a shallow, semi-enclosed bay on the western shores of Pakistan (Rabbani et al., 1990). Concentrations of *Prorocentrum minimum* of 45x10⁶ cells L⁻¹ were recorded in reddish-brown

waters and oxygen concentrations in post bloom waters dropped to <2 ml L⁻¹. The Arabian Gulf too has been subjected to an increase in HABs attributed to the deterioration of water quality owing to land reclamation and urbanization, and insufficient treatment of sewage and waste water discharge from industries (Rajan & Al Abdessalaam, 2008). Blooms of *P. minimum* and *Prorocentrum micans* have been prominent and in 2003 reached concentrations of 18x10⁷ cells L⁻¹ prior to events of oxygen depletion and the production of hydrogen sulphide, with subsequent fish mortalities.

Since 2000 the northern Arabian Sea has experienced a shift in phytoplankton composition with diatom blooms being replaced by the green *Noctiluca scintillans* which is now one of the dominant HAB-forming species (Figure 3.3.9) (Gomes et al., 2014). In the Sea of Oman a significant correlation has been found between fish kills and the incidence of HABs, with a seasonal trend in fish kills following a decline in oxygen, primarily driven by the decomposition of a series of blooms usually dominated by *N. scintillans* (Harrison et al., 2017).

3.3.4 Future trends in HABs and anoxia

Whereas HABs and resulting events of anoxia have for centuries, consistently characterized some coastal environments, other areas, particularly those subject to cultural eutrophication (as described in subsection 3.3.3), have demonstrated a notable increase in these events in recent decades. Recognition of the expansion of HABs was gained during the 1980s and 1990s and it is now accepted that most of the factors contributing to this expansion are the result of human activities (Anderson et al., 2012; Glibert et al., 2018a). Increases in nutrient loading, overfishing, aquaculture practices, ballast water discharge, and global climate change may all be important contributors. Human-assisted transport and dispersal of harmful species has been achieved by ballast water discharge and the translocation of shellfish. Fishing and the harvesting of shellfish have altered food chains, in some cases leading to a reduction in the control of HAB species through removal of primary grazers. There is emerging evidence that climate change is causing shifts in the composition of coastal phytoplankton communities and there is an expectation that future change will cause shifts in the spatial and temporal ranges of HABs (Wells & Karlson, 2018). Projected increases in stratification to which dinoflagellates are well adapted, as a result of warmer waters, increased precipitation and runoff, and altered

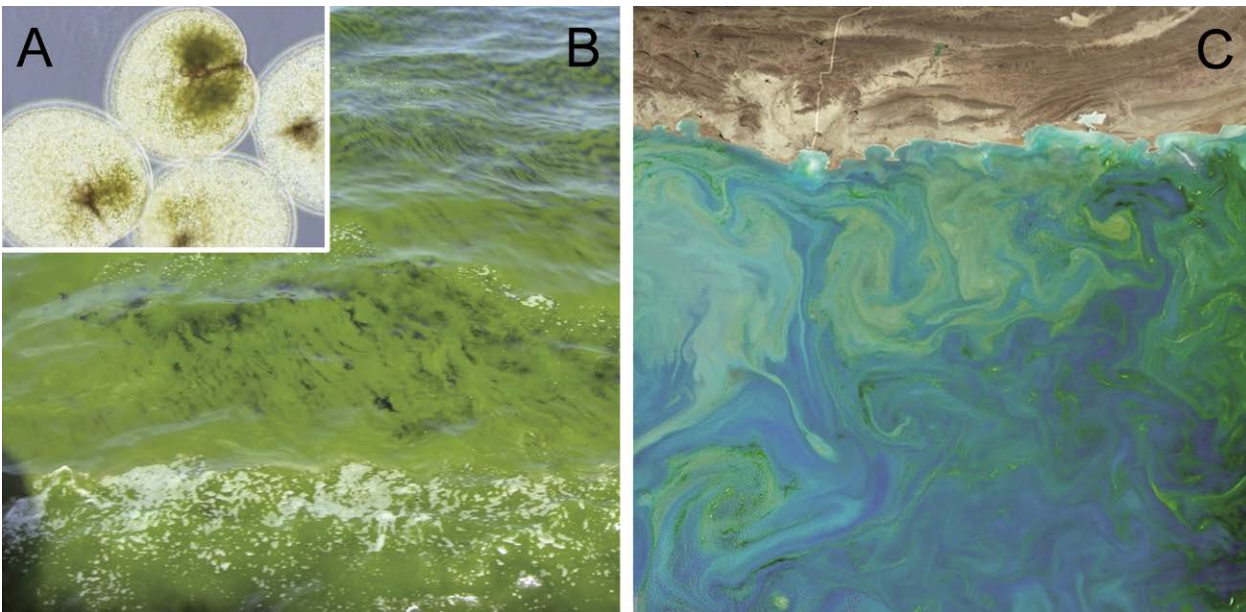


Figure 3.3.9 A) Green *Noctiluca scintillans* was first discovered in south-east Asia by Sweeney (1976). © Joaquim Goes. Compared to the better known red *Noctiluca scintillans* which is a heterotrophic dinoflagellate most common in temperate coastal waters, the green form is characterized by an endosymbiotic population of free swimming cells of *Pedinomonas noctilucae*. In the early 1990s the first large blooms of this dinoflagellate were recorded in the Gulf of Thailand and in Manila Bay of the Philippines, while their sudden appearance in the western Arabian Sea and in the coastal waters of Pakistan was observed in 2000 (Harrison et al., 2017). B) Blooms of green *Noctiluca* are now a regular feature along the coast of Oman. © Joaquim Goes, C) also observed by satellites from space. © Norman Kuring, NASA.

winds, serve as the foundation for much of the intuitive linkage between climate change and an increase in HABs. Furthermore, the direct effects of temperature, altered light fields, changing CO₂ levels, and ocean acidification, on phytoplankton physiology and metabolism are also likely to influence the prevalence of HABs. However, the fundamental driver of the global increase in HABs in recent decades, particularly in high biomass HABs, is the elevated anthropogenic nutrient input to which many coastal environments are subject (Glibert & Burford, 2017; Heisler et al., 2008).

Human activities, such as the use of synthetic fertilizers, energy production, and expansion of industrialized agriculture and aquaculture have had tremendous impacts on the global cycling of nutrients and carbon on land, in fresh waters, and in coastal waters, and an important consequence of such activities in aquatic systems is eutrophication with a resulting increase in HABs (Glibert et al., 2018b). The sources of nutrients that may stimulate blooms include sewage, atmospheric and groundwater inputs, and agricultural and aquaculture runoff and discharge (Anderson et al., 2002; Glibert & Burford, 2017). Global use of N fertilizer has increased nine-fold, and that of P has increased three-fold in the past four decades (Sutton et al., 2013), while agricultural crops take up only 50% of applied N fertilizers (Peoples et al., 1995). Animal production is

also increasing and animal waste is a major source of nutrient pollution. Moreover, aquaculture continues to grow with consequent inputs of nutrients from the culture of both shellfish and finfish. These nutrient sources have led to widespread coastal eutrophication throughout Europe, the USA and Asia (Glibert et al., 2018a) and the corresponding increase in HABs is one of the likely causes for faster declines in oxygen concentrations in the coastal ocean than in the open ocean (Gilbert et al., 2010).

The simplistic perception that more nutrients fuel more biomass through a direct dose-response relationship may still hold for high biomass blooms. However, it is now recognized that the relationship between nutrient pollution and species specific HABs is more complex, in that the composition and relative proportional availability of nutrient pools, and the range of physiological responses by different phytoplankton are all important in determining the linkage between eutrophication and HABs (Anderson et al., 2012). As an example, alterations in the composition of nutrient loads have been correlated with shifts to flagellate-dominated assemblages; more specifically the supply of N in excess of P is considered to promote dinoflagellate dominated HABs. It is therefore important to consider nutrient stoichiometry in addition to total nutrient load in determining any likely increase or decrease in HABs in

response to eutrophication (Glibert & Burford, 2017). It is also important to consider the receiving environment in that nutrient input into a retentive zone is likely to pose significantly greater risk than input into a system with less retentive properties (Glibert et al., 2018c).

The ability to predict how HABs may change with changes in nutrients, at scales from local to regional to global, is critical to the future management and control of HABs and requires a suite of modelling approaches (Glibert & Burford, 2017). A core need for modelling HABs in eutrophic systems is a good estimate of the nutrient load entering the receiving waters. Coupling nutrient discharge to the response of a single species or a group of species requires modelling of the hydrological properties of the receiving waters to determine the retention of the nutrient, and knowledge of the rates and pathways of nutrient consumption and recycling. Understanding the physiological responses of HABs to excess nutrient availability specifically needs to be advanced. Ultimately improved model formulations are needed that will link land-use models with ocean models that incorporate the dynamic physiological behaviour of blooms (Glibert et al., 2018b).

These models will provide management actions to help limit declining oxygen concentrations in response to increasing HABs through a better understanding of the required reduction of nutrients entering the ocean. Nevertheless, present model predictions show the likelihood for increased nutrient pollution and, correspondingly, for continued regional and global expansion of HABs. Scenario analyses for 2050 indicate that this risk will spread to developing countries in South America and Africa, and will continue to increase in the current high risk areas of eastern Asia (Glibert et al., 2018c). For this reason a first-order focus on reducing nutrient loads is critical in order to achieve a long-term reduction in HABs. Traditionally phosphorus reductions have been prescribed for freshwater systems and nitrogen reductions for coastal waters. However, because most systems are hydrologically interconnected dual nutrient reductions are likely to be required to achieve a positive controlling influence on HAB events and their cascading effects of hypoxia and anoxia (Paerl et al., 2018).

3.3.4 Conclusions

Despite the obvious and in many cases dramatic impacts of oxygen depleted waters that may follow the

decay of high biomass HABs there is a considerable need to advance our knowledge and understanding of these events. It is important that we better quantify the frequency and extent of these events, that we provide improved assessments of their impacts and are able to better document future trends. We should continue to improve our understanding, prediction, management and mitigation of HABs globally as guided by the science and implementation plan of *GlobalHAB (Global Harmful Algal Blooms)* – an international programme sponsored by the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO. As a listed objective of *GlobalHAB* we must continue to determine the extent to which increased eutrophication influences the occurrence of HABs and their harmful effects. However, in addition to the focus on the role of nutrient input and limitation in bloom development future studies should seek to establish the nature of phytoplankton mortality within HABs and the consequent role of microbial activity in carbon transformation and oxygen consumption. Measurements should be made to quantify microzooplankton grazing, virus-mediated cell lysis and programmed cell death as plankton mortality processes in order to contribute to the prediction of anoxia linked to HABs.

Moving forward, *GlobalHAB* should also seek to interact with the IOC-UNESCO expert group, the *Global Ocean Oxygen Network (GO₂NE)*, formed to address concerns relating to declining oxygen concentrations in the ocean. This international network of ocean oxygen scientists was established in response to the need for a joint global analysis of ocean deoxygenation and its impacts and will specifically benefit investigation of ocean deoxygenation in response to eutrophication and climate change. Formal collaboration between *GlobalHAB* and *GO₂NE* will explicitly serve investigation of the likely global increase in episodic oxygen depletion associated with increasing HABs in the coastal environment.

3.3.5 References

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3.4 Land-sea-atmosphere interactions exacerbating ocean deoxygenation in Eastern Boundary Upwelling Systems (EBUS)

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Summary

- While the biogeochemical and physical changes associated with ocean warming, deoxygenation and acidification occur all over the world's ocean, the imprint of these global stressors have a strong regional and local nature such as in the Eastern Boundary Upwelling Systems (EBUS). EBUS are key regions for the climate system due to the complex of oceanic and atmospheric processes that connect the open ocean, troposphere and land, and to the fact that they host Oxygen Minimum Zones (OMZs), responsible for the world's largest fraction of water column denitrification and for the largest estimated emission (0.2-4 Tg N yr⁻¹) of the greenhouse gas nitrous oxide (N₂O).
- Taking into account mesoscale air-sea interactions in regional Earth System models is a key requirement to realistically simulate upwelling dynamics, the characteristics of turbulence and associated offshore transport of water mass properties.
- Land-sea-atmosphere interactions modulate warming-induced ocean deoxygenation. For instance, the effect of nutrients delivered to the surface ocean by atmospheric deposition may be to stimulate primary production and CO₂ uptake but also to release N₂O, which could exacerbate warming, offset the increased CO₂ uptake, and thereby accelerate deoxygenation.
- Global warming will alter ventilation and source water properties, oceanic stratification, near-surface wind, mesoscale activity, upwelling rates, low cloud cover, and air-sea exchange of gases and particles. Understanding these changes and their compensating/synergistic influences on the future trajectory of ocean deoxygenation is challenging due to the scarcity of available biogeochemical data and global model biases in EBUS. Regional coupled physical-biogeochemical modelling offers an opportunity for addressing the range of variability in timescales relevant to OMZ dynamics (i.e. from hourly to decadal timescales) in a realistic framework.

Air-sea-land processes/phenomena in EBUS	Mechanisms of their impact on oxygen content in the ocean	Spatial scales
Wind-driven coastal upwelling.	Physical mechanism where cold, nutrient-rich and low-oxygen waters outcrop supporting the high abundance of ocean plants (primary productivity) that produce almost half of the atmospheric oxygen we breathe, absorb a large amount of CO ₂ , and supply food for fish; which under future scenarios (global warming) could modify the export production and deoxygenation as well as other services, e.g. fisheries.	1-100 km
Ocean-atmosphere exchange of gases.	When OMZ waters upwell and impinge on the euphotic zone, there is a potential release to the atmosphere of greenhouse gases such as N ₂ O, CO ₂ and CH ₄ which further exacerbates global warming with feedbacks onto stratification, biological productivity and the oxygen inventory.	1-1000 km
Near-coastal mesoscale atmospheric circulation-induced by orographic effects and underlying sea surface temperature.	Alongshore wind decrease towards the coast (drop-off) influences upwelling dynamics and thereby primary and export production together with oxygen and distribution.	1-100 km
Sub-meso and mesoscale air-sea interactions.	The current feedback (i.e. the effect of the relative wind in the estimate of wind stress) and the thermal coupling between wind and SST at the scale of the eddies are critical processes to determine the biogeochemical properties distribution, including oxygen, through their effect on oceanic mesoscale activity.	1-100 km
Low-level cloud cover and aerosols.	Stratocumulus clouds cover and aerosols particles of natural and anthropogenic origin control incoming solar radiation at the ocean surface, thereby playing a modulating role in either reducing or enhancing primary production with consequences on organic matter production and fate in the water column, and ultimately on subsurface oxygen depletion.	10-1000 km

3.4.1 Introduction

Ocean deoxygenation and acidification, along with ocean warming, form a trio of threats to marine life. These pressures are of critical importance to marine ecosystems because they are accelerating within a short timeframe (Breitburg et al., 2018a; Gruber, 2011; Levin, 2018; Mora et al., 2013). The future status of dissolved oxygen in the coastal and open ocean will in large measure depend on the scale and rate of global environmental change in warming, human population growth especially along coasts, and agricultural practices. Open-ocean deoxygenation, warming and ocean acidification are all driven by increased atmospheric CO₂.

While the biogeochemical and physical changes associated with ocean warming, acidification and deoxygenation occur all over the world, the imprint of these combined global stressors is expected to have a strong regional and local nature, which is exemplified by the Eastern Boundary Upwelling Systems (EBUS). Top predators in the marine food web such as pelagic

billfishes and tunas which might be important for the economic development of certain regions are impaired by deoxygenation, ocean acidification and temperature increase (Breitburg et al., 2018a, b; Stramma et al., 2011).

The EBUS are key regions for the control of the climate system because they connect the open ocean and the troposphere through a complex of oceanic and atmospheric processes, and they host Oxygen Minimum Zones (OMZs), vast oceanic regions responsible for the world's largest fraction of water column denitrification. These regions (Figure 3.4.1), which include: 1) the U.S. West Coast-Oregon and California, 2) the Humboldt Current off Chile and Peru, 3) the Canary Current/Iberian Peninsula, and 4) the Namibia/Benguela upwelling systems, are among the most productive marine ecosystems in the world and support some of the world's major fisheries (Bakun, 1990; Pauly & Christensen, 1995). Production in the EBUS is controlled by two main physical factors. Firstly, equatorward winds along the eastern boundaries of the

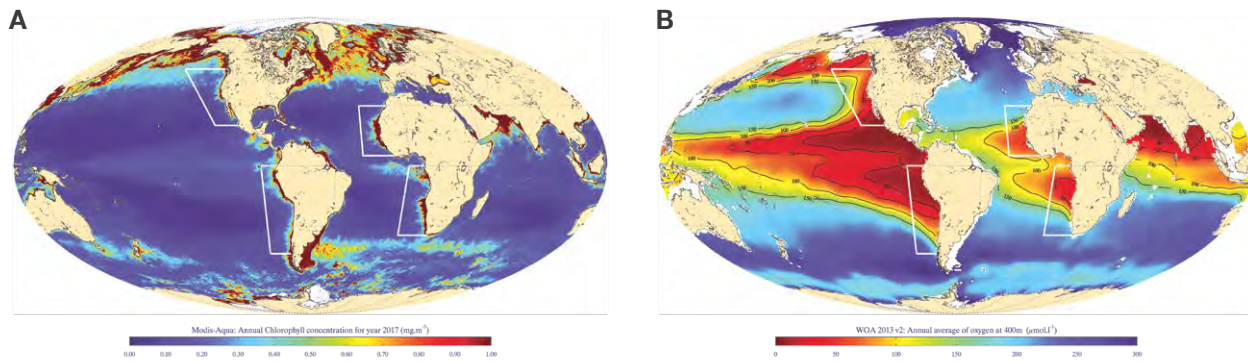


Figure 3.4.1 Eastern Boundary Upwelling Systems (EBUS) (white contour boxes) over an annual 2017 mean of A) chlorophyll-a concentration (derived from MODIS-Aqua), and B) dissolved oxygen concentration (derived from World Ocean Atlas, 2013) at 400m depth.

Atlantic and Pacific Oceans are linked to atmospheric mid-latitude high-pressure systems and force Ekman transport and pumping that drives upwelling of deep nutrient-rich waters into solar illuminated surface waters, enhancing export production and its ultimate decay (or consumption), with increased respiration and draw down of oxygen (Figure 3.4.2). Locally, mesoscale low-level atmospheric circulation may also be affected by land-sea-atmosphere interactions (Chelton et al., 2007; Oerder et al., 2016; Renault et al., 2016a, b) which impact upwelling and productivity (Astudillo et al., 2019; Renault et al., 2016c). Secondly, remote forcing may modulate upwelling at timescales from intra-seasonal (e.g. Kelvin waves) to inter-decadal (e.g. gyre circulation, El Niño-Southern Oscillation (ENSO)) and longer.

The physical state of EBUS oceanic regions varies on a range of time scales that includes intra-seasonal and longer. At interannual timescales, this variability is often associated with tropical modes (ENSO in the Pacific (Dewitte et al., 2012; Frischknecht et al., 2015), the Benguela Niño (Shannon et al., 1986) and the Atlantic Equatorial mode in the Atlantic (Zebiak, 1993)) but also with extratropical modes (the North Atlantic Oscillation (NAO) (Cropper et al., 2014) or the Northern and Southern Annular Modes (NAM and SAM, respectively) (Thompson & Wallace, 2000)) as well as lower-frequency climate modes operating at the basin scale (the Pacific Decadal Oscillation (PDO) (Mantua et al., 1997), the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al., 2008) and the Atlantic Multidecadal Oscillation (AMO) (Enfield et al., 2001)). Ecosystems respond strongly to these variations through the physical influence of winds, light, and temperature, and their effects on micro- and macro-nutrient supply to plankton and oxygen supply to marine life.

In tropical and subtropical regions, EBUS are characterized by high primary and export production that, in combination with weak ventilation, causes natural oxygen depletion and the development of midwater oxygen minimum zones (OMZs) (Karstensen et al., 2008). Low oxygen, low pH values and shallow aragonite saturation horizons co-occur within them, affecting nearly all aspects of ecosystem structure (Chavez et al., 2008) and function in the water column, including the present unbalanced nitrogen cycle (Paulmier & Ruiz-Pino, 2009). The coupling between upwelling, productivity, and oxygen depletion feeds back to biological productivity and their role as sinks or sources of climate active gases. There is for example a net nitrogen loss to the atmosphere of N_2O (particularly in the South-East Pacific OMZ, Arevalo-Martinez et al., 2015). In addition, where oxygen concentrations are extremely low, poisonous hydrogen sulphide (H_2S) gas may erupt to the surface (Bakun, 2017; Schunck et al., 2013; Weeks et al., 2003). EBUS also play a critical role in atmospheric chemistry and climate through emission of active trace gases (Law et al., 2013). In the context of climate change, ocean warming contributes to deoxygenation through two main processes: warmer water holds less oxygen and causes increased stratification which reduces ventilation of both the ocean interior and estuaries.

While there is no doubt that ocean deoxygenation is an ongoing process, there is still a critical gap in knowledge of understanding the exact driving mechanisms, the intensity, and the spatial and temporal variability of ocean deoxygenation as well as its impact on marine food webs and biogeochemistry. Therefore, understanding how land-air-sea interactions control the dynamics behind the OMZs and what may potentially exacerbate deoxygenation becomes not just a matter

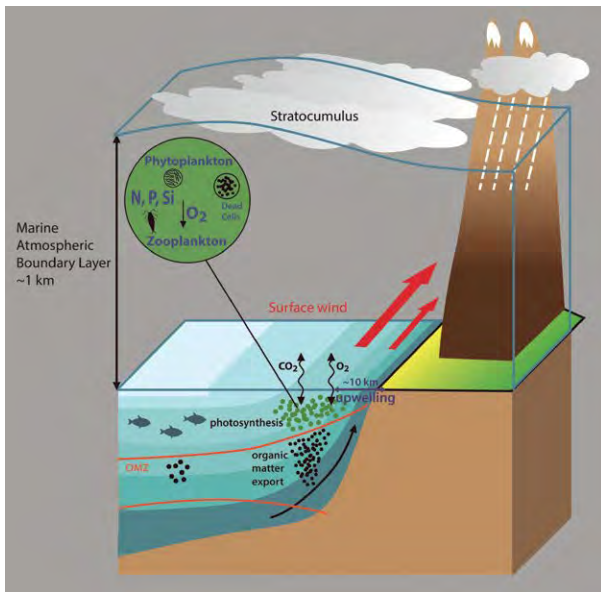


Figure 3.4.2 Schematic of air-sea-land coupled system in upwelling regions.

of scientific interest, but also a major societal concern. The economies of the countries neighbouring upwelling zones, are largely reliant on adjacent marine resources for food and employment (Figure 3.4.3). These countries urgently need improved capacity to predict variations in ecosystem structures and coastal water quality relating to deoxygenation and acidification to define sustainable management strategies for their marine resources.

This synthetic overview focuses first on intricate interactions between the ocean, atmosphere and land in the EBUS by emphasizing the processes driving these interactions, their time-scale modulations, their impacts on oxygen depletion and on future rates of deoxygenation within a changing climate. Second, on local forcing factors that are believed to be key to understanding the sensitivity of ecosystems and OMZs to changes in mean state, e.g. ocean-atmosphere



Figure 3.4.3 Banjul, Gambia, local fishing boats getting ready to leave © Salvador Aznar / Shutterstock.com.

interaction of gases; mesoscale atmospheric circulation (i.e. near-coastal cross-shore wind gradients); submeso- and mesoscale air-sea interactions; and cloud cover and direct and indirect effects of aerosols. Finally, the remote influence of climate modes and their changes in a warming climate is discussed.

3.4.2 Land-air-sea interactions over the EBUS

To study the intricate interactions between physical and biogeochemical processes in upwelling systems requires an integrative approach that links ocean, atmosphere, land, and coastal areas impacted by human activities as well as socio-economic dimensions. This approach has been adopted by the SOLAS 2025 Science Plan and Organization (Brévière et al., 2016) that addresses greenhouse gases, oceanic impacts on atmospheric chemistry and linkages between upwelling and air-sea exchanges of biogenic gases, ecosystem structure, deoxygenation, and acidification (Figure 3.4.4). The impacts of both submeso- and mesoscale variability in ocean (eddies, fronts, filaments) and near-surface atmospheric (winds and its spatial fluctuations) circulations on OMZ dynamics and air-sea exchange, which is also likely impacted by as yet unidentified variations in sea-surface surfactant activity in response to ecosystem variations, are not yet understood. How aerosols link ocean temperature and stratocumulus clouds that impact regional radiative budgets in upwelling zones is a further gap in knowledge that needs to be addressed. Finally, at low latitudes, upwelling systems are often bounded by desert landscapes, and the balance between micronutrient inputs from above versus below is still uncertain, particularly at different time scales.

Low resolution Coupled Model Intercomparison Project (CMIP)-class climate models do not resolve well the essential characteristics of the EBUS where alongshore winds exhibit mesoscale features such as a nearshore decrease in intensity (Astudillo et al., 2017) and the upwelling is confined to a coastal band of only tens of km in width (Estrade et al., 2008). Model errors are amplified by air-sea interactions, yielding a severe warm sea-surface temperature (SST) bias in EBUS (Richter, 2015) (Figure 3.4.5), which has eluded the interpretation of long-term trends in OMZs (Cabré et al., 2015; Stramma et al., 2008, 2012). In addition, processes occurring on a scale smaller than the model grid used may drive the relationship between key ecosystem properties and the physical system, making

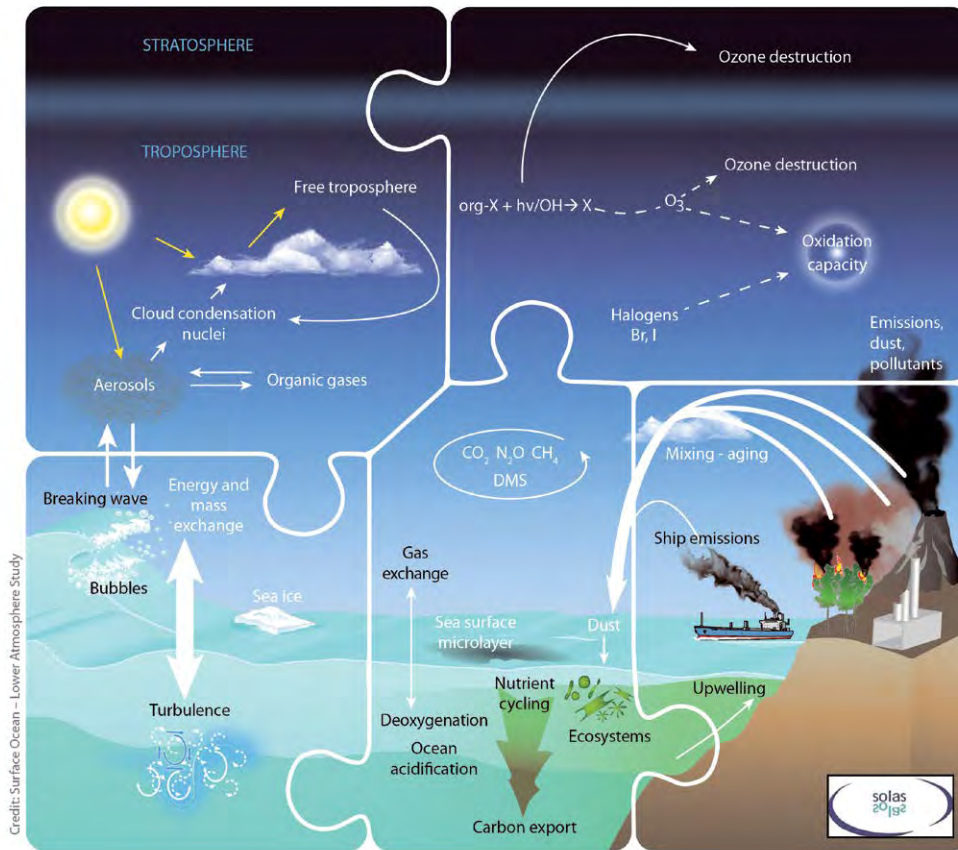


Figure 3.4.4 Jigsaw puzzle schematic of processes involved in ocean-atmosphere-land interactions (with permission from Brévière et al., 2016).

it difficult to understand the consequences of changes in the physical system for marine ecosystems based on the outputs of Ocean Model Intercomparison Project (OMIP) and CMIP class models alone. Several sources cause these biases and owing to ocean-atmosphere coupling it has been difficult to rank them by importance and criticality (Richter, 2015). Among them: i) underestimation of alongshore winds causes poor simulation of upwelling and alongshore currents and

the cooling associated with them, ii) underprediction of stratocumulus decks and their effects on shortwave radiation and low-level atmospheric circulation, iii) inadequate representation of offshore transport of cool waters by mesoscale turbulence is impacted by inadequate spatial resolution, and iv) aerosols provide a further problem for low resolution global models as the models overestimate their effects with respect to observations (Boucher et al., 2013). The large range

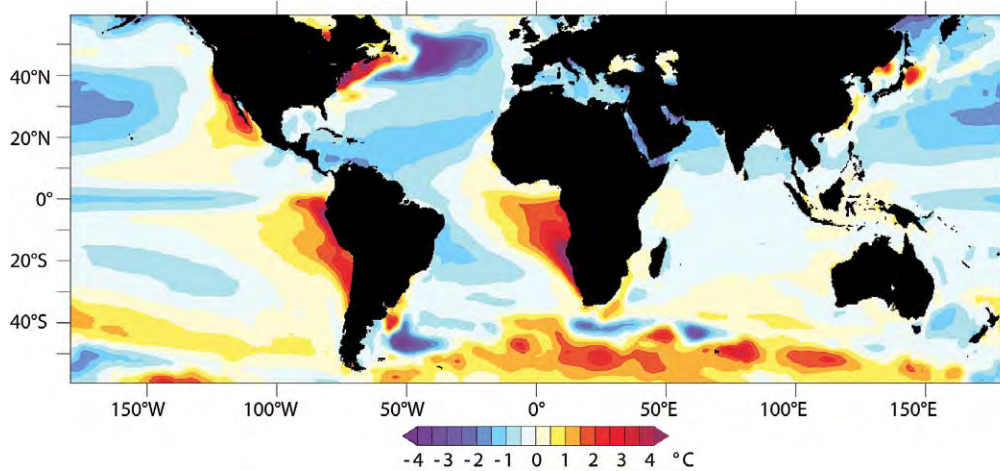


Figure 3.4.5 Annual-mean SST error, relative to the Reynolds SST dataset (Reynolds et al., 2007), of an ensemble of 39 coupled GCMs from the CMIP5 dataset in the historical integration (1982-2005).

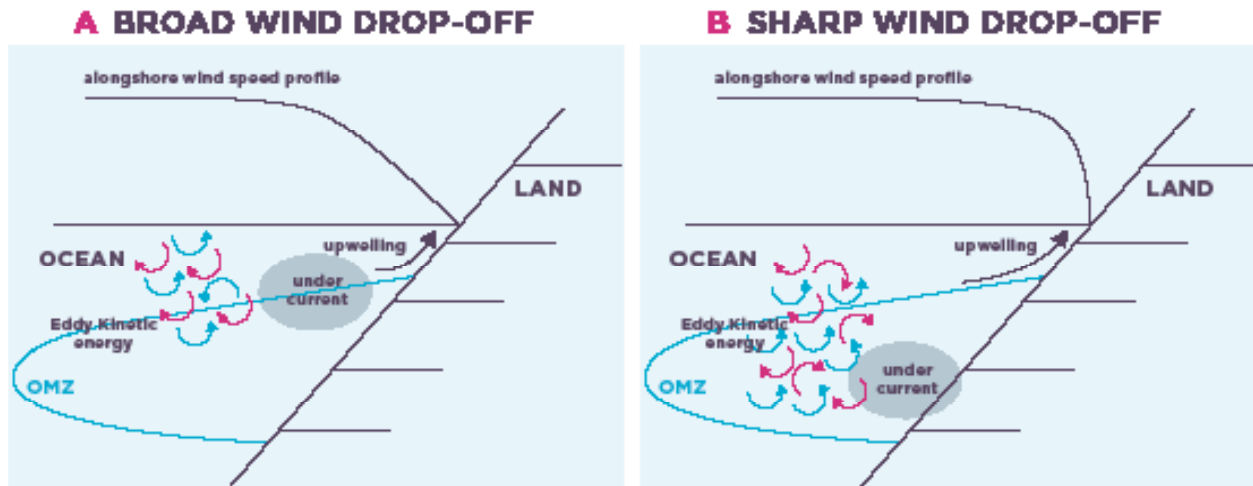


Figure 3.4.6 Schematic of the role of the wind drop-off in upwelling regions : A) Broad wind drop-off, B) Sharp wind drop-off.

of spatial and temporal scales of variability at which physical and biogeochemical processes interact make modelling and prediction of the location, strength and temporal variability of OMZs in EBUS a challenging task (Cabr e et al., 2015; Karstensen et al., 2008; Oschlies et al., 2017). In addition to physical causes for OMZ biases, biogeochemical causes include a particulate organic carbon flux at 100 m that is too high compared to observations, and a too deep expansion of the OMZ due to low remineralization in the upper ocean that is associated with a transfer of particulate organic carbon to depth that is too great (Cabr e et al., 2015).

By better constraining boundary conditions and allowing the relevant resolution to address coastal upwelling dynamics, regional coupled biogeochemical modelling nonetheless has provided a complementary approach to study the dynamics of OMZs and their relationship to climate (e.g. Gutknecht et al., 2013; Machu et al., 2015; Montes et al., 2014; Resplandy et al., 2012). However, the use of atmospheric reanalysis products for oceanic downscaling in EBUS has severe limitations (Astudillo et al., 2017; Cambon et al., 2013; Goubanova et al., 2011; Machu et al., 2015) calling for a regional focus in the treatment of atmospheric forcings.

3.4.3 Ocean-atmosphere interactions of gases

When OMZ waters upwell and impinge on the euphotic zone, they release significant quantities of greenhouse gases, including CO_2 , N_2O and CH_4 , to the atmosphere (i.e. Arevalo-Martinez et al., 2015; Babbitt et al., 2015; Cornejo & Farias, 2012; Cornejo et al., 2015;

Farias et al., 2015; Kock et al., 2012; Naqvi et al., 2010) exacerbating global warming with feedbacks to stratification, biological productivity and the oxygen inventory.

Keeling and Shertz (1992) documented changes in atmospheric oxygen concentrations and found they were dominated by the seasonal cycle of net biological production and by a long-term decline due to the burning of fossil fuels. These changes are small, however, in the order of parts per million and thus negligible compared to observed changes in oxygen in low latitude thermocline waters. Recently, Eddebbbar et al. (2017), using atmospheric potential oxygen ($\text{APO} \approx \text{O}_2 + 1.1 \cdot \text{CO}_2$), showed that air-sea O_2 exchange is modulated at interannual timescales by ENSO through its effect on equatorial upwelling rather than through its effect on biological productivity or thermally driven O_2 exchange, suggesting that the dominant processes behind air-sea interface gas exchange are likely to depend on timescales and regions. Closing budgets of dissolved elements is a key issue that deserves further investigation.

3.4.4 Mesoscale atmospheric circulation

Historically, upwelling indices have been mostly based on estimating Ekman transport from the magnitude of alongshore wind speed. However, within approximately 50-km from the coast alongshore winds are typically strongest offshore, becoming weaker towards the coast owing to orographic effects and, to a lesser extent, the cooler sea-surface temperature of upwelling that stabilizes the marine boundary layer

(Renault et al., 2016a). The wind stress curl induced by this wind drop-off modulates the position and intensity of the undercurrent. In the California system, a broader drop-off induces a shallower and more intense undercurrent (Capet et al., 2004; Renault et al., 2016c) while in the Central Chile upwelling system, the intensity of the wind drop-off is more influential on the surface current (Astudillo et al., 2019). In both cases, this influences the production of eddies near the coast through baroclinic and barotropic instability (Capet et al., 2008), with consequences on the off-shore export of water mass properties. For instance, in the California system, by modulating the coastal circulation, the wind drop-off changes the composition and origin of the biogenic material of coastal zones and thus the upwelling efficiency and OMZ properties (Renault et al., 2016c). The latter showed that the coastal wind shape, by modulating the baroclinic instabilities, modulates the Eddy Kinetic Energy (EKE) levels (Figure 3.4.6). In the open ocean, and in particular in low-nutrient environments, mesoscale processes increase the net upward flux of limiting nutrients and enhance biological production (Garçon et al., 2001; McGillicuddy et al., 2007; Oschlies & Garçon, 1998). In the EBUS, eddy activity can be a limiting factor, which progressively prevents high levels of net primary production as the number of eddies increases by subducting nutrients below the euphotic layer (eddy quenching) (Gruber et al., 2011; Nagai et al., 2015). Thus, in some EBUS, less EKE means a more productive system. Considering wind forcing at fine scales is thus essential to realistically simulate mean current flow in coastal systems, whose characteristics determine the level of mesoscale activity through instability processes (Capet et al., 2008) and thus off-shore transport of water mass properties with likely consequences for oxygen content. Another potentially important factor that is associated with mesoscale atmospheric circulation is related to low-level coastal jets in the atmosphere (as found off Central Peru (Dewitte et al., 2011), Central Chile (Muñoz & Garreaud, 2005), and off Namibia (Patricola & Chang, 2017)) that provide a source of oceanic mixing and variability of the undercurrent.

3.4.5 Submeso- and mesoscale air-sea interactions

Air-sea interaction at sub meso- to mesoscales (horizontal scales of the order of 100 m - 100 km) modulates the properties of the oceanic boundary layer

with rectified effects on the mean circulation in EBUS. For instance, sea-surface temperature gradients at ocean fronts and eddies can modify the surface wind field through processes previously considered for warm waters and larger scale circulation. These processes include the downward transfer of momentum flux to the ocean surface (Koseki & Watanabe, 2010; O'Neill et al., 2010), as well as changes in the pressure gradient across the SST front that generate low-level wind anomalies. Scatterometer observations together with micro-wave observations of SST have facilitated the collection of data that allows the investigation of these processes at the mesoscale. Chelton et al. (2004) and Small et al. (2008) identified a link between modification of the dynamics of the atmospheric boundary layer by SST and the feedback of this modification on the ocean through wind surface stress and heat flux. This link has been observed between sharp SST gradients and surface winds - the so called 'Chelton effect', where winds tend to accelerate over warm and decelerate over cold waters in frontal zones. This effect results in a quasi-linear relationship between the curl (divergence) of the wind and the SST gradient according to a perpendicular (parallel) direction to the wind. These fine scale interactions influence the ocean dynamics through acting on both momentum and heat fluxes and consequently distribution and evolution of biogeochemical properties.

Recent regional coupled modelling studies by Seo et al. (2016) and Renault et al. (2016b) have highlighted the importance of current-wind interaction for the energetics of the California Upwelling System, distinguishing the thermodynamics and dynamics associated with air-sea interaction. In particular, consideration of oceanic currents in estimating wind stress (so-called current feedback) yields a reduction in oceanic EKE in high-resolution models. Wang and Castelao (2016) showed also from satellite observations that a strong coupling between SST gradients and wind stress curl at fine scales is observed in many mid-latitude regions throughout the world, especially in regions with strong fronts like the Western and Eastern Boundary Currents, which challenges how high-resolution oceanic models should be forced by atmospheric re-analyses, the latter encapsulating the effect of the observed turbulent oceanic flow. These processes have yet to be implemented in high-resolution physical-biogeochemical atmosphere and oceanic models, which will help address still unresolved effects on mesoscale eddies, oxygen content and their distribution.



Figure 3.4.7 Stratocumulus clouds © Kingcraft / Shutterstock.com.

3.4.6 Cloud cover, aerosols direct and indirect effects

The EBUS regions are hotspots where global climate models diverge when trying to estimate the top-of-atmosphere radiative effect (Nam et al., 2012). They are characterized by persistent stratocumulus clouds topping a shallow, stable marine boundary layer maintained by the cool SST of upwelling. Stratocumulus clouds (Figure 3.4.7) are highly reflective and modify the net radiative balance at the top of the atmosphere more than any other cloud regimes. Yet, these cloud formations are also amongst the largest source of uncertainty in estimating the radiative budget of the Earth's atmosphere (Boucher et al., 2013).

Aerosol particles of natural and anthropogenic origin play a key role in the radiative budget and more globally in the climatic functioning of EBUS since they modulate the greenhouse effect of long-lived gases through their indirect effects on cloud formation (Boucher et al., 2013). The extent of interaction of the aerosols with radiation and clouds depends on their nature, in particular their chemical composition and size distribution. Aerosols may also influence primary production by modifying low level circulation and the re-emission of sensible heat by

altering the penetration of short-wave radiation into the marine boundary layer, with feedbacks to ocean dynamics, and fertilizing the surface ocean through dust deposition (Figure 3.4.4). Together they influence the biological feedbacks associated with variations in short-wave radiation penetration into the mixed layer that are associated with changes in production. For instance, by absorbing or reflecting light, the direct radiative effect of aerosols could induce a decrease of 15 to 20% in primary production along the Senegalese coast (Mallet et al., 2009). Atmospheric deposition to the ocean through the fertilizing role of micro- and macronutrient inputs has a direct positive effect on primary production (Capone & Hutchins, 2013; Ito et al., 2016; Neuer et al., 2004). Ito et al. (2016) showed in a modelling study that the effect of aerosol deposition on oceanic oxygen is most pronounced at low latitudes despite deposition being greatest in mid-latitudes, due to oceanic transport favouring a regional increase in productivity, respiration and consequently subsurface oxygen depletion. These competing effects of reduction and enhancement are probably modulated by the oceanic circulation. For instance, in the Benguela/Namibia upwelling system, aerosols produced by biomass burning attenuate light and thereby primary production. They stabilize the troposphere and thus reinforce low cloud cover (Adebiyi

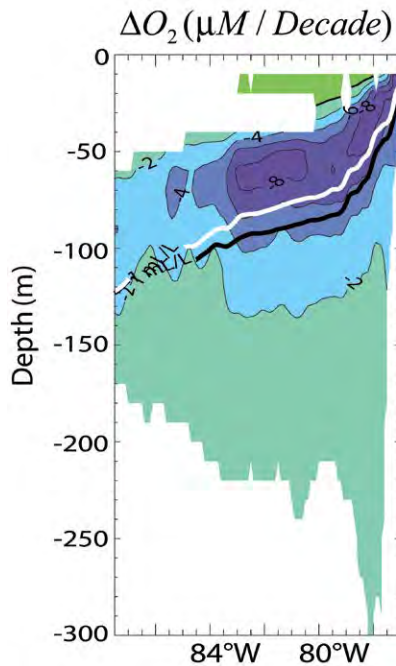


Figure 3.4.8 Long-term trend in dissolved oxygen (in $\mu\text{M decade}^{-1}$) at 12°S over the period 1958–2008 as simulated by a regional coupled model in a configuration similar to Dewitte et al. (2012). The black thick line indicates the iso-oxygen surface at 1 ml L^{-1} (i.e. oxycline depth) over the full period whereas the thick white line is for the period 2000–2008. Only the values significant at the 95% level are shown.

et al., 2015; Formenti et al., 2017). On the other hand, oceanic stratification is reduced (colder SST), inducing a more efficient upwelling and thus an increase in production. Jousse (2015) showed the importance of representing accurately aerosol spatial variability and the associated indirect effects on the Liquid Water Path for realistically simulating solar radiation in the north-east Pacific.

Atmospheric deposition of nitrogen to the ocean (NO_x and NH_3) has tripled since 1860 to 67 Tg N yr^{-1} and is expected to grow further (Duce et al., 2008). Including this increasing atmospheric forcing of anthropogenic nitrogen in model simulations, Ito et al. (2016) and Oschlies et al. (2017) both found a reduction of the simulated tropical thermocline oxygen, but with different amplitudes due to their treatment of nitrogen cycle feedbacks, in particular via nitrogen fixation. Since factors controlling nitrogen fixation and absolute rates are still poorly understood (Landolfi et al., 2015), the impact of atmospheric nitrogen deposition on ocean productivity and thereby on oxygen content still constitutes an important knowledge gap.

Deposition of volcanic ash during explosive eruptions can impact phytoplankton and marine foodwebs by

releasing iron especially and other nutrients into sea water (Garçon et al., 2015; Olgun et al., 2011, 2013). Explosive tropical volcanic eruptions are sufficiently strong to inject aerosols into the stratosphere. These aerosols backscatter incoming solar radiation and can reduce global surface temperature by a few tenths of a degree Celsius for up to two years. Ocean fertilization by volcanic eruptions may also affect marine biomass within the ash-fall and neighbouring areas. How these antagonistic mechanisms operating on different scales will impact primary productivity and oxygen concentrations is a topic which will require further study.

3.4.7 Influence of climate modes and changing climate

The contribution of climate modes to variability in the oxygen inventory is poorly understood mostly because of the scarcity of oxygen data. In the open ocean, changes in ventilation and oxygen supply are considered to be major drivers of trends in the oxygen inventory. How existing processes and pathways of ventilation are being perturbed by climate variability in the ocean within a regional context (in particular OMZs) or through implied mechanisms (e.g. zonal jets in the tropics, mid/high latitude subduction) is an active area of research. The scarcity of data has only allowed the temporal variability of dissolved oxygen to be documented at a few locations (e.g. Bograd et al., 2008; Farias et al., 2007; Fernandez et al., 2015; Graco et al., 2017; Gutierrez et al., 2008; McClatchie et al., 2010; Monteiro et al., 2011; Paulmier et al., 2006) and only over decadal time scales in the California upwelling system.

The investigation of the OMZ forcing by the climate modes requires dedicated modelling studies that incorporate as much as possible the aforementioned processes considering the chain of intricate interactions at different spatial and temporal scales. The influence of climate modes can be through either change in frequency of occurrence of climatic events or change in amplitude of the climate modes, which, through non-linearity, can change the regional mean circulation, producing a so-called “rectified” effect. This is illustrated by the results of a long-term integration with a regional coupled biogeochemical model of the Peru upwelling system which is connected to ENSO dynamics through the propagation of Kelvin waves along the coast. During extreme El Niño events, the coastal upwelling is switched off for several seasons. Conversely during

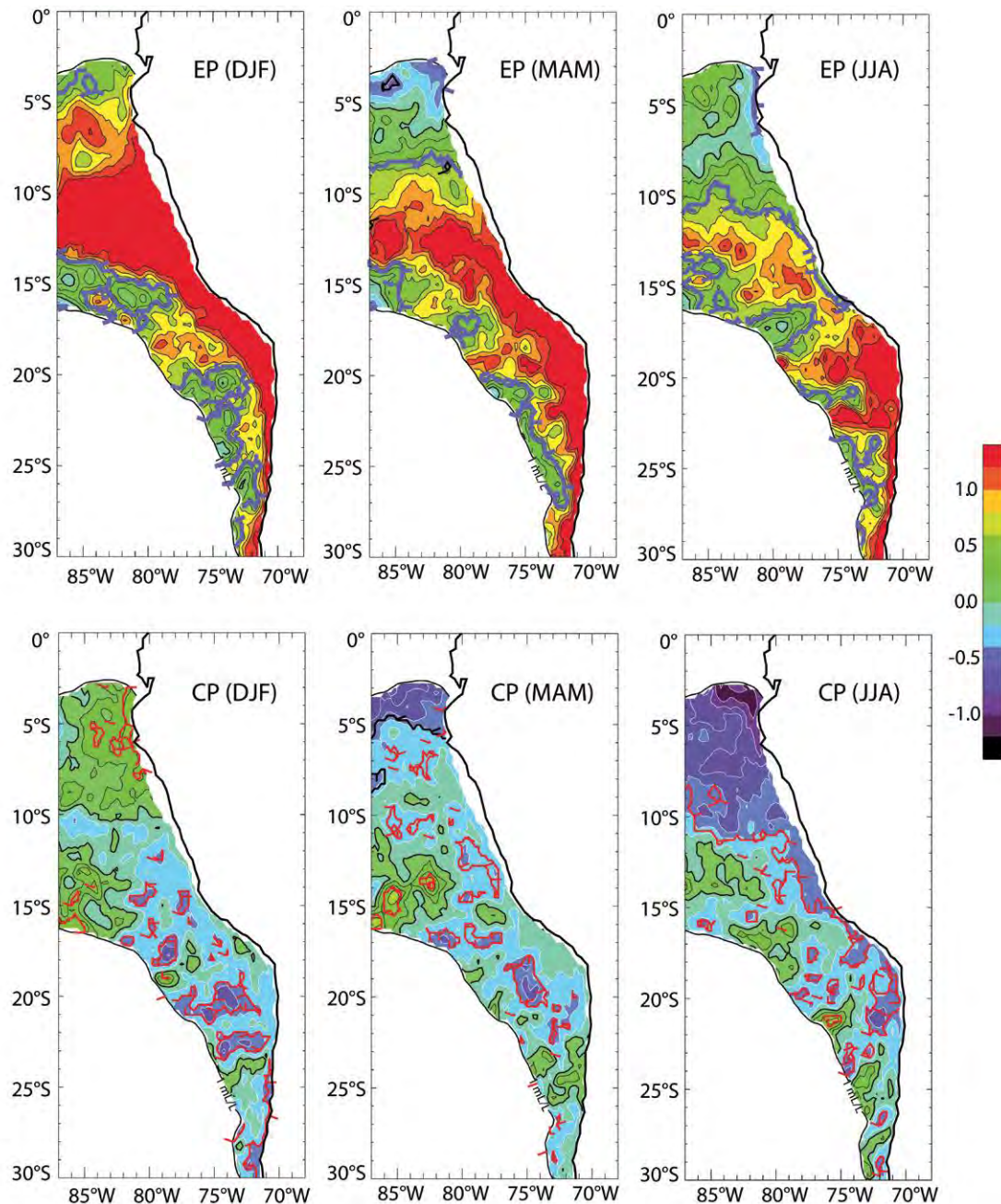


Figure 3.4.9 Composite evolution of dissolved oxygen concentration anomaly at 200m in the OMZ region to the west of South America during Eastern Pacific (EP, top panels) and Central Pacific (CP, bottom panels) El Niño events as simulated by a high-resolution biogeochemical coupled model. See Montes et al. (2014) for the biogeochemical model description and validation and Dewitte et al. (2012) for the ocean model setting and validation. Three seasons are considered with two, MAM and JJA following the peak season of El Niño (DJF). Anomalies are normalized by their variance over the length of the simulation (1958-2008) and so are in adimensionalized units. Anomalies are only shown inside the OMZ which is defined as the region where the O_2 concentration is lower than 1 ml L^{-1} . The significance of the composites is estimated using a bootstrap method with 6 CP and 5 EP events over the simulated period with the contours in red and blue indicating the 90% significance level for EP and CP events, respectively. Tick marks on the contours indicate the direction where the significance level is larger than 90%.

Central Pacific (CP) El Niño, near-normal to cool conditions prevail (Dewitte et al., 2012). The change in frequency of occurrence of the two types (CP and Eastern Pacific - EP) of El Niño as observed since the 1990s (i.e. more occurrence of CP El Niño events, cf. Lee & McPhaden, 2010) leads to an increase in mean

upwelling conditions at decadal timescales (Dewitte et al., 2012) which is consistent with observations (Gutierrez et al., 2011). In the modelling study of Dewitte et al. (2012), the upwelling favourable winds have no trend. Embedding the BioEBUS biogeochemical model into the oceanic model configuration of Dewitte

et al. (2012) yields changes that involve a long-term deoxygenation of the upper part of the OMZ off northern Peru (Figure 3.4.8). This deoxygenation trend above the oxycline of between -2 and $-4 \mu\text{M decade}^{-1}$ over 1958–2008 agrees reasonably well with multi-decadal trend estimates of between -1 and $-3 \mu\text{M decade}^{-1}$ over 1958–2015 estimated from the World Ocean Atlas (Ito et al., 2017), and can be interpreted as an ENSO-induced response of O_2 variations affecting the mean OMZ. Such a rectified effect results from the strong asymmetry of EP El Niño events in the far eastern Pacific (i.e. the fact that the EP El Niño events yield a strong warming off the coast of Peru converse to the CP El Niño or La Niña events). In particular the Peru-Chile Undercurrent brings O_2 deficient waters from the equatorial region (Montes et al., 2014) and is considerably reduced during EP El Niño events, which are associated with a depressed oxycline and have an anomalous positive O_2 concentration within the OMZ (Figure 3.4.9). Conversely during CP El Niño events, the OMZ is intensified, potentially favouring hypoxic conditions. This illustrates that the mechanisms by which climate modes influence OMZ dynamics are not straightforward and could not be limited to processes that influence the upwelling favourable winds (Bakun, 1990).

Similar to the Peru coast, the occurrences of interannual warm (Benguela Niño) and cold events along the coast of Africa have been intensively studied because of their effects on the local marine ecosystems, hypoxia events, and atmospheric circulation and rainfall. Using the same coupled physical/biogeochemical model, Bachèlery et al. (2016) showed that oceanic remote equatorial forcing explains more than 85% of the coastal interannual oxygen fluctuations along the Angolan and Namibian coasts up to the Benguela Upwelling System. These events, associated with poleward propagations of upwelling and downwelling coastal trapped waves, are at a maximum in the subsurface and are controlled by advection processes. The associated variation in the oxygen content in waters below the surface along the shelf may also affect the extension of the OMZ and enhance natural hypoxia.

Global model projections simulate an intensification of winds that favours upwelling in the 21st century at least in mid-latitudes upwelling systems (Ryckaczewski et al., 2015; Wang et al., 2015). A weak confidence in future projections of the evolution of oxygen is mainly due to uncertainty associated with the competing effects of intensifying winds and increasing thermal stratification.

Together they will determine the amount of nutrients entrained in the euphotic zone and thereby biological productivity and oxygen levels. This uncertainty in the modifications of ventilation processes and source-water pathways that supply the EBUS constitutes another difficulty. Indeed, Earth System model simulations suggest large changes in the oxygen inventory for the 21st century, although the agreement among models is weak and especially so for oxygen deficient regions (Bopp et al., 2017; Cabré et al., 2015). Observations in some EBUS have shown trends towards increased upwelling and declining oxygen levels (Garcia-Reyes et al., 2015). However, the degree to which these changes are attributable to climate change is unclear especially in tropical regions owing to the superimposition of natural variability in the climate and regional circulation, inducing a myriad of potential interactions. Understanding and predicting the resulting effects of all antagonistic/synergistic factors on the future trajectory of ocean deoxygenation is an immense and challenging task.

3.4.8 Conclusions / Recommendations

The relationships between upwelling dynamics, marine ecosystems, and atmospheric chemistry have implications for all coastal marine ecosystem services, including fisheries management and aquaculture, carbon sequestration, air cleansing, and cultural and recreational activities in these highly vulnerable coastal regions. Land-air-sea interactions that regulate EBUS-OMZ dynamics continue to be an area of high uncertainty in understanding the Earth system. Rapid changes in ocean-atmosphere interactions are under way and many knowledge gaps remain, raising questions such as:

- What is the magnitude of the EBUS OMZs net radiative forcing and associated climate effect?
- What is the role of these oxygen deficient environments in an oxygenated world for marine biogeochemical equilibrium cycles of: oxygen, nitrogen, carbon, phosphorus, silica, sulphur, etc., as well as for the resilience of marine ecosystems?
- How will these regions evolve under the combined action of multiple stressors (warming, stratification change, acidification and deoxygenation)?

These questions are at the heart of several international initiatives, the Global Ocean Oxygen Network GO₂NE

(<http://www.unesco.org/new/en/natural-sciences/ioc-oceans/sections-and-programmes/ocean-sciences/global-ocean-oxygen-network/>) (Breitburg et al., 2018a,b), the IMSOO (Implementation of Multi-disciplinary Sustained Ocean Observations)/GOOS OMZ demonstration theme with the VOICE (Variability in the Oxycline and Its Impacts on the Ecosystem) project (Garçon et al., 2018; Palacz et al., 2017a, b), and the SCOR Working group N°155 'Eastern boundary upwelling systems (EBUS): diversity, coupled dynamics and sensitivity to climate change' (http://www.scor-int.org/SCOR_WGs.htm) as well as part of the new science plans of several global research projects such as SOLAS, IMBeR and CLIVAR.

An assessment of the different levels of response is needed that includes further analysis of historical data and long-term observations, experiments and forecast models that take into account the impacts of multiple stressors at the physiological/biogeochemical, organism, and ecosystem levels. There is no doubt that the most effective solution to mitigate global environmental change and the deoxygenation trend is to curb carbon emissions. Recognizing and understanding these climate stressors which interact with other human activities is essential to sustainably manage ocean ecosystems. What the costs of no action will be is at present unclear due to a lack of information and understanding.

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Oxygen projections for the future

4

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Summary

- The loss of oxygen from the ocean, termed “deoxygenation”, is a consequence of climate warming. As the ocean warms, it loses oxygen due to the direct effect of temperature on gas solubility: warmer waters hold less oxygen. Additionally, reductions in vertical mixing associated with enhanced upper-ocean buoyancy stratification cause respiration-driven oxygen depletion at depth.
- The ocean as a whole is expected to lose about 3–4% of its oxygen inventory by the year 2100 under a “business-as-usual” scenario (RCP8.5) with most of this loss concentrated in the upper 1000 m where species richness and abundance is highest. There will be distinct regional differences in the intensity of oxygen loss as well as variations in ecological and biogeochemical impacts. There is consensus across models that oxygen loss at mid and high-latitudes will be strong and driven by both solubility reductions and increased respiration effects. Projections are more ambiguous in the tropics, where models suggest that there will be compensation between oxygen decline due to reduced solubility and oxygen increase caused by reductions in cumulative respiration. Thus, oxygen concentrations in the core of present-day oxygen minimum zones may increase; however, the total volume of waters classified as “suboxic” and “hypoxic” is still likely to grow substantially.
- Low oxygen conditions and increased temperature jointly limit the viable habitat for marine macro-organisms; warming accompanied by deoxygenation will drive habitat contraction and fragmentation in regions where oxygen levels decline below metabolic requirements. Expansion of suboxic zones will likely disrupt the cycling of nitrogen in the ocean; denitrification may increase, yielding greater rates of fixed nitrogen loss from the ocean. Perturbations to the nitrogen cycle may include substantial changes to nitrous oxide production, though this is highly uncertain.
- Warming-driven deoxygenation cannot be easily reversed; indeed, the ocean oxygen inventory is likely to take centuries to recover from warming projected under “business-as-usual” emissions scenarios. Deoxygenation is intrinsically linked to climate warming; reduction of human-driven warming is the only means of preventing widespread ocean oxygen loss. Stabilization of climate-changing emissions, however, can enable ocean ventilation to recover to some degree, thereby mitigating oxygen loss. Given the long persistence timescales of climate drivers, earlier mitigation action will yield maximum benefit.

Ocean hypoxia effect	Potential consequences
Climate warming drives ocean oxygen loss by a direct mechanism: sea water holds less oxygen as temperatures rise. However, warming also reduces circulation, thus shutting down the oxygen supply to the ocean depths. It is the compounding influence of direct warming effects amplified by changes in circulation that make oxygen so sensitive to climate.	<ul style="list-style-type: none"> • Vertical habitat compression for organisms in the upper ocean. • Expansion of regions with denitrification leading to enhanced loss of fixed nitrogen from the ocean and possible changes to nitrous oxide production. • Reduced oxygen levels in the open ocean, with effects propagating to coastal systems.
Model projections are relatively consistent for high-latitudes, where oxygen loss is driven by both solubility and respiration effects; there is less agreement across models in the tropics, where oxygen loss due to solubility reductions appears to be offset by diminished respiration.	<ul style="list-style-type: none"> • Oxygen projections at high-latitudes have less uncertainty than in the tropics. • Predictions of tropical oxygen distributions are highly uncertain.
Comparisons of models and observations suggests that models underestimate the true rate of ocean oxygen loss.	<ul style="list-style-type: none"> • Ocean deoxygenation may occur more rapidly and may be more severe than suggested by models.
Warming-driven deoxygenation cannot be easily reversed.	<ul style="list-style-type: none"> • Earlier action to limit carbon dioxide emissions and reduce warming will yield greater benefit.

4.1 Introduction

Warming of the climate system is driving declines in ocean oxygen content, presenting significant concerns for marine ecosystems. Global warming leads to ocean oxygen loss because O_2 is less soluble in warmer waters—and warming increases upper ocean stratification, curtailing the supply of oxygen to the ocean interior (Breitburg et al., 2018; Keeling et al., 2010). Model projections of deoxygenation under the recent Couple Model Intercomparison Project Phase 5 (CMIP5) (Taylor et al., 2012), suggest that by the year 2100, the ocean will have lost 3–4% of its O_2 inventory, with much of this loss concentrated in the upper ocean (above 1000 m) (Bopp et al., 2013; Cocco et al., 2013). This is a significant perturbation that is very likely to have widespread consequences for marine life and biogeochemical cycles.

4.1.1 Animals

Dissolved oxygen (O_2) is a fundamental control on marine habitat. Animals require oxygen and, except for marine mammals and reptiles, animals in the sea depend on the oxygen dissolved in sea water for their supply. Typically, animals are not sensitive to oxygen distributions as long as concentrations remain sufficiently high; as O_2 levels drop, however, organisms are unable to sustain aerobic metabolism and will eventually die (Vaquer-Sunyer &

Duarte, 2008). Concentrations of oxygen below about 60 mmol m^{-3} ($1 \text{ mmol m}^{-3} = 1 \text{ }\mu\text{M}$) are termed “hypoxic”; regions with oxygen persistently below this threshold are referred to as “dead zones”: normal respiration is severely limited in these regions and animals cannot function (Vaquer-Sunyer & Duarte, 2008). Importantly, the oxygen requirements for juveniles can exceed that of mature organisms; thus, even if oxygen concentrations are sufficient to sustain adults, they may still impinge upon the survival and development of larvae (e.g. Miller et al., 2002). Dead zones are found in many coastal systems, caused by nutrient pollution that drives eutrophication and oxygen depletion, though global ocean deoxygenation is also expected to exacerbate these effects (Breitburg et al., 2018; Diaz & Rosenberg, 2008; Rabalais et al., 2002). Hypoxic tolerances vary considerably across taxonomic groups and lethal thresholds have been found well above the conventional definition of hypoxia (Figure 4.1B) (Vaquer-Sunyer & Duarte, 2008). Furthermore, hypoxic tolerances can change as a function of temperature and body size, requiring consideration of multiple life stages and environmental factors when projecting the ecological impacts of deoxygenation (Deutsch et al., 2015; Pörtner & Farrell, 2008).

While dead zones may expand under climate warming, the impacts of ocean deoxygenation on marine macro-organisms may be more profound and widespread than

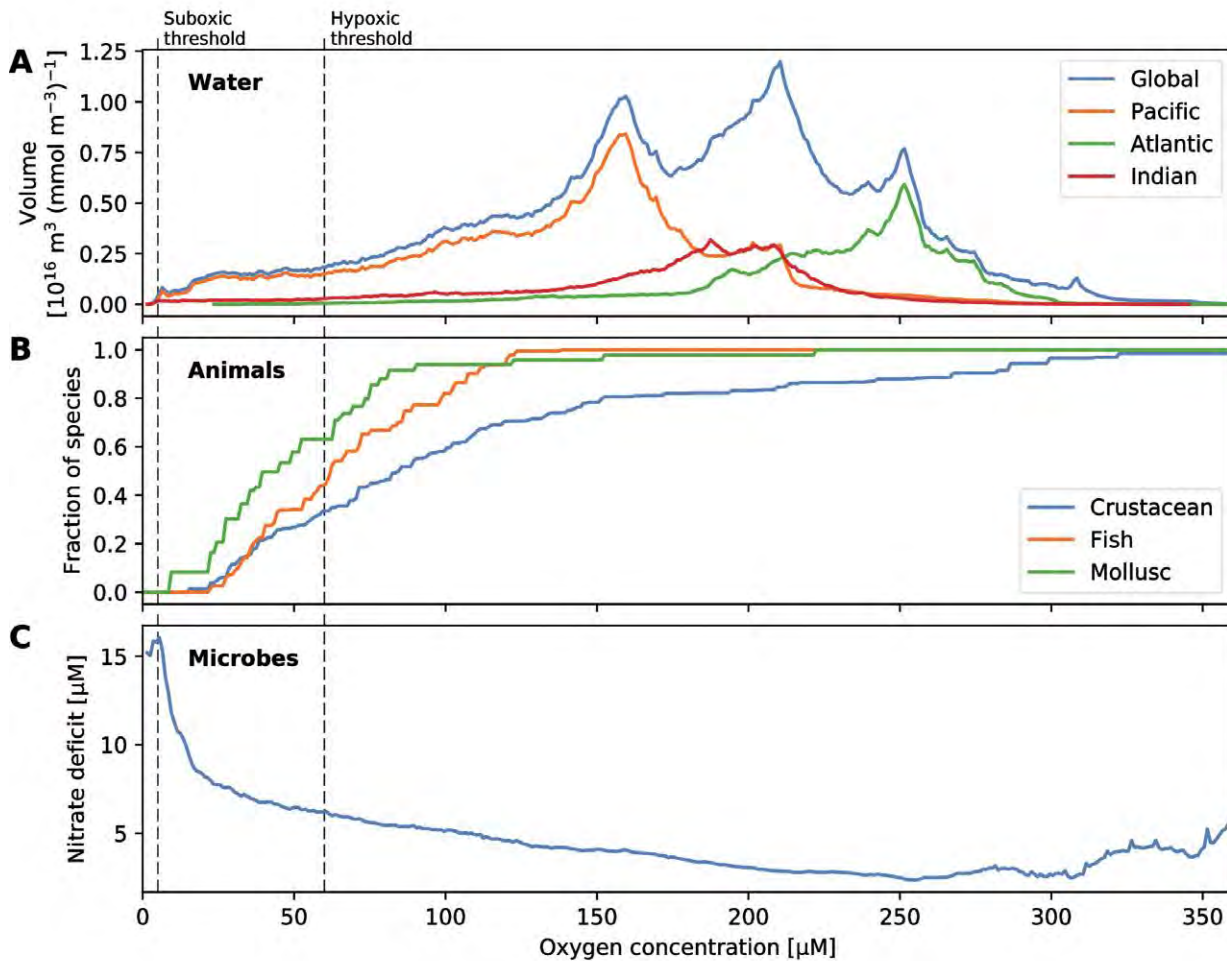


Figure 4.1 Distributions as a function of oxygen concentration: (A) the volume of water in the global ocean, and in each major basin; (B) the fraction of species in three groups of organisms that survive at a given oxygen concentration; and (C) the nitrate deficit relative to phosphorus, defined as $-N^* = N - r_{N:P} P$ (Gruber & Sarmiento, 1997), where $r_{N:P}$ is the stoichiometric ratio of remineralization of organic matter (we assume $r_{N:P} = 16$) (Anderson & Sarmiento, 1994). Mortality thresholds are from a compilation of empirical studies (Vaquer-Sunyer & Duarte, 2008).

suggested by projected changes in hypoxic volumes. Indeed, the large-scale biogeographic distributions of ectothermic organisms in the contemporary ocean are limited in part by the combined effects of temperature and oxygen (Deutsch et al., 2015). Metabolic rates increase in proportion to temperature; thus, an aerobic organism's demand for oxygen also increases in warmer waters. Viable habitat is bounded by the need for a sufficient supply of oxygen to meet temperature-dependent metabolic demand. Concomitant warming and ocean deoxygenation, therefore, can be expected to result in a contraction of metabolically viable habitat (Deutsch et al., 2015). Organisms are likely to be forced poleward, where cooler waters temper oxygen demand; additionally, since oxygen concentrations typically decline with depth, we can expect vertical habitat compression as the region of the near-surface ocean with sufficient oxygen shrinks (Koslow et al., 2011). This may be particularly important for deep ocean predators

such as tuna (Mislán et al., 2017). It is important to note that future changes in ocean oxygen and temperature will occur in concert with increasing concentrations of CO_2 and ocean acidification, which also have independent and possibly synergistic impacts on the health of ocean organisms (e.g. Doney et al., 2009; Hoegh-Guldberg et al., 2007; Pörtner et al., 2004)

4.1.2 Microbes

Just as higher animals are physiologically constrained when oxygen concentrations become low, oxygen also exerts a strong control on microbial metabolism. When oxygen in the ocean falls below “suboxic” concentrations ($\text{O}_2 < 5 \text{ mmol m}^{-3}$), aerobic metabolism becomes inefficient and alternative oxidation pathways become more energetically favourable: microbes that use compounds other than oxygen as an electron acceptor to oxidize organic matter begin to dominate. It

may initially seem strange to worry about impinging on microbes; much of our familiarity with microbes stems from disease. Microbes, however, play a fundamental role in sustaining all life on Earth by enabling nutrient cycling. The importance of nutrient cycles can be appreciated by considering that the energy that powers virtually all life on Earth is harvested from the Sun during photosynthesis. Life is carbon based—but nutrient elements such as nitrogen and phosphorus, are also fundamental building blocks required to make organic materials. Plants and algae use sunlight to make organic matter from carbon dioxide and nutrients; they split water, use the hydrogen energy to make biomass and release O_2 as waste. The organic matter created by photosynthesis enters the food chain; primary producers are eaten by secondary producers and so on, supporting complex ecosystems. In this manner, primary production in the ocean is the ultimate constraint on the biomass of the whole marine ecosystem. Secondary producers have fundamentally different metabolisms than the photosynthesizers they eat; rather than producing oxygen as waste, they require oxygen to oxidize organic matter during respiration; the resulting energy is harnessed, supporting synthesis of organic matter and functional activities such as acquisition of food, growth, predator avoidance, and reproduction. The inorganic nutrients incorporated during photosynthesis are carried up the food chain; ultimately, however, as organisms die, the organic material of which they are comprised is decomposed: microbes oxidize this material, converting its constituents back to their inorganic forms, returning nutrients to the pools upon which photosynthesis relies. Since the ocean is a single volume of fluid, interconnected by circulation, the marine cycles of nutrients like nitrogen and phosphorus are coupled on a global scale—entering the food chain during photosynthesis, returning to dissolved inorganic forms when organic matter is “remineralized” via microbially-mediated oxidation.

Oxygen plays a fundamental role in these global nutrient cycles. To illustrate this, we need to consider that the cycles of nitrogen and phosphorus are regulated by fundamentally different processes—yet organic matter is composed of nitrogen and phosphorus in specific relative amounts: more nitrogen is useless with insufficient phosphorus and vice versa. Phosphorus is supplied to the ocean from the land via weathering, run off, and atmospheric deposition of dust; it is removed from the ocean when organic material sinks and is buried in sediments. Nitrogen, by contrast, has only minor inputs from the atmosphere and runoff; it

is sourced primarily from the land, which consists of about 78% dinitrogen gas (N_2) (Gruber & Galloway, 2008). Most photosynthetic organisms cannot use N_2 directly; only certain types of cyanobacteria (diazotrophs) can “fix nitrogen,” converting N_2 gas into forms available to other organisms. Thus, microbes determine the rate at which fixed nitrogen enters the ocean—and, as it turns out, microbes also determine the rates of removal. As stated above, when oxygen concentrations decline to suboxic levels, aerobic processes become increasingly inefficient; ultimately, when oxygen is too scarce, microbes use other compounds as the electron acceptor needed to oxidize organic matter. In the ocean, nitrate (NO_3^-) is a widespread form of fixed nitrogen; nitrate is used to oxidize organic matter in suboxic regions, converting the nitrogen to N_2 , which is lost to the atmosphere. This process is termed “denitrification” and it accounts for the majority of fixed nitrogen loss from the ocean (Gruber, 2004; Gruber & Galloway, 2008). The signature of denitrification is evident as a “deficit” of nitrate relative to phosphate in suboxic regions of the global ocean (Figure 4.1C). As suboxic zones grow, the loss of fixed nitrogen to denitrification can increase, and may ultimately feedback to limit primary productivity (Deutsch & Weber, 2012). As ocean ecosystems are built on photosynthesis, climate-driven perturbations to oxygen that impact nutrient cycles can ultimately feedback to higher trophic levels. Microbially-mediated processes involved in the nitrogen cycle can also have direct impacts on climate. Denitrification and nitrification (the oxidation of ammonium to nitrate) can produce nitrous oxide (N_2O), which is a potent greenhouse gas (Bange et al., 2010). Expansion of hypoxic and suboxic volumes in the ocean may change the production and release of N_2O (Martinez-Rey et al., 2015; Nevison et al., 2003), though this involves substantial uncertainty.

4.1.3 Palaeo-perspective

The history of oxygen on Earth provides an important perspective on the future of oxygen in the ocean. Indeed, for roughly the first half of Earth’s 4.5 billion-year history, oxygen was not plentiful in the atmosphere; rather, significant concentrations of oxygen only arose between 2.4 and 2.1 billion years ago (Lyons et al., 2014). Photosynthesis is the primary source of oxygen in the atmosphere, illustrating how the evolution of life is intertwined with the character of Earth’s environment: the accumulation of oxygen in the atmosphere

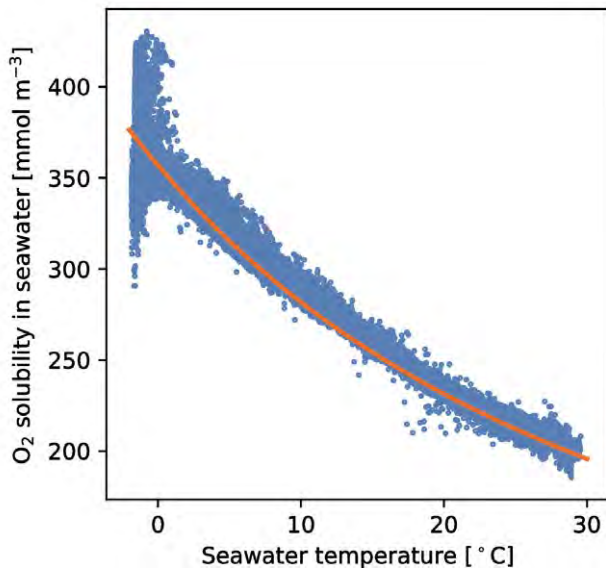


Figure 4.2 Relationship between dissolved oxygen and temperature for surface data in the World Ocean Atlas 2013 (Garcia et al., 2014). The orange line shows the saturation concentration of oxygen at equilibrium with the atmosphere (Garcia & Gordon, 1992). Strong deviations from saturation are evident at near-freezing temperatures, which is partially a function of sea-ice inhibition of gas exchange (Ito et al., 2004).

enabled animal life, whereas prior to the evolution of photosynthesis, aerobic metabolisms were not viable.

Earth's history has been punctuated by five major extinctions: catastrophic events when more than 65% of extant species disappeared. The present era has been characterized as Earth's sixth mass extinction event, caused by humans and leading to irreversible changes in ecosystems (Barnosky et al., 2011). Some of the mechanisms driving present extinction rates are unique to the global expansion of humans—for instance, habitat fragmentation, the spread of invasive species and disease through transportation, and pollution in the form of trace metals, pesticides, plastic, and other compounds. However, the liberation of massive amounts of geologically-sequestered carbon has happened before; thus, climate warming and the loss of ocean oxygen have well-documented analogues in the geologic record. The end-Permian extinction, for instance, which occurred ~252 million years ago, is the largest extinction event in Earth's history; nearly 95% of terrestrial and marine species perished (Erwin, 1993; Raup, 1979). Notably, the end-Permian extinction was coincident with massive volcanism, which led to elevated CO_2 and climate change; extinctions in the ocean during this event can be explained by changes in oxygen levels, CO_2 , and temperature (Song et al., 2014), thus this catastrophic event, while stronger in

magnitude, provides an analogue to the ocean of the 21st century (Payne & Clapham, 2012).

4.1.4 Climate-driven deoxygenation

Understanding of the basic mechanisms driving ocean deoxygenation is robust (Bopp et al., 2002; Breitburg et al., 2018; Gruber, 2011; Keeling et al., 2010; Matear & Hirst, 2003; Najjar & Keeling, 2000; Plattner et al., 2002). Increasing concentrations of greenhouse gases, primarily carbon dioxide, trap heat in the atmosphere, leading to a planetary energy imbalance (Trenberth et al., 2014). The ocean is the dominant thermal reservoir in the climate system and it is estimated that the ocean has absorbed more than 90% of the excess heat accumulating in the Earth system since the beginning of the industrial revolution (Cheng et al., 2016; Loeb et al., 2012; Rhein et al., 2013). As the planet has warmed, this extra heat has accumulated in the near-surface ocean (Abraham et al., 2013; Balmaseda et al., 2013; Levitus et al., 2012). Warmer waters hold less oxygen due to the temperature dependence of solubility; thus, as the surface ocean warms, oxygen concentrations can be expected to decline according to the solubility relationship with temperature (Figure 4.2). Reductions in solubility are compounded by an additional mechanism driving deoxygenation, which involves changes to ocean circulation in response to warming. The density of sea water is strongly temperature dependent; warmer waters are less dense or, equivalently, more buoyant. As extra heat is absorbed by the ocean, it tends to warm the surface ocean at a greater rate than warming at depth, increasing the density difference between surface and deep water. This enhanced density stratification inhibits exchange between the oxygen-rich surface ocean and waters in the interior where oxygen is consumed by respiration. Diminished surface-to-depth exchange reduces the quantity of oxygen supplied to the ocean interior, shifting the balance maintaining oxygen concentrations: consumption exceeds supply, oxygen concentrations decline. This reinforcing mechanism, wherein temperature-related solubility effects are amplified by the effect of density stratification, makes oxygen exceptionally sensitive to variations in climate. However, the enhanced stratification and slower circulation of the upper ocean has a countervailing effect: it simultaneously reduces the supply of nutrients from deep waters to the photic zone, reducing productivity at the surface and ultimately the respiration of organic matter below. The reduced oxygen demand offsets part of the reduced supply. This compensating mechanism,

in concert with the reinforcing mechanism noted above, creates the potential for complex regional and time-scale dependent behaviour in the O_2 changes. Indeed, as demonstrated below, dissolved oxygen is highly dynamic in the present-day climate, exhibiting dramatic variations on annual to multi-decadal timescales (Deutsch et al., 2011; Ito & Deutsch, 2010). These natural fluctuations in oxygen drive important shifts in marine ecology and biogeochemistry (Deutsch et al., 2014; Rabalais et al., 2010; Yang et al., 2016; Zamora et al., 2012)—and yet over the next century, the amplitude of oxygen changes is likely to be much greater, far exceeding the range of multi-decadal natural variability (Henson et al., 2017; Long et al., 2016; Rodgers et al., 2015).

4.1.5 Earth system models

While the basic mechanisms controlling deoxygenation are well-understood in principle, details of ocean circulation and biological productivity lead to regional differences in the rate and magnitude of oxygen loss. This chapter discusses projections of ocean oxygen under future emissions scenarios. The most sophisticated tools for developing such projections are Earth system models (ESMs); these consist of coupled atmosphere and ocean general circulation models (GCMs) and include representations of processes relevant to ocean biogeochemistry. The chapter objectives are to review the state of knowledge regarding the rate, magnitude and geographic distribution of expected deoxygenation trends, relying primarily on ESM projections.

To illustrate both the robust and uncertain projections for future ocean oxygen, results from two primary collections of model solutions are presented. First are results from a large ensemble of a single, fully-coupled ESM: The Community Earth System Model (CESM). The CESM Large Ensemble (CESM-LE) has more than 30 independent realizations of the historical period from 1920–2005 and future projections out to 2100 under the CMIP5 “business-as-usual” RCP8.5 forcing scenario (Kay et al., 2015). Second are results from a subset of the CMIP5 multi-model ensemble, providing a perspective on the degree to which CESM is representative of this broader collection of independently developed models. The models are from the Geophysical Fluid Dynamics Laboratory (GFDL) (Dunne et al., 2012, 2013); the UK Met Office Hadley Centre (HadGEM) (W.J. Collins et al., 2011; HadGEM2 Development Team, 2011); the Max Planck Institute (MPI) (Giorgetta et al., 2013); and the Institut Pierre Simon Laplace (IPSL) (Dufresne et

al., 2013). Also included are CESM’s CMIP5 solutions (Hurrell et al., 2013); this model is similar to the CESM-LE in many respects but has a different atmospheric model so does display distinct behaviour.

The “spread” across the CESM-LE and the CMIP5 ensembles reflects different sources of uncertainty (Hawkins & Sutton, 2009). Internal variability is an intrinsic feature of the climate system, arising from non-linear dynamical processes and interactions between the ocean, atmosphere and land surface that each integrate forcing over different timescales (Hasselmann, 1976). Earth system models generate internal climate variability representative of that in nature, thus the ensemble spread of the CESM-LE can be used to assess the contribution of natural variability to uncertainty in future projections, which is particularly important on regional scales (Deser et al., 2012; Lovenduski et al., 2016; McKinley et al., 2016). While internal climate variability contributes to the spread in the CMIP5 ensemble, each of the models in this collection has distinct behaviour reflecting differences in underlying formulations. Thus, spread across the CMIP5 models reflects a minimum bound on the contribution of “structural uncertainty” to future projections (Hawkins & Sutton, 2009; Lovenduski et al., 2016). Finally, human activity introduces substantial uncertainty into future projections. Indeed, the magnitude of surface warming during the next century is strongly dependent on the amount of greenhouse gases emitted over the next several decades (M. Collins et al., 2013). To account for this source of uncertainty, CMIP5 included four “Representative Concentration Pathway” scenarios intended to span a range of total radiative forcing at 2100 from 2.6 W m^{-2} (RCP2.6) to 8.5 W m^{-2} (RCP8.5) (Meinshausen et al., 2011). The differences in these scenarios illustrate the contribution of “scenario uncertainty” to future projections. The primary focus will be on the RCP8.5 scenario, but limited results from RCP4.5 and discussion of the benefits of climate change mitigation activities to the ocean deoxygenation problem (Henson et al., 2017) are also included.

4.2 Understanding dissolved oxygen

Several concepts are required to understand the mechanisms driving ocean deoxygenation. To review these, we first examine the large-scale structure of present-day oxygen distributions. An understanding of the basic physical and biological controls on these distributions provides perspective on the mechanisms by which climate warming drives oxygen loss. Our

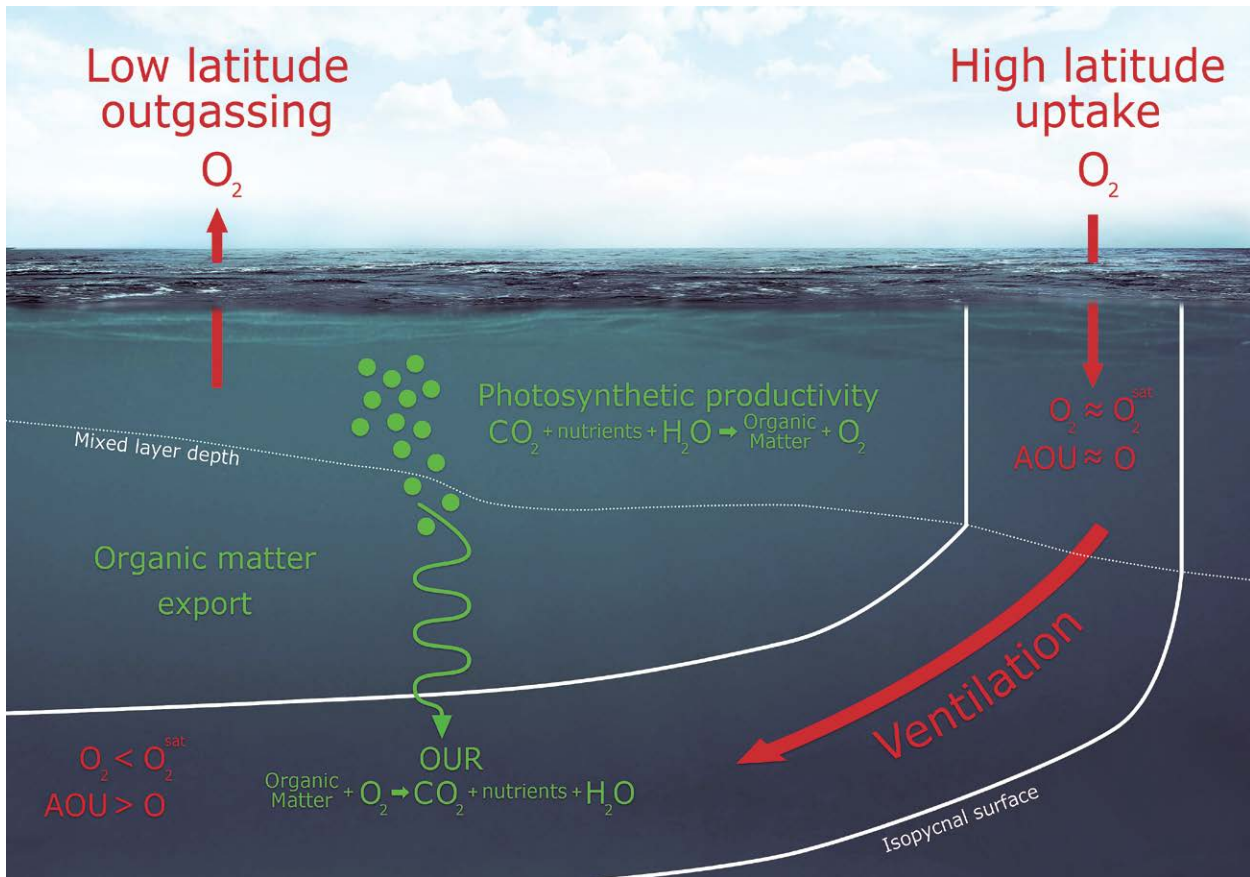


Figure 4.3 Schematic illustration of the mechanisms controlling oxygen distributions in the ocean. Oxygen is produced in the surface ocean by biological productivity, which generates organic matter. Air-sea exchange keeps oxygen in the surface ocean near saturation concentrations with the atmosphere (O_2^{sat}). Oxygen is consumed in the interior as organic matter is respired; the rate of oxygen consumption is termed the “oxygen utilization rate” (OUR). “Apparent oxygen utilization” ($AOU = O_2^{\text{sat}} - O_2$) provides an estimate of the amount of oxygen that has been consumed by respiration as a water parcel circulates in the ocean interior.

primary resource for understanding the global scale ocean oxygen distributions come from the World Ocean Atlas (WOA), produced by the National Oceanographic Data Center (United States). WOA is a compilation of observations that have been objectively-analysed to produce gridded fields at a spatial resolution of $1^\circ \times 1^\circ$. While only annual-mean distributions are considered here, WOA includes monthly data, enabling evaluation of the seasonal cycle. The observations upon which WOA is based, however, do not have sufficient coverage to enable a globally gridded-product with temporal resolution beyond the monthly mean annual cycle. Thus, efforts to evaluate global-scale trends in O_2 based on observations (section 4.2.1) have relied on independently-developed compilations of observations (e.g. Helm et al., 2011; Ito et al., 2017; Schmidtko et al., 2017).

Oxygen is supplied to the ocean via exchange with the atmosphere and photosynthetic oxygen production at the surface; the ocean surface, therefore, tends to be

well-oxygenated—which is to say the concentration of oxygen remains near the saturation concentration (O_2^{sat}) with respect to the atmosphere. Photosynthesis in the surface ocean produces organic matter; detrital remnants of this material sink to depth where they are broken down by microbial respiration, consuming oxygen (Figure 4.3). Thus, oxygen concentrations are elevated where freshly subducted surface waters flow into the interior, but concentrations decline downstream of these regions as a respiration signal accumulates. Large-scale patterns are set by the global overturning circulation, wherein oxygen is supplied to the ocean in ventilation regions, and is subsequently depleted as waters circulate in the interior. In the upper ocean thermocline, where respiration rates are relatively fast, oxygen concentrations span a range from full saturation at the surface to near zero at the tropical terminus (Figure 4.4A). In the abyssal ocean, where respiration rates are very slow, the high O_2 values obtained in polar surface waters decline to intermediate values at the end of the great ocean conveyor in the Pacific (Broecker, 1991).

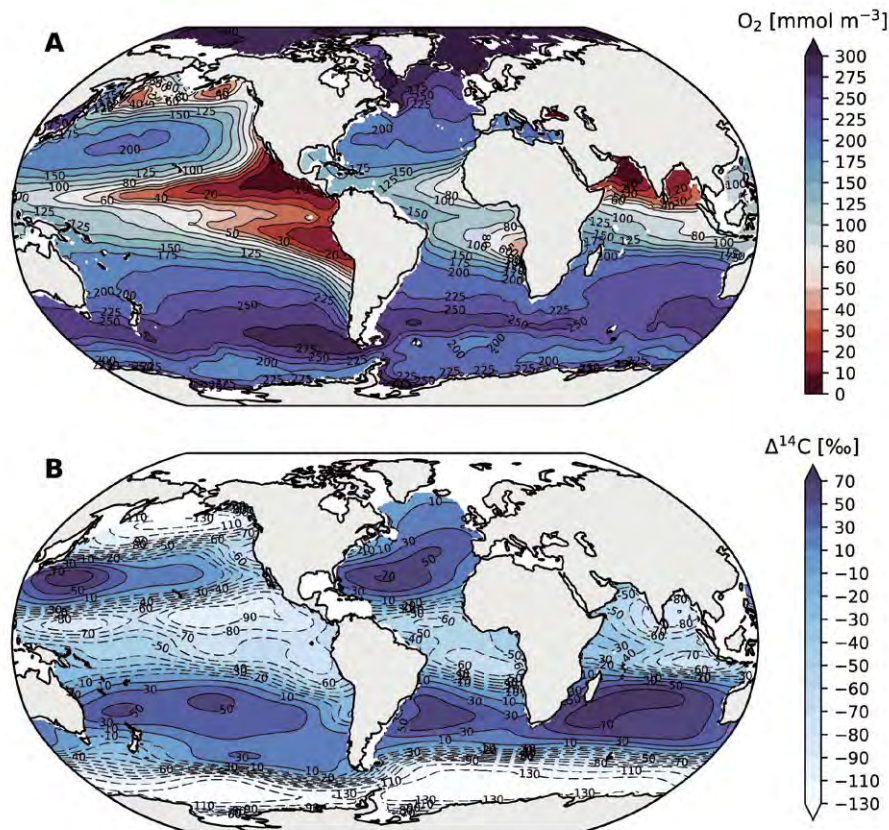


Figure 4.4 Oxygen distributions and a metric of water mass age averaged over 200–600 m depth based on observations. (A) The average dissolved oxygen concentration from the World Ocean Atlas, 2013, version 2 (Garcia et al., 2014); regions plotted in red are below 60 mmol m^{-3} , which is a common definition for an hypoxic threshold. (B) Total radiocarbon concentrations ($\Delta^{14}\text{C}$) from the Global Data Analysis Project (GLODAP) data synthesis (Key et al., 2004). Low $\Delta^{14}\text{C}$ is indicative of older waters; since these waters have been isolated from the atmosphere for longer, they are depleted in natural ^{14}C and contain limited anthropogenic ^{14}C . Most of the spatial structure in the total radiocarbon field at these depths is from the anthropogenic or “bomb” component (Key et al., 2004).

The “age” of waters in the ocean interior is a useful metric to consider in the context of ocean ventilation; age can be defined as the time since waters last contacted the surface. As waters grow older in the ocean interior, oxygen is continually depleted by respiration; the accumulated impact of this consumption is termed Apparent Oxygen Utilization (AOU) and is estimated based on the difference from saturation ($\text{AOU} = O_2^{\text{sat}} - O_2$), assuming that the oxygen concentration was close to O_2^{sat} at the time of subduction (Ito et al., 2004). Thus, AOU is an estimate of the amount of respiration integrated along the path waters take as they circulate in the ocean interior. Older waters can be expected to have greater AOU, and hence lower oxygen, because they have spent a longer time accumulating a respiration signal. This explains the contrast between dissolved oxygen concentrations in the thermocline of the North Pacific versus North Atlantic, for instance (Figure 4.4A). Freshly formed deep water fills the North Atlantic basin; this water is rich in oxygen from recent surface exchange and, as there is only modest accumulation of a respiration signal,

it remains relatively close to saturation concentrations (low AOU). The North Pacific, by contrast, is the last stop on the great ocean conveyor and as a result, deep water in this basin is substantially depleted in oxygen (Figure 4.5). Mode water ventilation (Hanawa & Talley, 2001) in the western North Pacific supplies oxygen to the subtropical thermocline, but the thermocline on the eastern side of the basin is characterized by strong oxygen depletion (Figure 4.4A). An examination of the global distributions of radiocarbon ($\Delta^{14}\text{C}$) in the thermocline depth range confirms that water mass age is a dominant control on oxygen: old waters are highly depleted in ^{14}C since they have been isolated from the atmosphere for longer; these waters have had longer to accumulate AOU, and thus tend to be more depleted in oxygen (Figure 4.4B).

The age of water dictates the time available to accumulate a respiration signal in the form of oxygen depletion; however, the rate at which oxygen is depleted by respiration—or, equivalently, the rate at which AOU

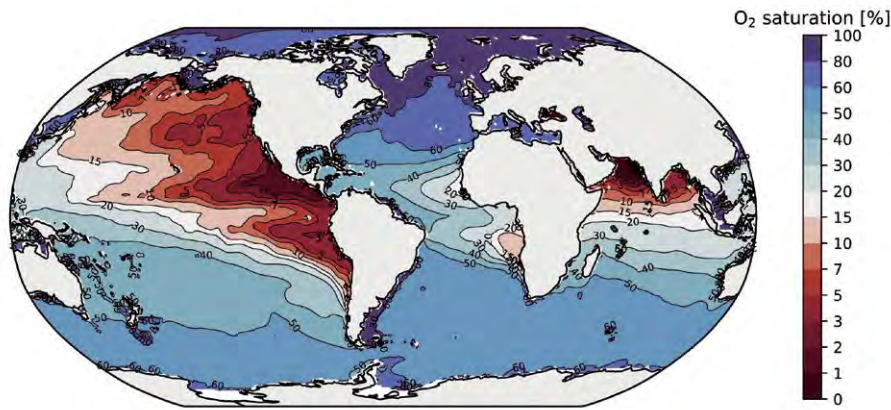


Figure 4.5 Oxygen saturation at the point in the vertical column where oxygen saturation is minimum; computed from the World Ocean Atlas, 2013, version 2 (Garcia et al., 2014). Saturation values less than 15% are coloured in red.

increases—can also vary. In particular, AOU increases at a rate that is largely proportional to the quantity of organic matter being respired. Regions with greater inputs of organic matter will have higher oxygen utilization rates (OUR), which drive faster increases in AOU. Depth is a dominant control on OUR because the downward flux of organic matter decreases approximately exponentially with depth. Most sinking organic matter is respired in the upper 1,000 m of the ocean, leading to higher OUR there; oxygen demand in deep waters is relatively low. This remineralization profile is an important driver of “oxygen minimum zones” (OMZs), which are regions of very low oxygen found on the eastern side of the ocean basins in the tropics (highlighted in red on Figure 4.4A). Oxygen concentrations approach zero in the core of the OMZs because the rate of fresh oxygen supply via mixing and advection cannot match the rate of organic matter consumption. As discussed above, oxygen minimum zones play an important role in global biogeochemical cycles of nutrients; in particular, nitrogen. As oxygen declines, a larger fraction of the oxidation of nitrogen in organic matter is shunted to N_2O , increasing the concentrations of this greenhouse gas in hypoxic waters. As O_2 is depleted to near zero concentrations, nitrate becomes the dominant electron acceptor used to oxidize organic matter, resulting in a loss of fixed nitrogen from the ocean; microbial communities also switch from N_2O production to consumption when O_2 is very low (Codispoti, 2010).

Climate warming drives deoxygenation via two pathways. The first is straightforward and involves reductions in thermal solubility of gases. The second is less straightforward; it includes the role of diminished ventilation (Figure 4.3) that results from density stratification. As ventilation declines, the age of waters

in the ocean interior increase, tending to lead to an increase in AOU insofar as supply of remineralizing organic carbon is not diminished. Notably, the same processes involved with ventilation play a role in sustaining surface ocean primary productivity. Primary productivity operates in the sunlit-surface layer of the ocean (the euphotic zone); nutrients are consumed in the process of carbon fixation, and ultimately exported to depth where they are remineralized; this collection of processes is referred to as the “biological pump”: it “pumps” carbon into the deep ocean in spite of the homogenizing influence of circulation (Volk & Hoffert, 1985). The biological pump is dependent on vertical mixing and advection to return nutrients from depth back into the surface layer; warming-driven stratification will curtail this nutrient supply, just as it does for the delivery of fresh oxygen to the interior ocean. Stratification, therefore, is expected to lead to a reduction in surface ocean primary production (Bopp et al., 2013; Steinacher et al., 2010), which will very likely have significant consequences for marine ecosystems and the fisheries they support (Stock et al., 2017). A reduction in the biological pump alleviates some demand for oxygen in the interior via reducing OUR; this effect, however, is not expected to fully compensate for the reduced ventilation because in regions with unused surface nutrients, a slower circulation need not slow the rate of organic matter production. Since stratification increases the residence time of surface waters, primary productivity is able to effect a more complete utilization of nutrients in the surface layer. To attribute changes in oxygen to the solubility and remineralization mechanisms, it is useful to consider nutrients in the ocean interior as the sum of “preformed” and “regenerated” components. “Preformed” phosphate (a major limiting nutrient), for instance, refers to the

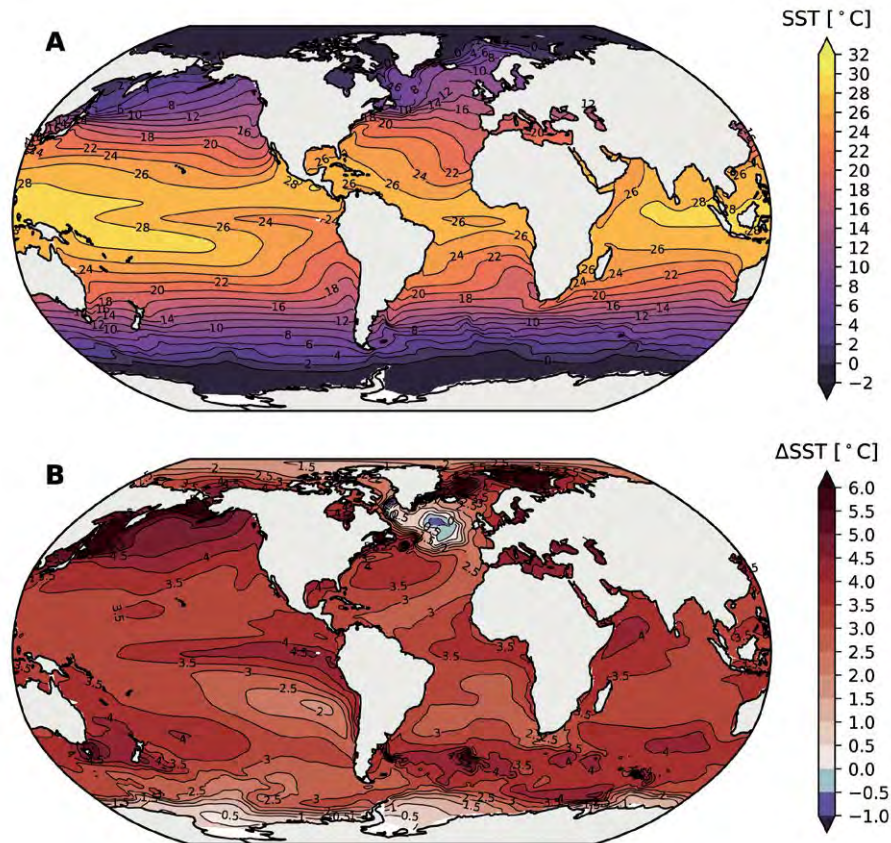


Figure 4.6 (A) Ensemble-mean sea-surface temperature (SST) in the mean climate; (B) the change in SST by the year 2100 as simulated by the CESM-LE under RCP8.5 (Kay et al., 2015).

phosphate concentration at the time of water mass formation—when the water first subducts in the ocean interior. In contrast, “regenerated” phosphate is closely related to AOU as it accounts for the cumulative (or path-integrated) amount of phosphate released by the microbial decomposition of organic matter since the water mass entered the interior. As nutrient utilization in the surface ocean becomes more complete, “performed” concentrations of nutrients in waters sinking into the ocean interior decline. The sources and sinks of phosphorus to the ocean are small relative to the global inventory; therefore, the residence time of phosphorus in the ocean is in the order of 50,000 years (Benitez-Nelson, 2000; Froelich et al., 1982; Paytan & McLaughlin, 2007). Thus, the oceanic inventory of phosphate can be treated as practically constant on timescales shorter than tens of thousands of years—so the global sum of performed and regenerated phosphate must be conserved. Therefore, the decline in performed phosphate must be compensated by an increase in remineralized (or regenerated) phosphate. On this basis, stratification can be expected to yield an increase in AOU and an associated decrease in oxygen.

4.2.1 Observed trends

A few studies have examined oxygen distributions on a global scale and found declines that appear consistent with expectations based on model simulations. Helm et al. (2011) found a globally-averaged decrease in upper-ocean (100 – 1000 m) oxygen an inventory trend of $-55 \pm 13 \text{ Tmol yr}^{-1}$ ($1 \text{ Tmol} = 10^{12} \text{ mol}$). This is consistent with Manning and Keeling (2006), who found a net oxygen outgassing from the ocean over the period 1993–2003 of -45 Tmol yr^{-1} . Schmidtko et al. (2017) reported somewhat larger numbers analysing data from full depth over the period 1960–2015, finding trends in the oxygen inventory of $-96.1 \pm 42.9 \text{ Tmol yr}^{-1}$. Ito et al. (2017), using a different compilation of similar datasets, found a trend of $24.3 \pm 12.4 \text{ Tmol yr}^{-1}$ over the upper 1000 m. Data coverage is a major limitation in assessing global trends; however, the observed changes are not inconsistent with the changes expected from anthropogenic warming. Notably, observationally-based studies have found that the direct solubility effect can account for about 15% of oxygen declines (Helm et al., 2011; Schmidtko et al., 2017); models show weaker oxygen declines

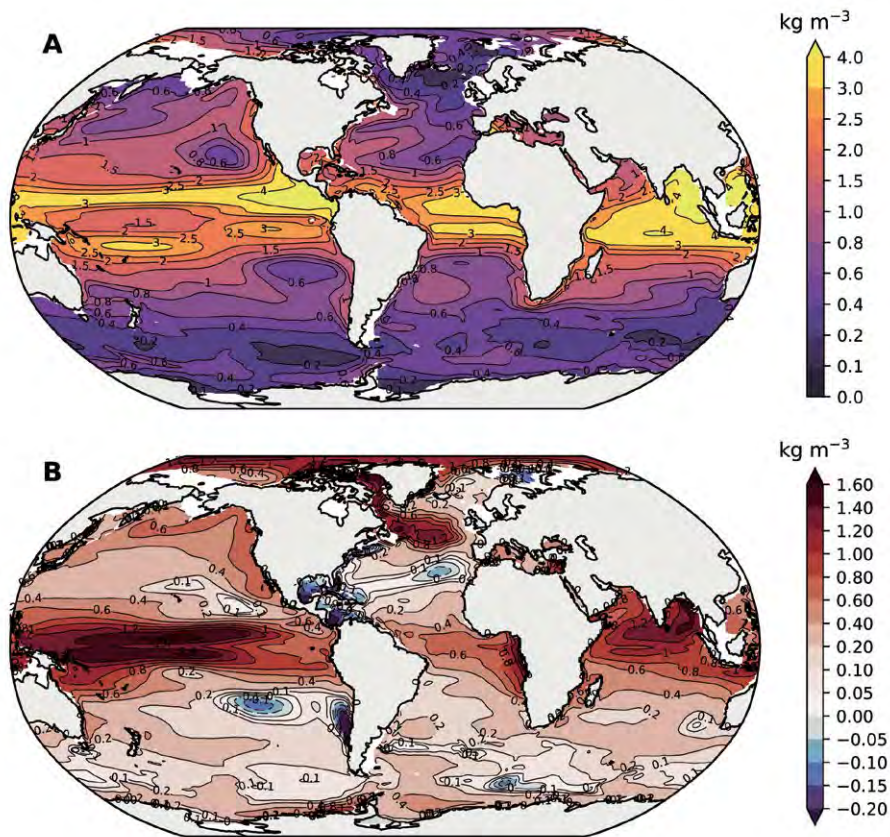


Figure 4.7 Upper ocean stratification: (A) Density difference between the upper-ocean (0–50 m) and upper-thermocline (100–200 m) in the mean climate from the CESM-LE; (B) changes in stratification by 2100.

than observations, which is attributable to a weaker contribution from remineralization-driven trends (e.g. Bopp et al., 2002).

While global data coverage is difficult to achieve, one might imagine that sufficiently long time series exist in particular oceanic regions, thereby enabling detection and attribution of forced trends. Indeed, many studies have evaluated low-frequency variability and long-term trends in local to regional scale O₂ observations, including at ocean time series sites (e.g. Andreev & Baturina, 2006; McClatchie et al., 2010; Ono et al., 2001; Whitney et al., 2007), repeat hydrographic sections (e.g. Emerson et al., 2004; Johnson & Gruber, 2007; Mecking et al., 2008; Sasano et al., 2015; van Aken et al., 2011) or compilation and optimal interpolation of historical observations (e.g. Helm et al., 2011; Stendardo & Gruber, 2012; Stramma et al., 2008). While statistically significant trends in interior oxygen distributions have been observed in specific oceanic regions, and in some cases over long time periods (50 years) (Stendardo & Gruber, 2012), definitive attribution of these trends to externally-forced climate change is challenged by the presence of significant background “noise” associated

with internally-driven, low-frequency climate variability (Garcia et al., 2005; Ito & Deutsch, 2010).

4.3 Future projections

Just as the distribution of oxygen in the modern ocean can be understood on the basis of the combined influences of temperature, ventilation rates, and patterns of oxygen consumption, the future of dissolved oxygen can be predicted on the basis of expected perturbations in these factors. The proximal driver of these perturbations is the warming of the ocean; thus, it is necessary to first examine expected changes in ocean heat content and its impact on stratification.

4.3.1 Ocean heat uptake

In each of the CMIP5 scenarios (RCP2.6, RCP4.5, RCP6.0 and RCP8.5), increasing atmospheric CO₂ concentration is the dominant driver of changes in radiative forcing, accounting for about 80–90% of the total anthropogenic influence on climate (Collins et al., 2013). All scenarios result in substantial warming of the ocean, which moderates the effect of climate change

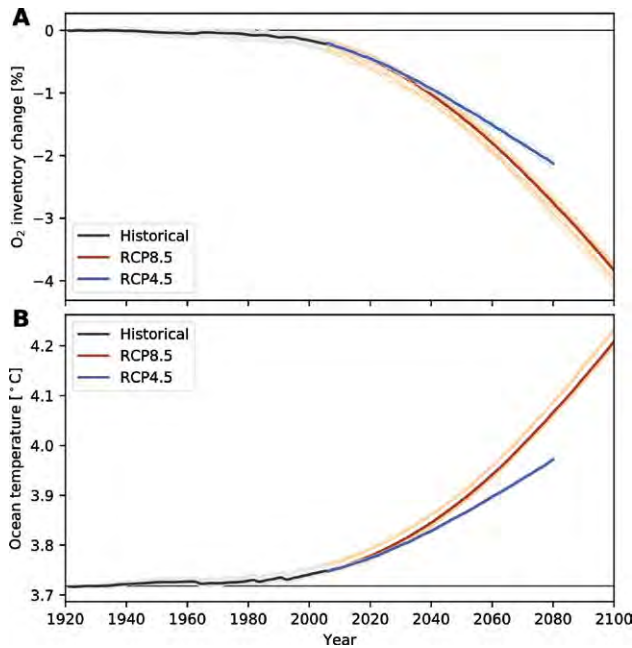


Figure 4.8 Change in global-mean ocean properties as simulated in the Community Earth System Model Large Ensemble (CESM-LE): (A) percentage change the ocean oxygen inventory relative to the “control” climate; (B) ocean temperature. Red lines show results from RCP8.5, blue lines show results from RCP4.5. The ensemble mean over the period 1920–1939 is used to define the “control” climate.

on land, but results in impacts on sea-level rise and ocean circulation (Gattuso et al., 2015). The CMIP5 collection of models suggests that by 2100, the top 100 m of the ocean will have warmed by about 0.6 °C under RCP2.6 and up to 2.0 °C under RCP8.5 relative to preindustrial levels (Collins et al., 2013). Figure 4.6 illustrates the distribution of sea surface temperature (SST) change in the CESM-LE under RCP8.5; there is a near-ubiquitous increase in tropical and subtropical SSTs by 3–4 °C and very strong warming in the Subarctic North Pacific. A “warming hole” appears in the North Atlantic (Figure 4.6B), a feature associated with reduced meridional overturning circulation that limits northward heat transport (Drijfhout et al., 2012).

The distribution of warming in future projections is consistent with an amplification of observed patterns of temperature change (Levitus et al., 2012) and manifests in part from ocean circulation. Low latitude oceans are relatively well-stratified (Figure 4.7A), which inhibits mixing and advection of heat away from the surface and into the ocean interior; heat trapped in surface waters drives large temperature increases. High-latitude regions tend to be weakly stratified, by contrast, leading to smaller changes in temperature as heat is mixed over a larger volume of ocean. The

Southern Ocean is exceptional in this regard; recent decades have been marked by little surface warming in this region, explained by upwelling and subsequent northward advection of deep water (Armour et al., 2016).

A key feature of the ocean warming expected under future scenarios is that it is strongly surface intensified. Half of the excess heat absorbed by the ocean by 2100 under RCP4.5, for instance, is expected to be confined to the upper 700 m of the water column (Collins et al., 2013). This is expected on the basis of theoretical understanding of ocean response timescales to transient forcing (Held et al., 2010; Stouffer, 2004). The mixed layer in the surface ocean responds rapidly to changes in radiative forcing in the atmosphere, but the deep ocean requires millennia to equilibrate (Hansen et al., 2011; Li et al., 2013). A consequence of this vertical progression of warming is a strong increase in upper ocean stratification, particularly while transient forcing remains in effect (Xu et al., 2012, 2013). Figure 4.7B shows the change in upper ocean stratification simulated by the CESM-LE. The change in stratification is strongest in the tropics and in the Arctic Ocean; there are widespread increases in stratification at mid- to high-latitudes, with some localized and weak reductions in stratification. Stratification in the Subarctic North Pacific is expected to increase dramatically. The “warming hole” in the North Atlantic is associated with a strong increase in the supply of fresh water and associated stratification in the deepwater formation region (Drijfhout et al., 2012) that prevents warming.

4.3.2 Global oxygen declines

Earth system model simulations indicate that the global ocean will begin to lose oxygen at an accelerating rate in the early 21st century, with a tight correspondence to increases in ocean heat content (Bopp et al., 2013). This phenomenon is illustrated in Figure 4.8, which shows results from the CESM-LE, including RCP8.5 and RCP4.5 scenarios. In these simulations, oxygen declines are evident in the late 20th century, but rates of change strongly increase in the early to mid 21st century. Notably, ensemble spread is limited at the global scale; this is because spatial averaging reduces the contribution of natural variability to trends, leaving a signal that is mostly driven by external forcing. Differences between RCP8.5 and RCP4.5 start to become evident for global ocean temperature around 2040, but manifest somewhat later for global O₂, reflecting, in part, the greater variability

(ensemble spread) in the simulated O_2 inventory relative to temperature.

The acceleration in the rate of oxygen depletion is a common feature across the CMIP5 models (Bopp et al., 2013; Cocco et al., 2013). In the CESM-LE under RCP8.5 (Figure 4.8A), the ensemble mean trend in the global-ocean oxygen inventory during the first two decades of the 21st century increased in magnitude from about -20 Tmol yr^{-1} to nearly -60 Tmol yr^{-1} . By mid-century (2050s), the model suggests that the ocean will be losing about 100 Tmol yr^{-1} of oxygen and this rate of loss will continue to increase to more than 130 Tmol yr^{-1} by the end of the century. Notably, however, Schmidtko et al. (2017) reported an observationally-based estimate of the rate of oxygen loss between 1960–2015 that was about $-100 \text{ Tmol yr}^{-1}$. The trends simulated by the models over this period are much weaker; indeed, the CESM-LE, for instance, has a mean linear trend of only about -14 Tmol yr^{-1} over 1960–2015; internal variability cannot account for the discrepancy of this trend with the observations, as the strongest trend in the ensemble is only -20 Tmol yr^{-1} (the weakest is -9 Tmol yr^{-1}). This suggests that models may underestimate the true deoxygenation rates. The reasons for this discrepancy are not fully understood, but there are indications that strong trends observed in the tropical oceans (Stramma et al., 2008, 2012) are not replicated in the simulations (Oschlies et al., 2017).

The global-scale O_2 declines depicted in Figure 4.8A result from a combination of the direct warming-induced reduction in solubility and changes in cumulative respiration brought about by stratification. Changes in respiration can be quantified by changes in AOU, presuming that oxygen in the surface ocean remains relatively close to saturation. As explained above, an increase in AOU indicates greater path-integrated respiration, which corresponds to a decrease in the oxygen concentration. Therefore, the total change in oxygen concentrations under climate warming, ΔO_2 , can be written as the sum of changes due to warming effects on saturation concentrations (ΔO_2^{sat}) and respiration effects quantified by the negative of changes in AOU ($-\Delta \text{AOU}$):

$$\Delta O_2 = \Delta O_2^{\text{sat}} - \Delta \text{AOU} \quad (1)$$

Figure 4.9 illustrates this interplay of mechanisms driving oxygen loss for a global-mean vertical profile computed from the CESM-LE. The total global O_2 change at

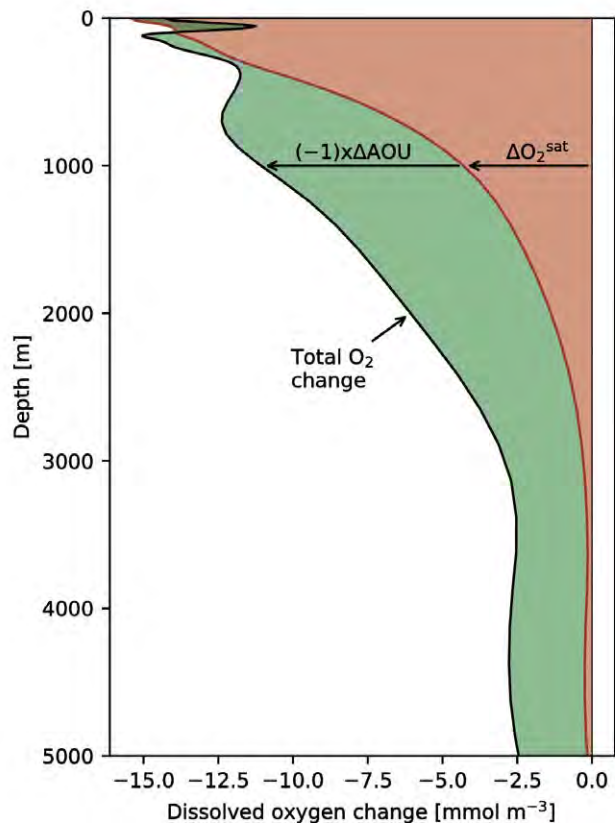


Figure 4.9 Mechanisms driving global oxygen change in the CESM-LE. The total oxygen decline (black) and the contribution of reduced solubility (orange area) and increase respiration (AOU, green area). The ensemble mean over the period 1920–1939 was used to define the “control” climate.

2100 (ΔO_2) is shown as a black line; the contribution of changes in oxygen solubility (ΔO_2^{sat}) and respiration ($-\Delta \text{AOU}$) are highlighted with orange and green shading, respectively. Oxygen depletion is strongest in the upper 1000 m, exceeding -10 mmol m^{-3} over this depth range. Solubility-driven declines in oxygen decay rapidly with depth, consistent with the expectation of a vertical progression of ocean warming (section 4.3.1). In the near-surface ocean, the direct effect of warming on solubility is the dominant driver of oxygen loss, accounting for global-mean reduction of near 15 mmol m^{-3} at the surface; below about 3000 m depth, the solubility effect is negligible. The respiration-driven component of oxygen change ($-\Delta \text{AOU}$), by contrast, is actually weakly negative in the near-surface ocean. AOU is the difference between the oxygen concentration and the saturation concentration; thus, this decline in the absolute magnitude of surface AOU suggests that, although saturation concentrations are lower due to warming, surface oxygen is closer to saturation in the future climate. This effect can be understood as a result of shoaling mixed layer depths and reduced sea ice concentrations; these factors enable oxygen in the

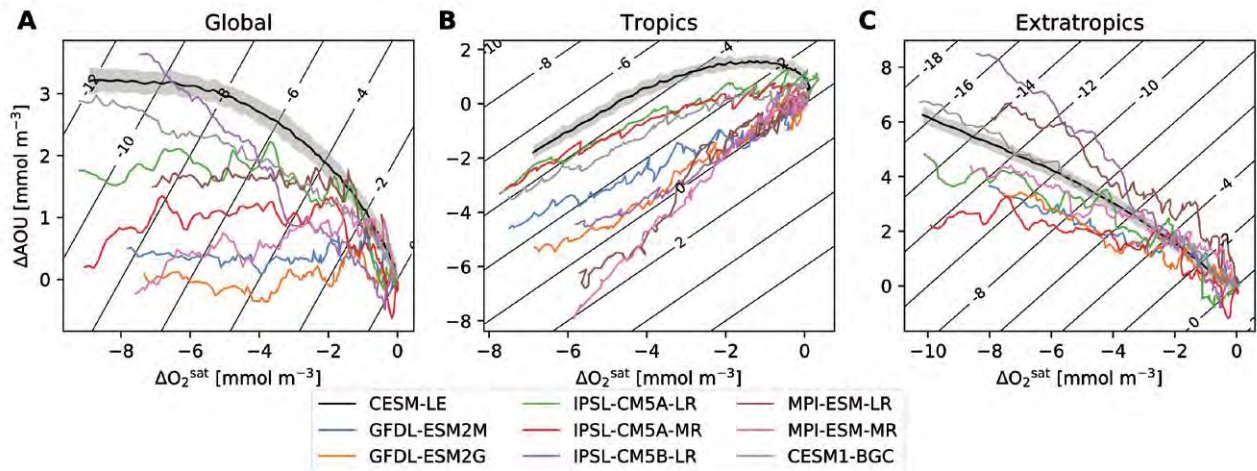


Figure 4.10 Simulated relationships between upper ocean (above 1000 m depth) (ΔAOU) and $\Delta\text{O}_2^{\text{sat}}$ changes: (A) globally, (B) in the “tropics” (20°S – 20°N), and (C) in the “extratropics” (poleward of 20° latitude). The black line shows results from the CESM-LE (shading shows the region within one standard deviation of the ensemble spread). The coloured lines show a subset of the CMIP5 models. Contours show the total oxygen depletion.

surface ocean to more effectively reach equilibrium with the atmosphere (Ito et al., 2004). In spite of reductions in surface AOU, respiration-driven declines in oxygen rapidly become substantial below about 500 m depth and dominate oxygen depletion in the deep ocean (Figure 4.9). These changes in respiration are indicative of reduced ventilation due to increases in surface stratification. At the global-scale, increased stratification limits surface-to-depth exchange, cutting off the supply of oxygen to waters in the ocean interior.

Figure 4.10 presents another perspective on deoxygenation in the upper ocean (above 1000 m) and includes simulations from the CMIP5 models as well as the CESM-LE. These plots show a phase-space defined by changes in cumulative respiration (ΔAOU) and changes in solubility ($\Delta\text{O}_2^{\text{sat}}$); total oxygen change is directly proportional to changes in both these factors (equation 1), which are illustrated with contour lines: a trajectory perpendicular to these contour lines is consistent with reinforcing changes in respiration and solubility; trajectories following a particular contour line indicate exact compensation between changes in respiration and solubility (i.e. no change in oxygen). Each coloured line shows the evolution of a CMIP5 model simulation from 1970 to 2100; the lines begin at the origin ($\Delta\text{O}_2^{\text{sat}}=0$, $\Delta\text{AOU}=0$) at 1970 and their trajectory demonstrates the degree to which AOU and solubility change over the 21st century. The CESM-LE is shown as a black line with grey shading to represent the ensemble spread. All models simulate substantial changes in upper ocean oxygen concentrations, spanning a range from about -7 to -12 mmol m^{-3} averaged over the upper 1000 m. While deoxygenation is universal, the models show

widely divergent behaviour with respect to the relative balance of $\Delta\text{O}_2^{\text{sat}}$ and ΔAOU driving oxygen change. The global oxygen changes in the CESM-LE, for instance, are initially dominated by increases in AOU (upward trajectory) but are later dominated by solubility (Figure 4.10A). Global oxygen change in the GFDL models, by contrast, is strongly dominated by changes in solubility out to 2100, with very little change in AOU; the IPSL-CM5B-LR model behaves more like the CESM-LE, with substantial changes in both solubility and AOU (Figure 4.10A). Oxygen loss in the CESM-LE is more strongly dominated by changes in AOU than most of the models in the CMIP5 collection (Figure 4.10A).

The divergent behaviour within the CMIP5 models in the mechanisms driving upper ocean deoxygenation globally is partially a result of fundamentally different dynamics in the tropics versus high latitude regions; the models show more consistent behaviour when these regions are considered separately (Figure 4.10B, C). Deoxygenation in the extratropics (poleward of 20° latitude) is more intense than in the tropics and involves a combination of strong solubility and respiration effects; most models show trajectories near-perpendicular to the oxygen-change contours (Figure 4.10C). The CESM-LE simulates high latitude changes near the centre of the CMIP5 model spread. In contrast to AOU increases in the extratropics, all CMIP5 models considered simulate decreasing AOU in the upper ocean within the tropics (equatorward of 20° latitude; Figure 4.10B). Decreasing AOU means less respiratory consumption of oxygen; therefore, while the models simulate warming-driven solubility declines in the tropics, reductions in AOU compensate, tempering oxygen declines such that in

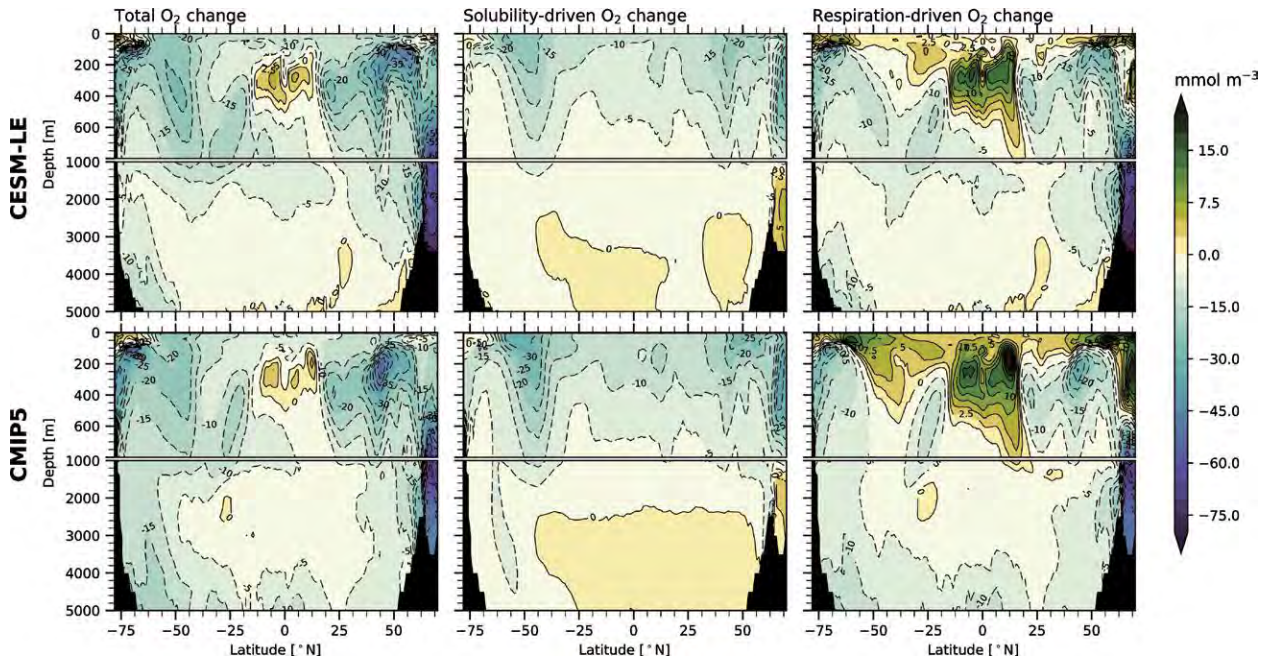


Figure 4.11 Zonal-mean, ensemble-mean change in the concentration of dissolved oxygen in the ocean simulated by the Community Earth System Model Large Ensemble (CESM-LE) (top row) and the CMIP5 multi-model collection (bottom row) under RCP8.5.

some models, tropical oxygen is actually projected to increase by 2100 (Figure 4.10B). The CESM-LE is an end-member model in the simulation of tropical oxygen change; its initial trajectory includes modest oxygen decline driven by increased respiration (positive ΔAOU); AOI subsequently declines, however, at a rate that largely compensates for warming (Figure 4.10B). It is this initial reinforcing behaviour in tropical and extratropical AOI and subsequent cancellation that leads to the global trajectory for CESM-LE shown in Figure 4.10A.

Figure 4.11 shows the change in dissolved oxygen along a zonal-mean, depth section; the left column shows the total simulated oxygen change at 2100, while the middle and right columns show the contribution of solubility and respiration to oxygen change. This figure presents a picture consistent with that shown in Figure 4.10: Oxygen declines are most intense at high latitudes due to the reinforcing effects of solubility and respiration-driven change. Opposing solubility and respiration effects mean that oxygen declines in the tropics are more modest—there is even a local oxygen increase in the low latitude thermocline. The imprint of ocean ventilation pathways is evident on Figure 4.11 as regions of strong deoxygenation extending from surface to depth at mid-latitudes; these features are similar to those found in observations of oxygen declines (Helm et al., 2011). Reductions in AOI are evident at the surface globally (as seen in Figure 4.9), however, while

the CMIP5 ensemble mean shows some AOI declines in the extratropical southern hemisphere, the tropics are where pronounced AOI declines above about 600 m

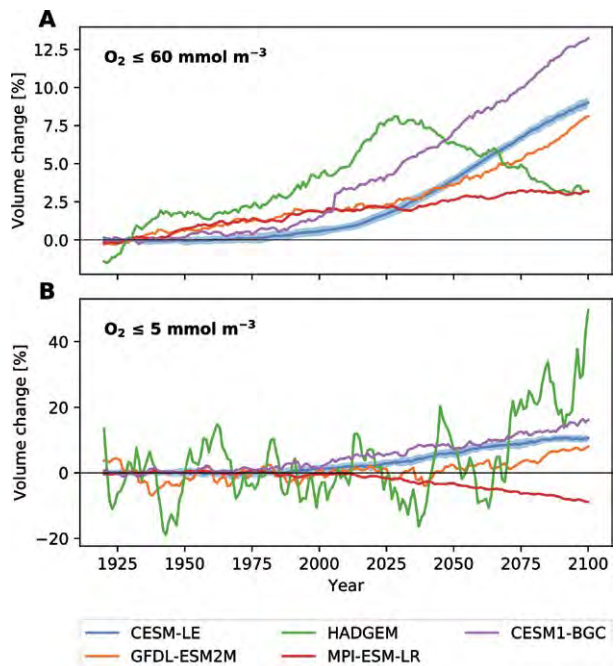


Figure 4.12 Change in the volume of (A) hypoxic ($\text{O}_2 \leq 60 \text{ mmol m}^{-3}$) and (B) suboxic ($\text{O}_2 \leq 5 \text{ mmol m}^{-3}$) waters in the CESM-LE (blue) and a subset of the CMIP5 models relative to a 1920–1939 baseline. The CESM-LE has an average hypoxic volume of $1.1 \times 10^{17} \text{ m}^3$ over the period 1920–1939, whereas the CMIP5 ensemble mean hypoxic volume is $9.2 \times 10^{16} \text{ m}^3$. The suboxic volumes are $1.6 \times 10^{16} \text{ m}^3$ and $2.5 \times 10^{16} \text{ m}^3$ for the CESM-LE and CMIP5 ensemble mean, respectively.

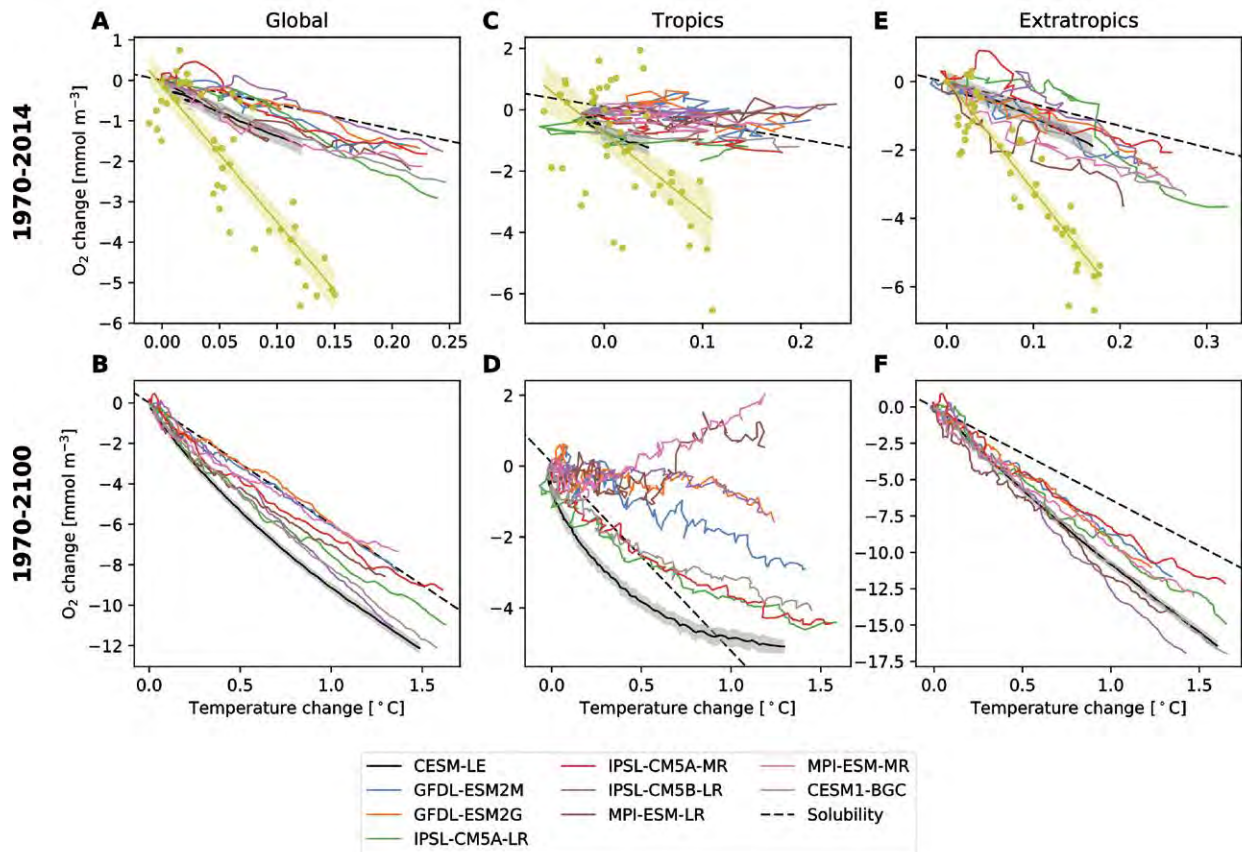


Figure 4.13 Modelled and simulated relationships between upper ocean (above 1000 m depth) mean O_2 and temperature changes. Top row shows model and observational data over the period 1970–2014; the bottom row shows the models from 1970–2100; annual means are plotted, and all change is relative to the year 1970. A) and B) show data averaged globally; C) and D) show data averaged in the tropics (20°S – 20°N); and E) and F) show the extratropics (poleward of 20° latitude). Simulation data are taken from a subset of the CMIP5 models (noted in legend) and the CESM-LE. Observational data are taken from Ito et al. (2017). The dashed line in each panel indicates the expected relationship if all change in oxygen was solubility-driven.

depth compensate for solubility, leading to oxygen increases.

Figure 4.12A and B show the projected time-evolution of hypoxic ($O_2 \leq 60 \text{ mmol m}^{-3}$) and suboxic ($O_2 \leq 5 \text{ mmol m}^{-3}$) volumes respectively in the CESM-LE and a subset of the CMIP5 ensemble. All of the models show an increase in hypoxic volume by 2100, though hypoxic volume actually peaks mid-century in the HadGEM model. Suboxic volume increases in all but one model, though the range of increase is large. The coarse resolution of the ESMs precludes adequate representation of complex coastal processes; thus, these changes predominantly reflect changes to open-ocean regions in the tropics. While ecologically and economically important, coastal regions comprise a small fraction of global hypoxic volumes (Breitburg et al., 2018).

The distribution of O_2 in the current ocean implies that suboxic zones are particularly sensitive to changes in

regional oxygen concentrations. A decline in mean O_2 of the tropical upper ocean of only $\sim 2 \text{ mmol m}^{-3}$, substantially smaller than the global average, is enough to double the current volume of suboxia globally (Deutsch et al., 2014). This expansion of suboxic zones would be associated with enhanced denitrification. Assuming a constant volumetric rate of nitrogen loss in suboxic zones, integrated rates of denitrification would rise in proportion to the volume of suboxic waters and may therefore also be exceptionally sensitive to deoxygenation. Models of microbial nitrogen cycling in these regions indicate that the efficiency of nitrogen removal also increases as the volume of suboxic zones increases, so that the sensitivity of nitrogen loss to deoxygenation is further enhanced (Penn et al., 2016). Historical reconstructions of nitrogen loss from the North Pacific based on sedimentary records and model hindcasts support a high sensitivity of denitrification, implying a 3-fold change in the integrated rate of denitrification in recent decades (Deutsch et al., 2014; Yang et al., 2016). The impacts of historical changes

in nitrogen loss can be seen in the nitrate deficit (N^* ; see Figure 4.1 caption) well outside the suboxic zone, in the productive California Current System (Deutsch et al., 2011), with presumed impacts on the N-limited net primary production in that upwelling zone. Large uncertainties still surround the future projections in the impacts of deoxygenation on nitrogen cycling and its effects on remote productivity. Resolving these uncertainties will require models that better reproduce the mean state of the suboxic zones, the microbial dynamics in these regions, and the rates and pathways by which their nitrate deficits are transported to nitrogen limited surface regions, all of which are crudely represented in ESMs.

4.3.3 Relationships with heat content

Deoxygenation is driven by the direct impact of temperature on solubility and the indirect effect of changes in circulation that lead to changes in respiration as estimated by AOU. The CMIP5 models and the CESM-LE show that deoxygenation in the extratropics results from a synergy between these factors, which drive reinforcing changes in oxygen (Figure 4.10C). In the tropics, by contrast, the models suggest that solubility and respiration effects work in opposition; reductions in respiration tend to win-out slightly in some models, leading to modest increases in tropical oxygen (Figure 4.10B). While the models are relatively consistent with regard to these tendencies when the tropics and extratropics are considered independently, divergent behaviour results at the global scale due to averaging over regions with opposing tendencies. Additionally, the opposing respiration-driven changes at high-latitudes and in the tropics lead to cancellation, such that global deoxygenation in the multi-model mean is mostly solubility driven (Figure 4.10A). Another reason why the models might show different relative amounts of deoxygenation relates to the physical climate simulation: the models simulate different amounts of warming over the 21st century (Bopp et al., 2013). This motivates us to consider the relationship between changes in oxygen with simulated changes in ocean heat content.

Figure 4.13 shows the change in upper-ocean oxygen in each model plotted against the concomitant change in temperature; Figures 4.13A, C, E show the period 1970–2014 and includes observational estimates; Figures 4.13B, D, F show 1970–2100. Observational estimates of oxygen variability are from the data compilation of Ito

et al. (2017) and the ocean heat content estimates are from the European Centre for Medium-Range Weather Forecasts Ocean Reanalysis (ORAS4) (Balmaseda et al., 2013). While the models were shown to have substantial differences in the mechanisms driving simulated oxygen decline, there is a fairly tight correspondence across the models between oxygen and temperature at the global scale (Figure 4.13A, B); indeed, the relationship between the global mean O_2 and global mean temperature above 1000 m depth tends to collapse into a quasi-linear relationship. The dashed lines in Figure 4.13 show the O_2 -heat relationships that would arise if changes in O_2 were purely solubility-driven. Declines in O_2 that exceed the solubility slope are due to the effect of respiration.

Notably, the observations indicate a much stronger O_2 -heat relationship than is evident in any of the models. Over recent decades, the global scale simulated O_2 -heat relationship (Figure 4.13A) is in the range of -7 to $-13 \text{ mmol m}^{-3} \text{ }^\circ\text{C}^{-1}$; the observations, by contrast, show much more O_2 loss for a given temperature increase, with a relationship of $-33.6 \pm 2.98 \text{ mmol m}^{-3} \text{ }^\circ\text{C}^{-1}$. The observational estimates of O_2 -heat relationships in the extratropics ($-32.2 \pm 2.47 \text{ mmol m}^{-3} \text{ }^\circ\text{C}^{-1}$; Figure 4.13E) and tropics ($-25.5 \pm 5.53 \text{ mmol m}^{-3} \text{ }^\circ\text{C}^{-1}$; Figure 4.13C) are also stronger than simulated. The average slope of the simulated O_2 -heat relationship is $-11.7 \text{ mmol m}^{-3} \text{ }^\circ\text{C}^{-1}$ in the extratropics, which is only slightly stronger than pure-solubility (Figure 4.13E), and the slope is very close to solubility ($-3.27 \text{ mmol m}^{-3} \text{ }^\circ\text{C}^{-1}$; Figure 4.13C) in the tropics.

Ocean warming between 1970 and 2014 is quite modest in comparison to the changes projected by 2100 (Figure 4.13A, B). Over the full 1970–2100 time period, the models show distinct behaviour in the tropics and extratropics. At the global scale and in the extratropics, deoxygenation is tightly coupled to temperature, with a slope that exceeds solubility in most models (Figure 4.13B, F). In the tropics, by contrast, all the models show less deoxygenation than would be predicted on the basis of solubility changes alone and the spread across the models in simulated oxygen change is wide (Figure 4.13D). Tropical oxygen loss in the CESM-LE, for instance, begins with a temperature relationship much stronger than solubility, but the rate of decline with respect to temperature diminishes, ultimately yielding a relationship integrated out to 2100 that is less than would be predicted from pure solubility-driven changes (Figure 4.13D).

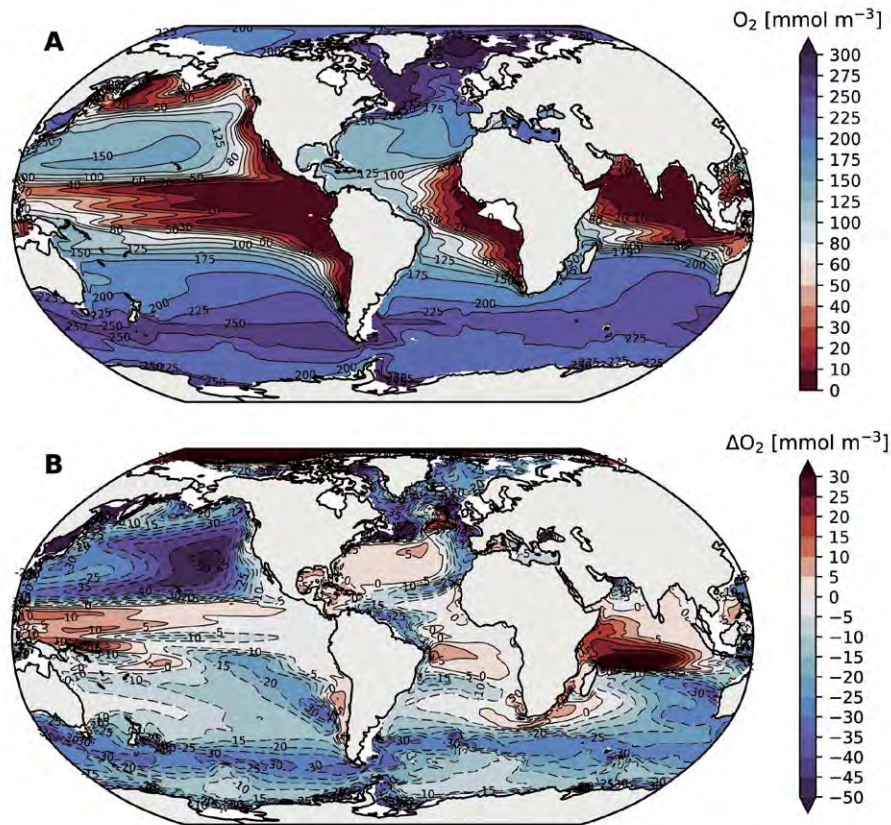


Figure 4.14 Thermocline (mean over the 200–600 m depth range) oxygen distributions simulated by the CESM-LE: (A) O_2 concentration in the control climate; (B) change in O_2 concentration at 2100. The ensemble mean over the period 1920–1939 is used to define the “control” climate.

It is not clear what causes these large differences in the sensitivity of ocean oxygen content to the heat uptake. The observations themselves involve substantial uncertainty (e.g. Bianchi et al., 2012), much of which arises from the fact that oxygen measurements are relatively sparse in space and time—and particularly sparse in the tropics. Furthermore, as we lack long-term records of oxygen trends on the global scale, it is possible that the observations include periods or regions strongly influenced by natural variability, which may involve a different mix of solubility and respiratory (AOU) changes. It is also possible that the models are missing a mechanism that is actually driving O_2 declines in nature. For instance, Ito et al. (2016) showed that polluted aerosol deposition has driven substantial declines in tropical Pacific oxygen concentration over recent decades. If ESMs lack such forcing, which may be strongly correlated temporally with ocean heat content, they should predict an O_2 -temperature relationship that is too weak. Similarly, the models may omit important changes due to ocean acidification, stoichiometry and specifics of tropical wind forcing (Oschlies et al., 2017 and references therein).

In summary, the collection of CMIP5 models and the CESM-LE are relatively consistent in their simulation of O_2 -heat relationships in the extratropics; however, there is little agreement on this relationship in simulations of the tropics. Observations indicate a stronger O_2 -heat relationship than is simulated by any of the models, which suggests that the models underestimate the amount of respiration-driven deoxygenation. If we believe that the observations provide an accurate assessment of the true O_2 -heat relationship, the implication is that the simulated deoxygenation is a substantial underestimate of the oxygen loss that will be realized for a given warming scenario.

4.3.4 Oxygen change in the thermocline

While the global trends in oxygen are characterized by consistent secular declines (Figure 4.8A), regional patterns of change, as has been illustrated, are more complicated; thus, we next examine patterns in oxygen over the thermocline, i.e. the 200–600 m depth range. The focus on the thermocline depth is motivated by relevance to ecological impacts. As the base of the oxygenated surface layer, oxygen declines in this

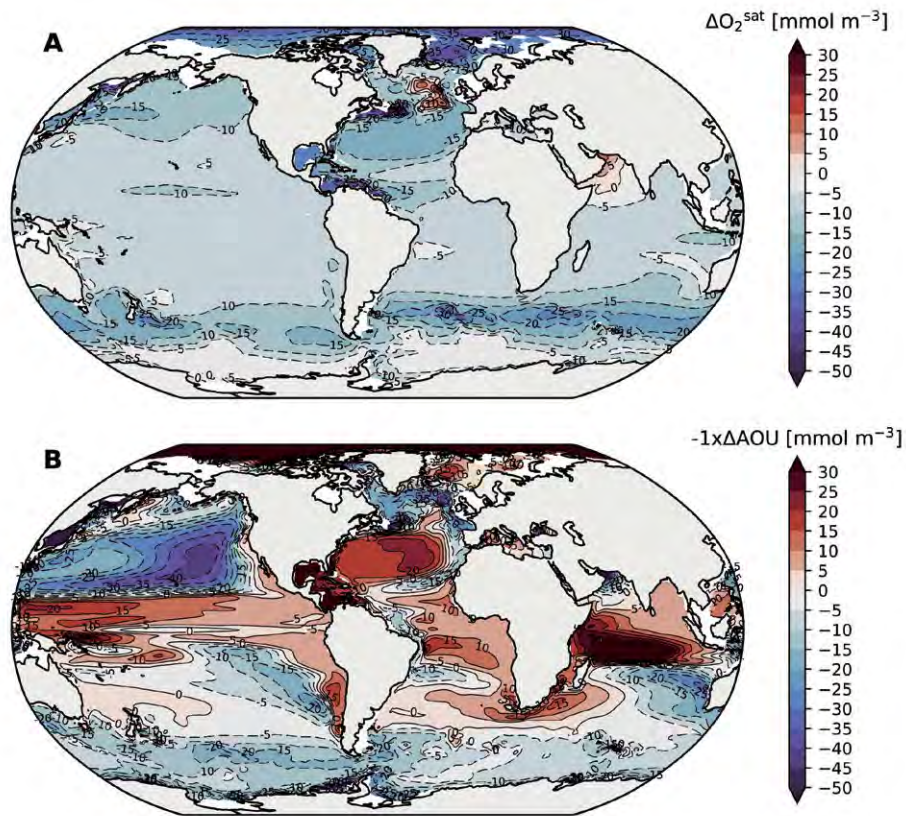


Figure 4.15 Solubility and respiration-driven changes in thermocline (200–600 m mean) oxygen at the year 2100; computed from the CESM-LE ensemble mean: (A) Solubility-driven oxygen change (ΔO_2^{sat}). (B) Respiration-driven oxygen change (the negative of ΔAOU).

depth range might drive vertical habitat compression, impacting marine organisms that are concentrated in the near surface (Deutsch et al., 2015; Stramma et al., 2011).

Figure 4.14A shows the distribution of oxygen in the “control” climate of the CESM-LE. It is important to note the discrepancies between this simulated oxygen distribution and that inferred from observations (Figure 4.4A): Oxygen concentrations in CESM-LE tend to be too low and hypoxic regions are too extensive. These biases, a well-known and common feature of coarse-resolution ESMs, are partially attributable to sluggish circulation yielding weak ventilation and are discussed further in section 4.4.1. In spite of the biases in simulated oxygen distributions, however, the basic spatial structure of the oxygen field is well represented (i.e. the pattern correlation with observations is relatively high); thus, we are confident that this model (and other ESMs) can provide some insight into the mechanisms driving deoxygenation—though projections for oxygen variability and trends in tropical OMZs are to be treated with particular caution.

Thermocline oxygen depletion at 2100 is most pronounced in extratropical regions, with particularly strong changes in the North Pacific (Figure 4.14B). Consistent with what we have already seen, there are modest increases in oxygen in the tropics in all ocean basins, with moderately strong increases in the western equatorial Pacific and Indian Oceans. In order to understand the mechanisms modulating the intensity of deoxygenation and its spatial structure, it is instructive, once again, to examine the direct temperature effects on oxygen decline (ΔO_2^{sat}) and respiration-driven declines (ΔAOU). These fields are shown in Figure 4.15, noting that, as in Figure 4.9, it is a plot of the negative of the ΔAOU , which can be directly interpreted as the change in oxygen due to changes in respiration, presuming that surface waters remain close to equilibrium with atmospheric O_2 . The structure in ΔO_2^{sat} is a direct reflection of changes in ocean temperature in the thermocline depth range; ΔO_2^{sat} is strongly negative in the Southern Ocean, the Arctic, and parts of the North Atlantic. The Southern Ocean dominates ocean heat uptake in the present-day climate (Talley et al., 2015) and is expected to persist in this role under future warming scenarios (Frölicher et

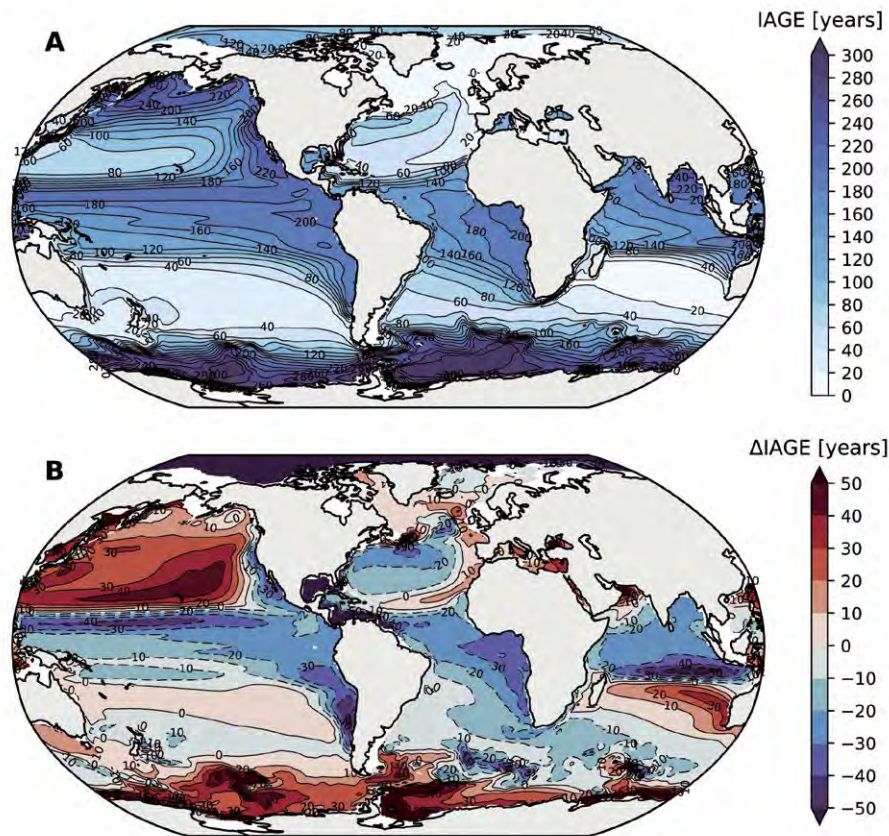


Figure 4.16 Thermocline (mean over the 200–600 m depth range) ideal age (IAGE) distributions simulated by the CESM-LE: (A) IAGE in the control climate; (B) change in IAGE at 2100.

al., 2015). The North Atlantic, as a site of substantial deepwater formation, also plays a strong role in ocean heat uptake; however, the patterns associated with the “warming hole” lead to localized cooling where solubility-driven changes in oxygen are positive (Figure 4.15A). There is no substantial deepwater formation in the Arctic basin; however, this region is subject to strong sea ice declines and warming associated with polar amplification (Screen & Simmonds, 2010) leading to widespread reductions in solubility in this region.

While the direct effect of temperature on oxygen is almost universally negative (driving declines), changes associated with respiration are more complicated (Figure 4.15B). By examining the changes in AOU, it can be seen that strong oxygen depletion in the thermocline of the North Pacific is a result of increases in respiration-driven oxygen depletion (increased AOU) that reinforce temperature effects. This contrasts with the North Atlantic, where respiration-driven declines in oxygen (increased AOU) are confined to the subpolar gyre; AOU in the mid-latitude North Atlantic thermocline decreases, which mitigates solubility driven oxygen declines there. Tropical regions are characterized by

widespread declines in AOU, indicative of reduced oxygen consumption by respiration, consistent with the picture gleaned from the analysis of the $\Delta\text{AOU}-\Delta\text{O}_2^{\text{sat}}$ phase space for the tropics (Figure 4.10B).

This raises the question, why are there decreases in cumulative respiration (AOU) in the tropical thermocline under climate warming? The first clue to answering this question comes from looking at the distribution of water mass age in the CESM-LE simulation. Figure 4.16 shows the mean distribution and change in a tracer called “ideal age” (IAGE) in the CESM-LE. Ideal age is transported by the OGCM; it is set to zero in the surface layer and increases at a rate of 1 year per year in the ocean interior—thus providing a direct estimate of the average time since a water-mass was last in contact with the atmosphere. Just as seen in section 4.2, there is a tight correspondence between the age of waters in the thermocline (Figure 4.16A) and their oxygen content (Figure 4.14A); older waters tend to have lower O_2 concentrations. Similarly, the change in the age of thermocline waters at 2100 (Figure 4.16B) is a relatively good predictor of changes in oxygen; waters that become older show O_2 declines, whereas

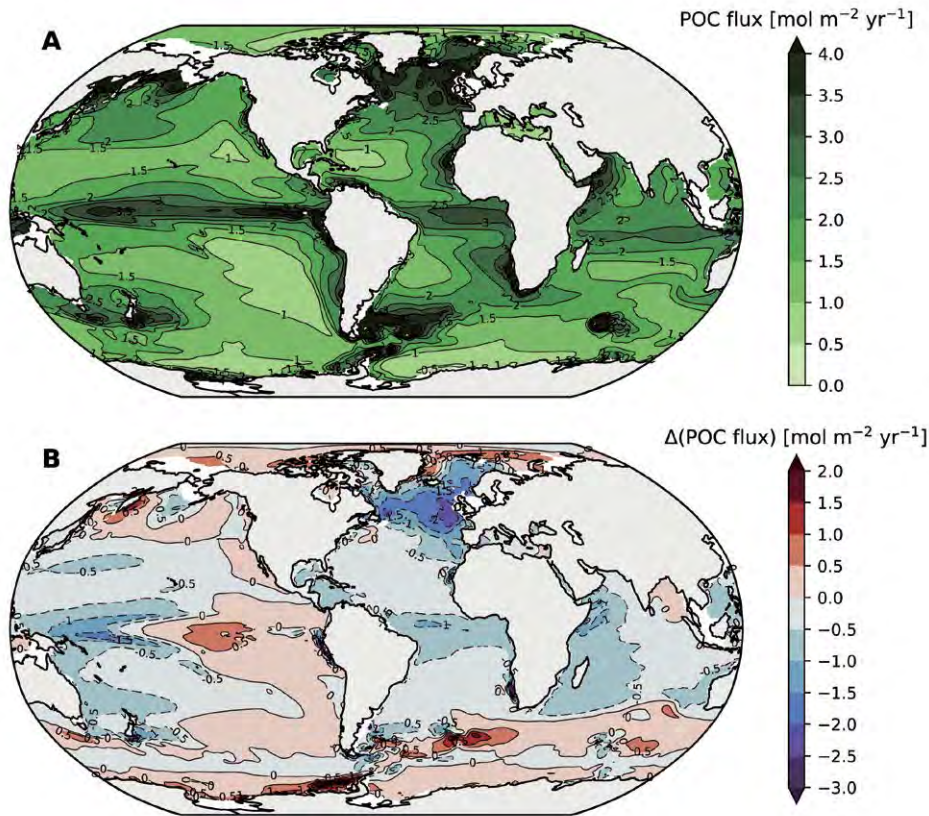


Figure 4.17 Carbon export at 100 m in the CESM-LE: (A) in the control climate and (B) the change by 2100.

waters that become younger have modest increases in oxygen. As discussed above, water mass age controls AOU by determining the time available for a respiration signal to accumulate. If we imagine the flow in the ocean interior as consisting of a one-dimensional pipe, a reduction in age is akin to moving upstream in that pipe, where water mass properties are closer to those of the inlet at the ocean surface. The reduction in ideal age with the tropical thermocline is likely due to a shift in the relative balance of water masses contributing to these regions (Gnanadesikan et al., 2007). In particular, as upwelling in the tropics is diminished under climate warming, the contribution of old deep waters to the thermocline is reduced, leading to a local reduction in age.

Another mechanism that might lead to local increases in oxygen is a reduction in OUR; indeed, changes in AOU can be thought of as originating from changes in age and/or changes in OUR. As noted in section 4.2, net primary productivity in the surface ocean is expected to decline under climate warming, which will drive diminished export of organic matter, thereby alleviating the demand for oxygen in the ocean interior.

Most of the CMIP5 models do indeed simulate declines in net primary productivity under climate warming, although there are substantial differences between the models; some do simulate an increase (Laufkötter et al., 2015). A reduction of OUR was found to be the dominant mechanism driving multi-decadal changes in suboxic zone volume and denitrification in retrospective model simulations of the tropical Pacific that reproduce observed changes in nitrogen cycle tracers (Deutsch et al., 2011, 2014). Figure 4.17B shows the change in carbon export in the CESM-LE. There is a global reduction in export production, with the strongest reductions in the North Atlantic; export production increases, however, over broad regions of the Southern Ocean and tropical Pacific). The widespread reduction in export production in the North Atlantic might be expected to temper oxygen declines in that basin, consistent with the reduction in AOU (Figure 4.14B). The changes in OUR in the tropical Pacific, however, are more complicated and further analysis is necessary to assess the role of changes in OUR in driving oxygen change there.

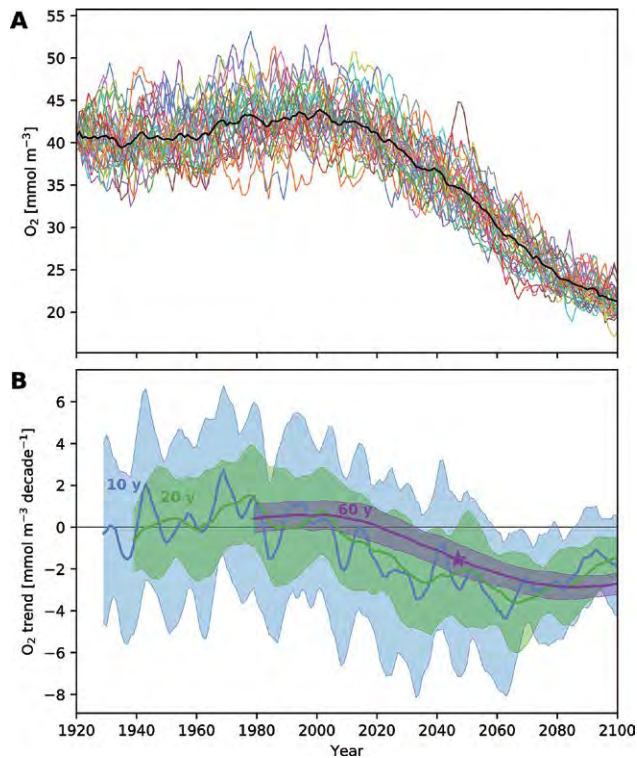


Figure 4.18 Oxygen concentrations and trends in the thermocline of the California Current System (CCS) simulated by the CESM-LE. (A) Oxygen concentrations in the CCS; coloured lines show individual ensemble members, the black line is the ensemble mean. (B) Retrospective trends computed from the data displayed in (A).

4.3.5 Time of emergence

One question that arises in the context of interpreting observations is whether trends are attributable to human-driven climate change. A key challenge in making definitive assessments of attribution is the role of natural climate variability, which has the potential to drive long-term trends in ocean oxygen. Indeed, variations in weather from year-to-year can produce thermally-driven surface O_2 anomalies, modulate surface-to-depth exchange, and alter the structure of the upper ocean environment, thereby impacting organic matter production and OUR in the interior (Deutsch et al., 2011; Ito & Deutsch, 2010). Observations collected in the Labrador Sea, for instance, have linked regional variations in O_2 to changes in deep convection on decadal or shorter timescales (van Aken et al., 2011). In the subpolar North Pacific, oxygen displays significant variability (Deutsch et al., 2006), which has been linked to fluctuations in the winter-time atmospheric forcing of the ocean (Andreev & Baturina, 2006). Variability of thermocline O_2 ventilation in the North Pacific is mainly controlled by the areal extent of winter mixed layer water intersecting the density layers

through which atmospheric O_2 is supplied to the ocean (Kwon et al., 2016).

The view of global-scale changes in ocean oxygen leaves an impression of smooth changes and clear trends (Figure 4.8A). Indeed, at the global-scale, spatial averaging reduces the contribution of natural variability to fluctuations in oxygen concentrations, which is reflected in relatively little ensemble spread. The case is different moving to regional scales; here, natural variability is evident as a major driver of trends. Figure 4.18A, for instance, shows oxygen concentrations simulated by the CESM-LE in the thermocline depth range in the California Current System (CCS; $33^\circ\text{--}46^\circ\text{N}$, within ~ 800 km of the coast). Notably, there is substantial variability in oxygen at this regional scale with each coloured line in representing the oxygen concentration in the CCS for a particular ensemble member; these lines can each be considered equally plausible realizations of the historical period (Figure 4.18A). There is substantial spread because the timing of modes of natural climate variability are out of phase across the ensemble; the fluctuations amount to weather-like noise and are entirely natural. Changes driven by increasing greenhouse gas concentrations, however, are superimposed on the natural variability; this “forced” signal is evident most clearly in the ensemble mean. Just as spatial averaging to the global-scale decreases noise, averaging across the ensemble tends to cancel out the effects of natural variability, leaving only the forced signal.

Given the role of natural variability in driving random fluctuations, detection and attribution of human-driven climate change amounts to a signal-to-noise problem. For detection to be possible, forced signals must develop a magnitude and persistence sufficient to transcend the noise, which is characterized by the envelope of background variability (Hasselmann, 1993; Santer et al., 1994, 2011). In this context, internally-generated variability inherently limits detection of climate-change signals regardless of practical observing capabilities; inferring trends from sparse observations is an obvious additional complication.

To illustrate the issues associated with detection and attribution of human-forced climate change, it is important to consider the “time of emergence” (ToE) of the forced signal in the CCS region. We use a relatively narrow definition of ToE, in which the magnitude of trends in oxygen to the variability of similar trends across

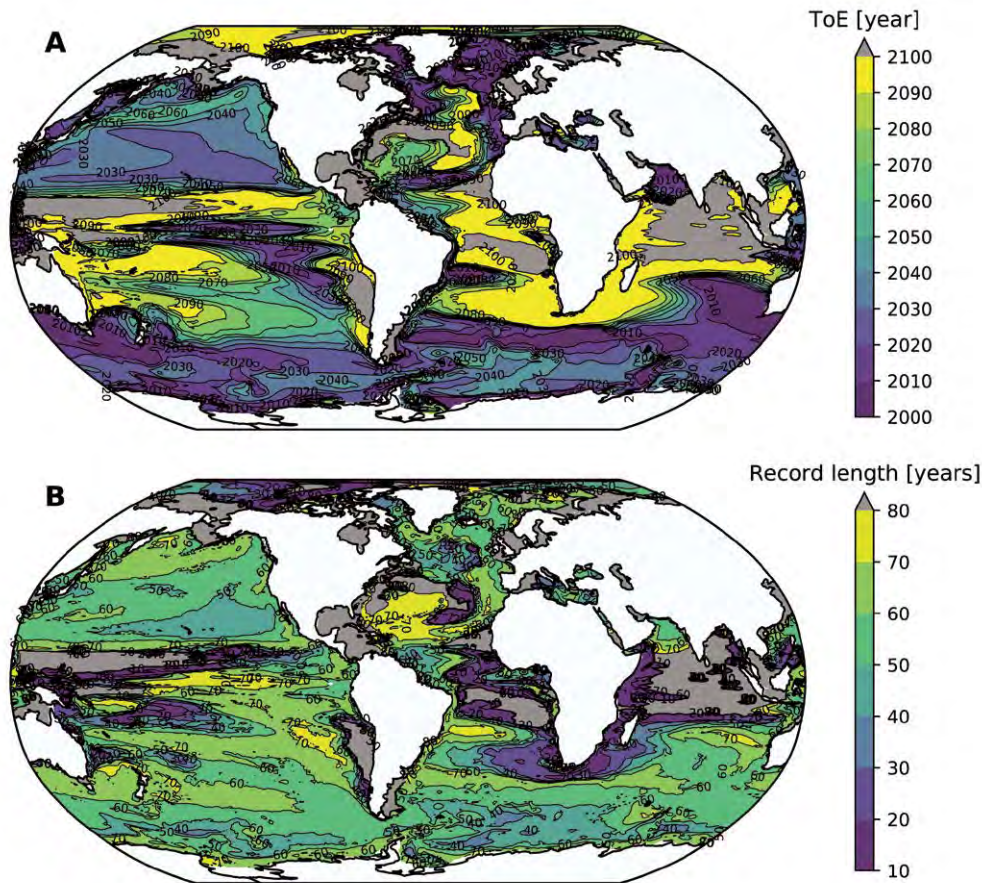


Figure 4.19 Time of emergence for trends in thermocline (mean over the 200–600 m depth range) oxygen, as simulated by the CESM-LE: (A) the year at which a significant trend is detected on average across the ensemble; and (B) the length of record required to detect a significant trend. Grey areas are regions where detection was not possible by 2100; in some cases these are regions where oxygen increased.

the ensemble are compared. We compute retrospective trends in each ensemble member starting at year 2000 and continuing through year 2100. For each year, trends are computed over record lengths from 10 to 100 years and normalized by the standard deviation of trends within the full CESM-LE, yielding a signal-to-noise ratio estimate. ToE is diagnosed as the earliest year in which a trend of any length is more than two standard deviations (2σ) outside the variability in trends across the ensemble and does not return to within 2σ for all remaining years in the simulation.

The results of this computation for thermocline oxygen in the CCS are illustrated in Figure 4.18B. Each line shows the ensemble mean trend and the shaded region shows the range within one standard deviation of the mean; blue shows 10-year trends, green shows 20-year trends and purple shows 60-year trends. As is evident from the 10-year trends, there is substantial decadal variability in oxygen in the CCS within the CESM-LE simulation; trends span a wide range from strongly increasing to strongly decreasing O_2 . As the trend length moves to

20 years in duration, the spread across the ensemble is diminished and the variability in the ensemble mean trend is reduced. However, even with 20-year trends, it is not possible to identify a ToE for forced O_2 change in the CCS in this simulation—even out to 2100. Trends of 60 years in length further reduce the noise, however, and detection of anomalous trends is possible around 2050 (the purple star).

Figure 4.19 shows the results of this same computation applied to thermocline oxygen globally. Interestingly, while the North Pacific has some of the strongest deoxygenation signals at 2100 (Figure 4.14), the detection of ToE on the basis of trends in this region is delayed until the 2030s and 2040s. Detection of the anthropogenic signal is possible relatively early (i.e. in the early 2000s) over broad regions of the Southern Ocean and high latitude North Atlantic (Figure 4.19A), however, that detection of the forced signal can require fairly long observational records (Figure 4.19B). Indeed, over much of the areas where early detection is possible, identifying ToE requires records of 40–60 years in length.

In addition to trends, there are other elements of the time-evolving signal-to-noise relationship that can facilitate identifying ToE (Santer et al., 1994). First, changes in the mean value of dissolved oxygen concentrations may be compared to the variability over a period known to have little influence from external forcing. In this context, as concentrations pass outside the range of unforced variability, these changes might be classified as externally forced (Christian, 2014). Second, the large-scale spatial structure associated with the forced signal can be evaluated relative to the dominant spatial structures associated with natural oxygen variability. Detection in this context relies on the extent to which the pattern associated with a forced signal is distinct from the patterns associated with natural variability. A key point from all approaches is that high quality, sustained observing systems are critical to enabling early detection (Long et al., 2016).

There is no doubt that the ocean is losing oxygen due to anthropogenic forcing, but it is important to emphasize that natural climate variability can make substantial contributions to oxygen trends at local to regional scales—and this must be considered in the interpretation of observations. It is scientifically useful to understand the mechanisms driving O_2 fluctuations, and ideally be able to attribute variability to natural versus human-driven causes. Ultimately, with sufficient investment in observing and modelling capabilities, it may be possible to forecast large-scale oxygen anomalies years in advance. Improvements in our understanding of oxygen variability and trends could reduce uncertainty in the nature, magnitude, and impact of climate change on marine ecosystems, thereby providing a more reliable basis for adaptation strategies and understanding cost/benefit trade-offs associated with climate change mitigation.

4.4 Implications and uncertainties

The focus thus far has been to describe how large-scale oxygen distributions are expected to change. We have relied on ESMs because these provide a comprehensive basis for assessing interactions between climate and ocean biogeochemistry under future forcing scenarios. As has been alluded to many times above, however, ESMs are far from perfect; their deficiencies merit additional attention to enable an understanding of structural uncertainty in model projections. In addition to uncertainty, there are several implications of deoxygenation that are not directly simulated by the

ESMs discussed above. These include the impacts on N_2O production as a result of hypoxic and suboxic zone expansion. Additionally, the deoxygenation problem is likely to manifest at spatial scales smaller than those easily amenable to study with global ESMs. In particular, it is very likely that coastal marine systems will be impacted by ocean deoxygenation. Finally, our ability to understand how the structure and function of ecosystems will change in response to deoxygenation is a major challenge. We discuss an approach to characterizing the projected future environmental change directly in ecophysiological terms.

4.4.1 Structural uncertainty

The ESM projections suggest that the ocean will lose substantial oxygen over the 21st century. Deoxygenation will be most intense at high latitudes due to the combined effects of solubility and respiration-driven reductions. Oxygen loss in the tropics is more ambiguous; the models project modest increases in oxygen within the tropical thermocline, where declines in solubility are offset by declines in respiration that are largely driven by changes in circulation (Figure 4.11). Most models show an increase in hypoxic and suboxic volumes, indicating that while the intensity of oxygen depletion in the core of oxygen minimum zones is diminished, these zones will expand in future. However, while the models provide a relatively consistent picture in their projections of high latitude deoxygenation, there is limited consensus on the balance of mechanisms driving projected tropical oxygen change (i.e. Figures 4.10B and 4.13B). The implications of this uncertainty are discussed in an attempt to provide perspective on why model solutions might be biased.

First, it is well recognized that the state-of-the-art ESMs struggle to accurately reproduce the observed mean state of oxygen distributions, and biases are most pronounced in the tropics, where oxygen levels are very low (Bopp et al., 2013). Common biases are characterized by oxygen distributions that are generally too low and oxygen minimum zones that are (vastly) too extensive, though not all models have this combination of biases (Bopp et al., 2013). The distribution of very low oxygen involves a subtle interplay of physical and biological mechanisms; getting the balance of these correct is clearly challenging. For instance, the derivative of the oxygen solubility relationship with respect to temperature (Figure 4.2) is approximately $-5 \text{ mmol m}^{-3} \text{ } ^\circ\text{C}^{-1}$. This suggests that a $1 \text{ } ^\circ\text{C}$ bias in sea surface temperatures

can make a substantial difference in downstream waters near the suboxic threshold of 5 mmol m^{-3} .

ESMs are also limited by their relatively coarse spatial resolution, which is constrained by computational cost. Ocean dynamics are characterized by motions on scales ranging from sub-metre to planetary; most of the kinetic energy in the ocean is contained within currents that have spatial scales ranging from 10 to 100 km; this range of spatial scales is defined as the ocean mesoscale (Stammer, 1997). The resolution of the OGCMs used by ESM is too coarse to explicitly represent mesoscale dynamics; thus, these motions must be approximated with subgrid-scale parameterizations (e.g. Gent & McWilliams, 1990). These approximations, however, do not represent certain mesoscale features known to be present in equatorial current systems. Indeed, observations indicate that circulation in the tropics is characterized by zonally-coherent, zonal jets that alternate in direction with latitude (Cravatte et al., 2012). These jets contribute to OMZ ventilation but are not well-simulated at coarse resolution (Brandt et al., 2008, 2012; Dietze & Loeptien, 2013; Duteil et al., 2014; Getzlaff & Dietze, 2013). Lacking a primary physical mechanism mediating delivery of oxygen to the eastern side of tropical basins, OMZs in coarse resolution models grow too large; moreover, omitting these processes may preclude representing important drivers of change. The situation is similar for other unresolved physical processes, such as vertical mixing, which is mediated by fine-scale turbulence. Mixing over rough topography and the role of tides, boundary currents and mesoscale phenomena are particularly challenging to represent accurately in models; insufficiently accurate parameterization of this process may contribute to low oxygen biases in the Subarctic North Pacific, for instance (Nakamura et al., 2006).

Finally, in addition to physical processes, the extent of simulated OMZs is sensitive to biogeochemical parameterizations used in the models. The biological pump begins with net primary productivity and ends as organic matter sinks and is remineralized at depth. Many opportunities arise for inaccurate simulation in the complex collection of processes mediating this production and transit. Models include simplified representations of phytoplankton physiology; for instance, they often simulate growth with fixed stoichiometric ratios between carbon and nutrients, whereas natural phytoplankton assemblages are known to display systematic geographic variation (Devries & Deutsch, 2014). Changes in nutrient

ratios (stoichiometry) impact OUR, and thus OMZs, by modulating oxygen demand: for a given nutrient supply rate, a surface ecosystem will generate more carbon export and hence more oxygen demand if carbon-to-nutrient ratios are greater. In addition to phytoplankton physiology, carbon export is controlled by a range of ecological and biogeochemical processes, including grazing and packaging of carbon by zooplankton (e.g. Wilson & Steinberg, 2010), physical and chemical aggregation mechanisms (Burd & Jackson, 2009; Passow, 2002), and ballasting of organic matter by biogenic or mineral materials (Armstrong et al., 2002; Klaas & Archer, 2002). Variations in these factors drive geographic variability export production, as well as in the efficiency with which carbon is transferred from the base of the sunlit surface layer to depth (Buesseler & Boyd, 2009; Weber et al., 2016). These variations result in variability in the depth distribution of OUR that may not be captured by models. Ultimately, accurate simulation of oxygen distributions depends on correctly representing AOU in the context of the model's circulation field. Most of the models considered here have a reasonable simulation of the large-scale structure in oxygen distribution patterns; it is not surprising, however, that they struggle to exactly match simulated oxygen supply with simulated demand; indeed, this a delicate balance in nature (Watson et al., 2017).

The ability to capture mean states does not necessarily guarantee convergence of future productions (Tagklis et al., 2017), but it does provide important perspectives on the uncertainties of model-based projections. The negative bias in the simulated mean state of tropical thermocline oxygen is problematic if one anticipates a decreasing O_2 trend, for instance. Since the models start with much lower O_2 levels than the real ocean, they simply lack the O_2 to lose. A key question arising from our presentation of the observationally-based relationship between oxygen loss and ocean heat content anomaly (Figure 4.13) is whether model projections of oxygen loss are too conservative. The observations suggest a greater rate of oxygen loss for a given heat content anomaly than simulated by the models. The solubility-driven line for oxygen loss (Figure 4.13) is a fixed thermodynamic reference in the O_2 -temperature phase space; departures from this line can only be achieved if respiration responds to warming, thereby driving increases in AOU. Thus, the fact that models underestimate oxygen loss relative to observations suggests that their simulation of AOU is insufficiently sensitive to changes in temperature.

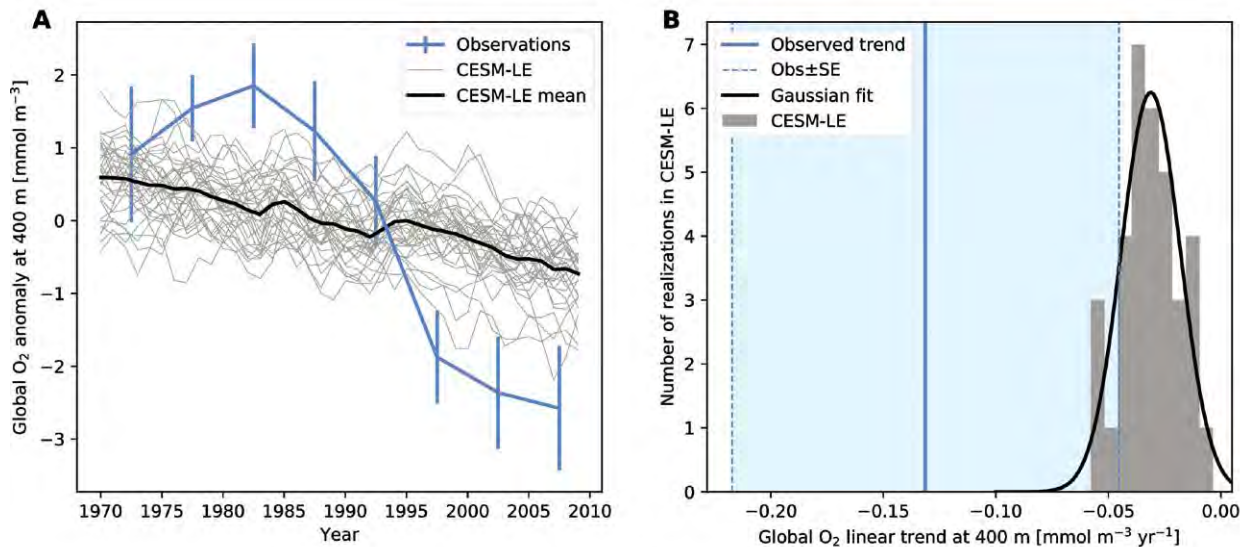


Figure 4.20 Global O₂ trends from observations and CESM-LE. (A) Globally average O₂ concentration at the depth of 400m from 1970 to 2010. The thin solid lines represent individual ensemble members of the CESM-LE, and the thick solid line is the ensemble mean. Blue line is the pentad time series of objectively mapped O₂ dataset based on the World Ocean Database (Ito et al., 2017). Error bars indicate one standard deviation of the pentad data. (B) Histogram of linear O₂ trend at 400 m. The black line is a gaussian fit, and the blue solid line is the observed trend; the dashed lines and shaded region show its uncertainty as measured by one standard error.

It is important to keep in mind that natural variability exerts substantial influence on oxygen trends (section 4.3.5). While it is not expected that natural variability is a dominant driver of decadal-scale variability on the global scale (i.e. Figure 4.8), observations do not provide comprehensive global coverage, introducing the possibility that inferred global trends arise from a peculiarity of the sampling distribution. As discussed earlier, the historical O₂ datasets include large data gaps and irregular sampling frequencies, which makes the quantification of the long-term trends difficult. Trends arising in model simulations, therefore, can only be evaluated in the context of large observational uncertainty.

Earth system models generate their own natural variability that is representative of that in nature—but does not necessarily evolve according to the temporal sequence followed in the real world. A large number of simulations with randomized initial conditions, therefore, can provide a means of quantifying uncertainty due to natural variability. For instance, with a perfect model, we might expect individual realizations of the historical period in that model to have trends weaker or stronger than those observed, depending on the particular evolution of natural variability in each case. However, while individual realizations may not match observations, the observed trends will fall within the spread of a sufficiently large ensemble of a perfect model. The question is: To what extent are O₂ trends within the CESM-LE consistent with observationally-estimated trends?

Figure 4.20A shows the comparison of the global O₂ time series from the objectively-mapped historical O₂ dataset (Ito et al., 2017) and CESM-LE. They are both evaluated at 400 m depth for the period of 1970 to 2010. The model and observations both show declining global O₂ trends but the model appears to underestimate the global O₂ trend evident in the observations. The objectively mapped historical O₂ dataset indicates a trend of -0.13 ± 0.09 mmol m⁻³ yr⁻¹, where the uncertainty is the standard error of the regression coefficient. The significant uncertainty arises because the observed time series substantially departs from a linear trend (Santer et al., 2011), which is due to the superposition of large, decadal-scale change evident as an apparently sinusoidal variation (Figure 4.20A). Figure 4.20B contrasts the observed and simulated linear trends of O₂. The overlap between observations and the model is quite marginal. The model underestimates the magnitude of the global O₂ decline, as no single ensemble member reproduces the observed trend. The ensemble mean trend (-0.03 mmol m⁻³ yr⁻¹) is a factor of 4 smaller in magnitude than the observationally-based estimate, but—due to the large uncertainty in the observations—the lower quartile trend (-0.04 mmol m⁻³ yr⁻¹) still overlaps with the upper bound of the observational uncertainty range (blue dashed line in Figure 4.20B). The effect of natural variability, as represented by the spread of histogram in Figure 4.20B, provides some sense of an expected range in the simulated trend, but there is a strikingly

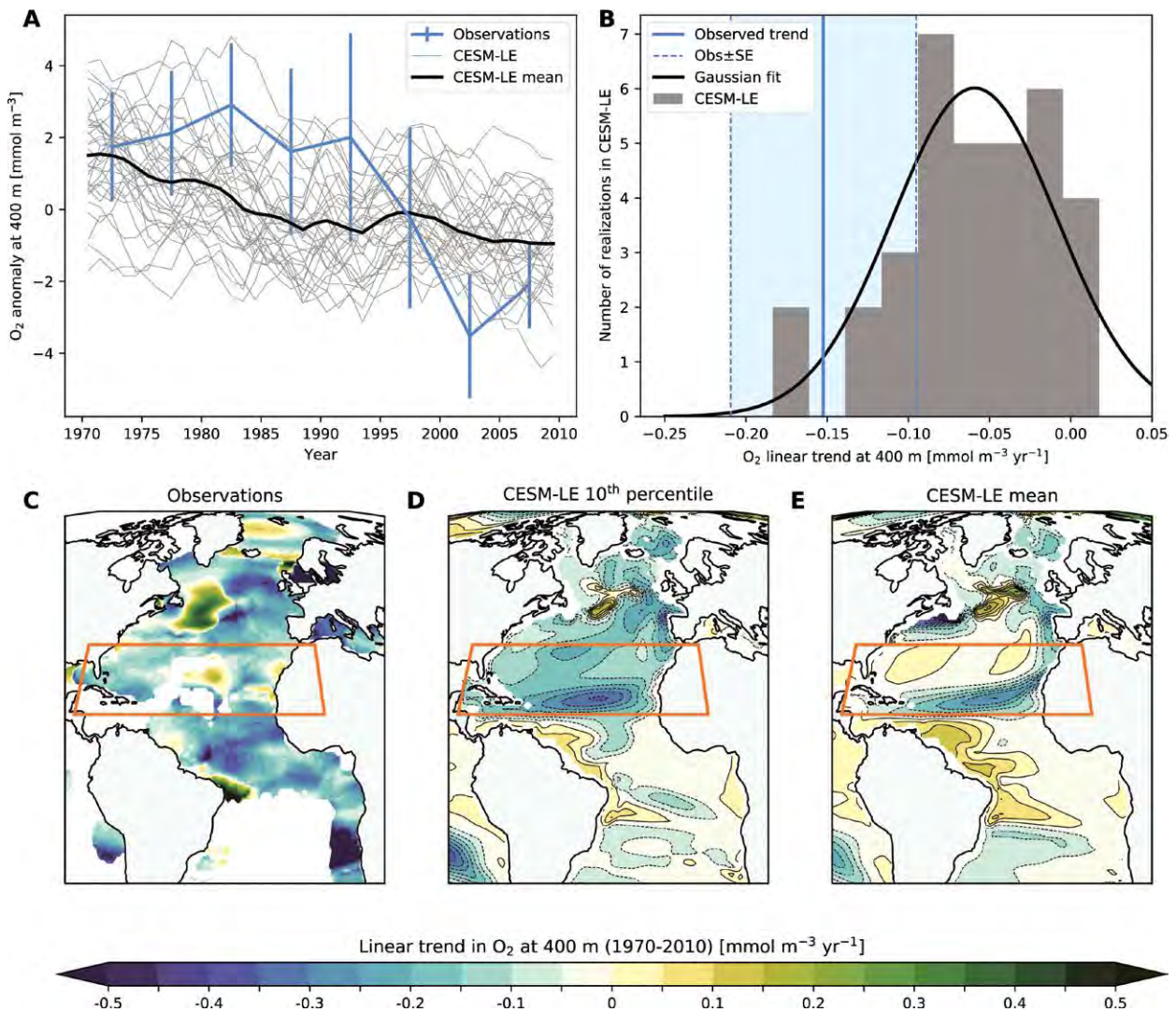


Figure 4.21 O_2 trends in the Subtropical North Atlantic (STNA; 15° – 35° N) from observations and CESM-LE. (A) STNA average O_2 concentration at 400 m depth from 1970 to 2010. The thin solid lines represent individual ensemble members of the CESM-LE, and the thick solid line is the ensemble mean. The blue line is the pentad time series of objectively mapped O_2 dataset based on the World Ocean Database (Ito et al., 2017). Error bar indicates one standard deviation of the pentad data. (B) Histogram of linear O_2 trend at 400 m. The black line is a gaussian fit, and the blue solid is the observed trend; the dashed lines and shaded region show its uncertainty as measured by one standard error. (C) Observed pattern of linear trend at 400 m depth from 1970 to 2010. The trend is plotted for $1^{\circ} \times 1^{\circ}$ grid cells within which at least 20-years' of observations are available. (D,E) 10th percentile and ensemble mean trend from the CESM-LE for the same depth and time period. The orange box on the maps shows the region for which time series and trends are presented in panels (A) and (B).

large difference between the spread in the ensemble members and the standard error of observed trend. This indicates that the model may be underestimating the natural variability, and/or the existing observations lacks the spatial coverage to accurately determine the decadal fluctuation of global O_2 time series. Considering the poor data coverage in the historical observations, consistent and accurate monitoring of global O_2 fields is a primary challenge.

Assessing global trends places significant demands on observations for comprehensive coverage. We might expect to be able to assess model behaviour more

robustly at regional scales but unfortunately, some regions of intense interest, such as the thermocline of the Eastern Tropical Pacific, have been poorly sampled in the historical dataset, making the model-observation comparisons difficult. Even with such large observational uncertainty, Oschlies et al. (2017) showed a persistent discrepancy in observed and simulated trends of O_2 at 300 m depth, wherein the observations show trends that are consistently stronger than the models. The subtropical North Atlantic, in contrast, has relatively high sampling density. This is also a region where the models and observations agree relatively well (Figure 4.21A). Comparing the observed and simulated time series of

O₂ in the subtropical North Atlantic (15°–35°N), however, the ensemble mean again underestimates the long-term trend of O₂. The observed linear trend (1970–2010) is $-0.15 \pm 0.06 \text{ mmol m}^{-3} \text{ yr}^{-1}$, where the uncertainty is a standard error of the regression coefficient (Santer et al., 2011). The ensemble mean trend ($-0.06 \text{ mmol m}^{-3} \text{ yr}^{-1}$) is a factor of 2.5 smaller than the observed trend. However, a few ensemble members exceed the magnitude of observed deoxygenation in this region (as measured by the linear trend; Figure 4.21B). Figures 4.21C–E compare the pattern of deoxygenation in the North Atlantic between observations, the 10th percentile composite from the CESM-LE, and the ensemble mean. The ensemble mean clearly lacks the strong deoxygenation of the central subtropical gyre; however, there is a subset of ensemble members that exhibited trends nearly as intense as those observed. Further investigation is required to partition the roles of natural variability versus external forcing in driving observed O₂ trends in this region; however, while this analysis emphasizes that natural variability can indeed play a substantial role in modulating trends, it also suggests that the CESM-LE and other CMIP5 models may underestimate deoxygenation.

4.4.2 Nitrous oxide production

Nitrous oxide (N₂O) affects climate in two distinct ways. First, it is a strong greenhouse gas; thus, increasing N₂O concentrations in the troposphere have a potent effect on radiative forcing (Solomon et al., 2007). Second, since N₂O is relatively long-lived, it is mixed upward to the stratosphere, where it is a major contributor to the production of ozone depleting substances (NO and NO₂) (WMO, 2011; Wuebbles, 2009). Global-mean atmospheric N₂O concentrations have increased markedly from preindustrial levels, around 270 ppb, to near 330 ppb in 2017, mainly as a result of human activities (Forster et al., 2007; NOAA ESRL Global Monitoring Division, Boulder, Colorado, USA). N₂O is produced naturally in soils and the ocean; agricultural land use changes, and industrial activities account for anthropogenic sources (Denman et al., 2007). The IPCC Fourth Assessment Report estimated that the ocean accounts for about 35% of the natural sources of N₂O to the atmosphere (Denman et al., 2007).

N₂O is produced by two microbially-mediated processes in the ocean: (1) under well-oxygenated conditions, microbes produce N₂O as a byproduct of nitrification ($\text{NH}_4^+ \rightarrow \text{NO}_2^- \rightarrow \text{NO}_3^-$); and (2) at suboxic concentrations,

denitrification produces N₂O as an intermediate during the conversion of nitrate to N₂ ($\text{NO}_3^- \rightarrow \text{NO}_2^- \rightarrow \text{N}_2\text{O} \rightarrow \text{N}_2$) (Bange et al., 2010). When oxygen concentrations are very near zero, there is net consumption of N₂O during denitrification and little N₂O accumulation (Bange et al., 2010). The N₂O yield of nitrification is sensitive to oxygen levels, however, increasing significantly as oxygen declines (Löscher et al., 2012; Santoro et al., 2011); thus, suboxic regions and surrounding hypoxic waters account for a substantial fraction of marine N₂O production (Codispoti, 2010).

The expansion of suboxic and hypoxic waters (i.e. Figure 4.12) is very likely to impact the production and decomposition of N₂O. Enhanced denitrification will lead to greater rates of fixed nitrogen loss from the ocean, with unknown implications on primary productivity. The role of increasing denitrification on N₂O production remains even less clear; however, it is likely that N₂O yields from nitrification will increase, on average, as oxygen levels decline. Moreover, oxygen loss in relatively shallow waters might enhance N₂O production because respiration rates are higher near the sunlit surface where primary productivity generates sinking organic matter (Codispoti, 2010). Our understanding of the collection of processes driving N₂O production, however, is insufficient to make definitive predictions. Indeed, ocean warming may drive shifts in bacterial community composition, potentially impacting N₂O production (Freing et al., 2012). Nitrification has been shown to decrease at low pH, thus suggesting the potential for ocean acidification to impact N₂O production (Beman et al., 2010). Modelling studies have projected decreased global N₂O emissions from the ocean, driven by reductions in primary productivity, which limits nitrification, and the direct effects of stratification, which traps N₂O at depth (Martinez-Rey et al., 2015). These projections, however, are highly uncertain in part because models lack fully mechanistic representations of the processes mediating microbial transformations in the nitrogen cycle and the resultant N₂O yields; indeed, our empirical understanding of these processes is still developing (Codispoti, 2010).

4.4.3 Coastal deoxygenation

Coastal ocean hypoxia has emerged as a growing threat to marine ecosystems and fisheries with high economic and societal value (Diaz & Rosenberg, 2008; McClatchie et al., 2010). Oxygen decline in many coastal waters is driven by nutrient pollution. The widespread use of

chemical fertilizers and discharge of waste waters increases the nutrient content of surface waters on land; as these waters are discharged into coastal systems, elevated nutrient loads stimulate productivity (Rabalais et al., 2010). Additionally, fossil fuel combustion and agricultural activities are associated with increases in atmospheric deposition of nutrients to the ocean. In particular, reactive nitrogen loads have increased substantially over the last century, enabled by industrial-scale artificial nitrogen fixation via the Haber-Bosch process (e.g. Gruber & Galloway, 2008). Nutrient pollution drives “eutrophication”, wherein primary productivity increases, leading to oxygen declines as excess organic matter decomposes in subsurface waters.

Coastal habitats can be particularly vulnerable to future deoxygenation because of the compounding effects of nutrient runoff from the land and the large-scale ocean deoxygenation. These areas are also of particular concern as they serve as the nurseries for larval stages of many species which have been shown to be particularly vulnerable to hypoxia (e.g. Miller et al., 2002). A major concern is that ocean deoxygenation drives declines in the oxygen content of offshore waters, lowering the baseline concentrations from which coastal eutrophication causes further oxygen depletion. The CCS, for instance, is one of the most productive and biodiverse marine systems in the world (Block et al., 2011; Carr, 2001). In the California Current System (CCS), like other coastal ocean upwelling systems, changes in the oxygen content are controlled by complex interactions between circulation and biogeochemistry, and show prominent fluctuations on interannual and decadal timescales both in observations and models (section 4.3.5; Bograd et al., 2008; Deutsch et al., 2011). Over the continental shelf region, where the marine ecosystem is most sensitive to low oxygen conditions, natural oxygen variations are associated with fluctuations in the strength of the coastal upwelling (Chan et al., 2008; Connolly et al., 2010). The subsurface waters in the offshore CCS region are charged with nutrient-rich, low-O₂ waters, which can trigger high production of new organic matter as water upwells onto the continental shelf. Coastal upwelling is driven by winds, which vary in intensity and seasonality due to both natural variability and anthropogenic climate warming. The seasonal timing of upwelling-favourable winds has a strong impact on the CCS system; for instance, Barth et al. (2007) demonstrated that delayed upwelling strongly impacted net primary productivity and food web structure in the CCS. Theory suggests that the seasonal timing and intensity of upwelling-favourable

winds are likely to change significantly in a warmer climate (Bakun, 1990). Indeed, consistent with this, a collection of the CMIP5 models suggest that upwelling-favourable winds in the CCS system will occur over a prolonged seasonal duration and become more intense at high latitudes (Wang et al., 2015). The likely impacts of these changes on coastal ecosystems and marine biodiversity are not well-understood and merit further study. It is clear, however, that changes in the properties of offshore source waters have a significant impact on hypoxia in the CCS system (Bograd et al., 2008; Grantham et al., 2004). Moreover, the frequency of hypoxic events may be modulated by the slow, decadal changes in these subsurface water properties feeding the CCS upwelling. Pozo Buil and Di Lorenzo (2017), for instance, demonstrated that low-frequency changes in the oxygen levels of the CCS upwelling are driven by large-scale ocean circulation dynamics. Oxygen anomalies are generated in regions well offshore in the Subarctic North Pacific and are advected across the basin in the North Pacific Current; these anomalies contribute to variations in hypoxia within the CCS on decadal to multi-decadal timescales (Pozo Buil & Di Lorenzo, 2017). Notably, the time required for the oxygen anomalies to cross the Pacific basin is about 10 years, indicating that with sufficiently robust observing capabilities, oxygen variability in the waters offshore the CCS might be predictable many years in advance.

In light of these dynamics, a major concern for the CCS and other similar coastal systems is the systematic and widespread depletion of oxygen in offshore waters. While there is limited research on the future of coastal hypoxia taking into account different scenarios of coastal eutrophication and emissions, it is reasonable to expect large-scale oxygen declines to propagate down to local scales (Bianucci et al., 2015). Oxygen depletion in coastal upwelling systems happens naturally; however, as the oxygen levels decline offshore, hypoxic and anoxic events may become much more frequent and severe. This is a critical consideration, especially since these coastal systems are profoundly important in both ecological and economic terms.

4.4.4 Habitat of the future

The impact of ocean deoxygenation on marine conservation goals depends on the number and ecological roles of the species for which the loss of dissolved O₂ crosses a critical biological threshold. Based on compilations of lethal O₂ levels from laboratory studies

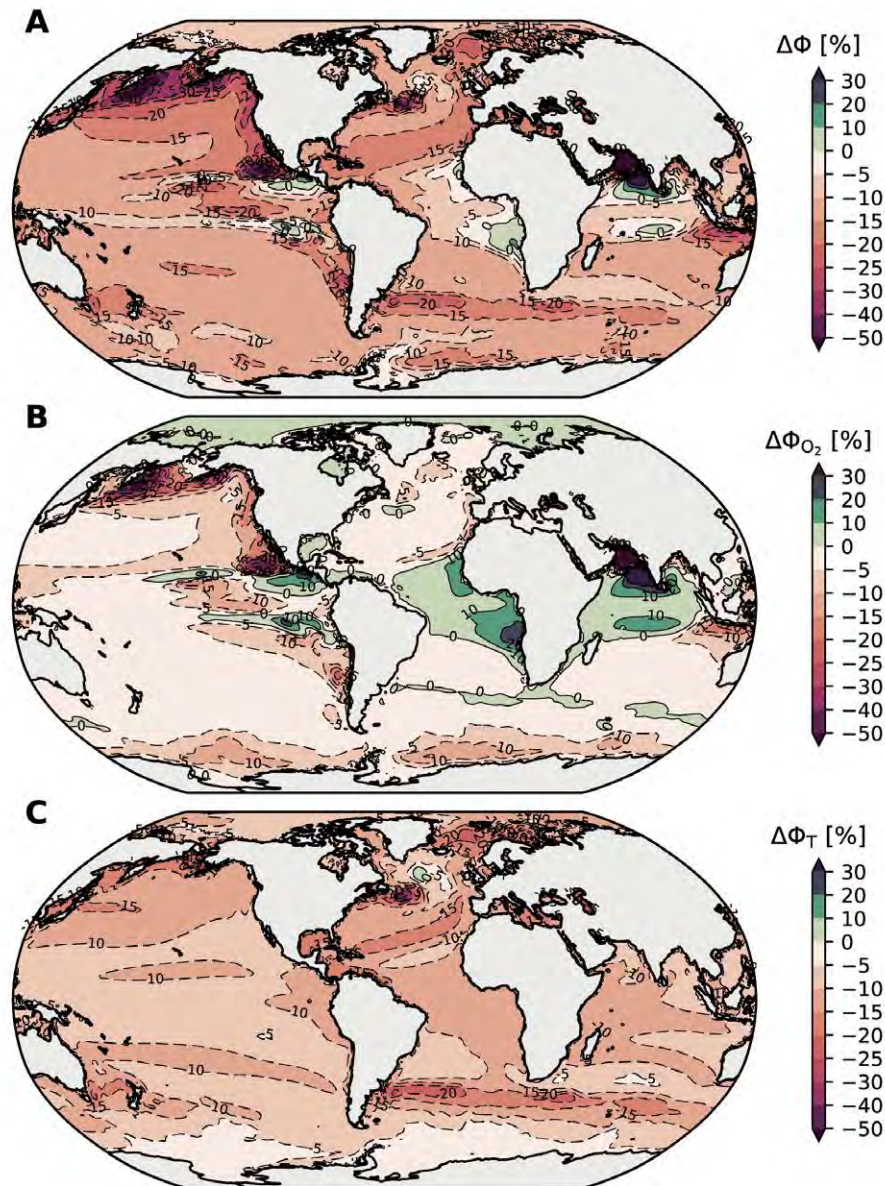


Figure 4.22 Relative change in the Metabolic Index (Φ ; equation 2) at year 2100 over the top 400 m of the ocean according to the bias-corrected, CMIP5 ensemble mean: (A) the total relative change in Φ , i.e. $\Delta\Phi=100\times(\Phi^{2100}-\Phi^{2000})/\Phi^{2000}$; (B) the relative change in Φ due purely to changes in O_2 ; (C) the relative change in Φ due purely to changes in temperature. The relative change has no dependence on A_0 or B^0 ; the total and temperature-driven components of change depend on E_0 . For this presentation, we have used $E_0=0.4$, which is the mean of the several taxa for which E_0 has been characterized (Deutsch et al., 2015).

and the distribution of O_2 in the ocean (i.e. Figure 4.1A, B), it would appear that the impact of deoxygenation will be confined to those species residing in the relatively small volumes of the oceans already at or near O_2 levels below a nominal hypoxic level of $\sim 60 \text{ mmol m}^{-3}$.

This view, however, neglects at least two critical facts about the provisioning of energy to aerobic marine organisms. First, the energetic demands of an organism's metabolism rise with temperature. Thus, as the oceans warm, even a constant O_2 may not suffice to meet organisms' energetic demands. Second, lethal

thresholds measured in laboratory studies are carried out under conditions designed to quantify oxygen demand at the minimum metabolic rate in a state of rest. Ecological survival in the real environment will typically require substantially more energy (and hence O_2 supply) than would be indicated by the physiological survival evaluated by laboratory studies. Indeed, among terrestrial taxa, active metabolic rates are found to be 1.5–7 times resting rates (Peterson et al., 1990), suggesting that O_2 thresholds for ecological survival may be several times higher than lethal thresholds would imply.

An ecophysiological framework has recently been developed to investigate metabolic habitat constraints imposed by temperature and oxygen, for the contemporary, past, and future oceans. The framework is built on a Metabolic Index (Φ), which can be calibrated with laboratory and biogeographic data (Deutsch et al., 2015). The Metabolic Index uses physiological data on hypoxia tolerance across a range of temperatures and body sizes to calibrate the ratio of oxygen supply (S) to an organism's resting demand (D). The supply of oxygen is a function of the ambient partial pressure of oxygen (pO_2) and the efficiency with which an organism can acquire and utilize O_2 . This can be written as $S = \alpha_s B^\delta pO_2$, where α_s is a mass-normalized coefficient expressing the rate of gas transfer between an organism and its environment and B^δ is the scaling of supply with biomass B (Piiper et al., 1971). Resting metabolic demand can be expressed as $D = \alpha_D B^\epsilon \exp(-E_o/k_B T)$, where α_D is a taxon-specific basal metabolic rate, B^ϵ is the scaling of this rate with biomass, E_o is the temperature dependence, and k_B is the Boltzmann constant (Gillooly et al., 2001). We construct the Metabolic Index as the ratio S/D :

$$\Phi = A_o B^n \frac{pO_2}{\exp(-E_o/k_B T)} \quad (2)$$

where $A_o = \alpha_s/\alpha_D$ is the ratio of rate coefficients for gas exchange (O_2 supply) and minimum metabolic rate (O_2 demand) and n is the difference between the scaling exponents applied to body size (B) for O_2 supply and demand. If Φ falls below a critical threshold value of 1, organisms must either suppress aerobic activity or initiate anaerobic metabolism, conditions that are physiologically unsustainable. Conversely, values above 1 enable organismal metabolic rates to increase by a factor of Φ above resting levels, permitting critical activities such as feeding, defence, growth, and reproduction. Thus, for a given environment and species, Φ estimates the ratio of maximum sustainable metabolic rate to the minimum rate necessary for maintenance.

For marine animals, this ratio of active to resting energetic demand can be inferred by mapping Φ alongside the species biogeographic distribution (Deutsch et al., 2015). Among all taxa studied to date ($n \approx 20$, species geographic range boundaries are found to coincide with Metabolic Index values of between 1.5–7, identical to the range predicted by terrestrial energetic demands.

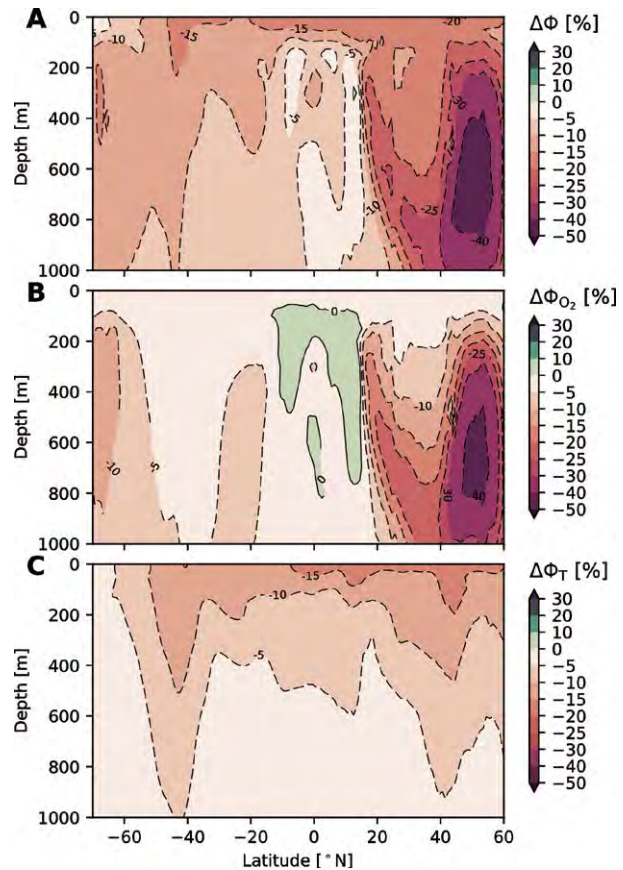


Figure 4.23 Zonal mean relative change in the Metabolic Index (Φ ; equation 2) at year 2100 according to the bias-corrected, CMIP5 ensemble mean: (A) the total relative change in Φ ; (B) the relative change in Φ due purely to changes in O_2 ; (C) the relative change in Φ due purely to changes in temperature. See the caption of Figure 4.22 for further details.

Where the ocean's supply of O_2 falls below this critical threshold, termed Φ_{crit} , the Metabolic Index acts as a fundamental energetic barrier for species habitat. In other words, if climate warming and O_2 loss reduce the Metabolic Index for an organism below its species-specific Φ_{crit} , the environment would no longer have the aerobic capacity to support the organism's energetic requirements. The Metabolic Index can therefore be used to quantify the loss of aerobically viable habitat for marine animals due to the combined effects of climate warming and attendant O_2 loss. It can also be used to track the relative role of each stressor in governing viable habitat across space and depth. This is particularly useful as the magnitudes of warming and deoxygenation can differ dramatically among regions of the ocean (Figures 4.6 and 4.14).

Figure 4.22A shows the total relative change in Φ over the top 400 m of the ocean for an organism with an average metabolic temperature sensitivity ($E_o = 0.4$). There are widespread declines in Φ over

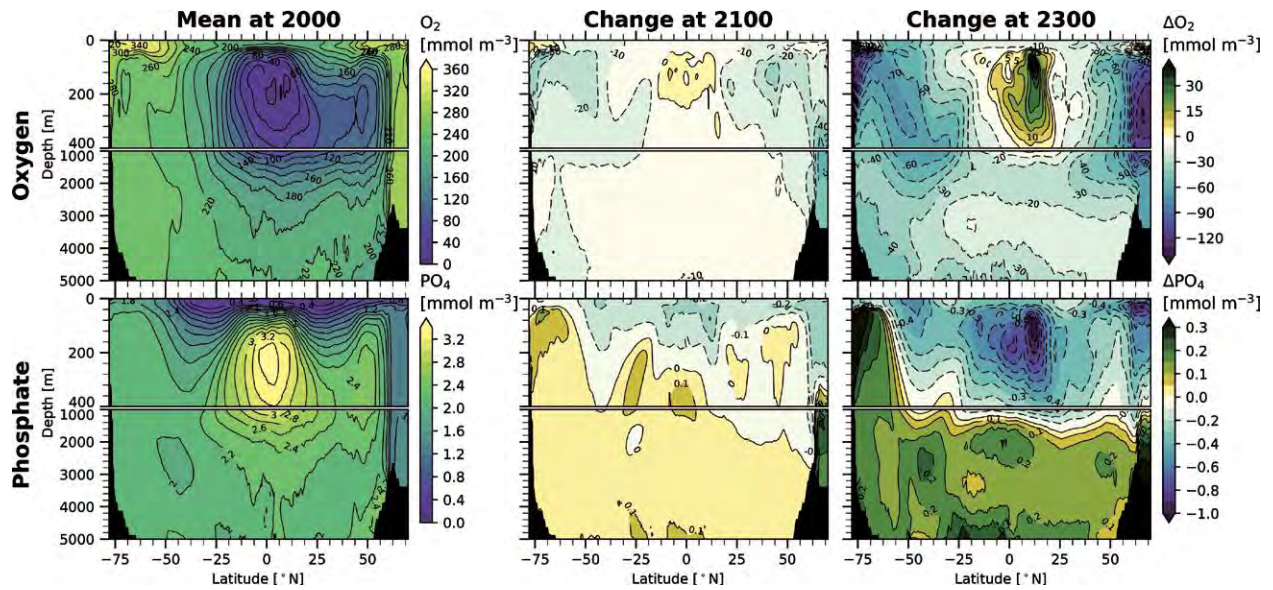


Figure 4.24 Zonal mean oxygen (top) and phosphate (bottom) in a CESM1-BGC simulation, averaged over 1995–2005 (left column). The middle column shows the change in zonal mean oxygen and phosphate at 2100 (2090–2100 minus 1995–2005); the right column shows the change at 2300 (2280–2300 minus 1995–2005).

most of the ocean; only in small pockets in the tropics does Φ modestly increase. Relative changes in Φ in excess of 40% are found in the Subarctic North Pacific, suggesting that this region may be particularly impacted by climate change and deoxygenation. Figures 4.22B and 4.22C demonstrate why it is important to consider changes in temperature and oxygen together. Figure 4.22B shows the change in Φ that would be realized if oxygen was changed in isolation. The subarctic North Pacific stands out again in this field, but much of the tropics where models simulate oxygen increases show improvements in Φ . Temperature-driven reductions in Φ , however, are nearly ubiquitous, which we might expect from the distribution of surface warming (Figure 4.6). The fact that metabolic rates scale with temperature means that even present-day distributions of oxygen may not be sufficient to meet metabolic demands in some regions in the future. The depth structure of changes in Φ are shown in Figure 4.23. Strong reductions in Φ are predicted for the upper 1000 m of ocean over much of the high-latitude northern hemisphere (Figure 4.23A). The oxygen-driven and temperature-driven changes in the zonal-mean Φ have a fundamentally different structure (Figure 4.23B, C). Oxygen-driven changes are most intense below 200 m, which is where oxygen depletion is most pronounced (Figure 4.11). The modest increases in oxygen in the tropical thermocline yield oxygen-driven increases in Φ locally.

The restrictions of habitat imposed by the need to balance O_2 supply and demand vary across species, and the tightening of those constraints during ocean warming will depend critically on the relative magnitude and patterns of ocean warming and deoxygenation. Thus, a generalized prediction of the responses of marine species to ongoing global change must rely on adequate characterization of species diversity with respect to Metabolic Index traits, and on a regional basis, since temperatures and O_2 levels can operate in both synergistic and counteracting directions.

4.5 Action

Ocean oxygen concentrations are strongly linked to ocean heat content (Figure 4.13); therefore, substantial deoxygenation is unavoidable without mitigating climate change. Even in the best circumstances, some degree of continued ocean warming is unavoidable and, given the longevity of perturbations to atmospheric CO_2 (Archer et al., 1997), current emissions commit the climate system to sustained alteration. Efforts to conserve marine ecosystems must account for the synergistic effects of multiple variables changing simultaneously (e.g. Boyd et al., 2014; Brewer & Peltzer, 2009; Deutsch et al., 2015; Pörtner, 2010). Indeed, ocean warming, acidification, oxygen loss, and reductions in primary productivity are key components of a suite of multiple stressors effecting ecosystem change. Specifically, in the context of ocean deoxygenation, we can frame our discussion about mitigation actions around two

questions. (1) What are the consequences if nothing is done to mitigate climate warming? (2) What are the benefits of mitigation actions?

Warming over the 21st century is very likely to lead to disruptive consequences; an examination of model projections under an extended RCP8.5 scenario out to 2300, however, suggest that long-term effects of unmitigated human-driven climate change could be catastrophic. While this scenario may be unlikely, assuming international efforts to mitigate climate change persist, it does provide a perspective on the risks of inaction. Figure 4.24 presents a zonal-mean view of oxygen and phosphate in the present-day climate as well as changes to these fields at 2100 and 2300. The scenario used to integrate the model out to 2300 follows historical and then the RCP8.5 forcing out to 2100; this entails an increase of atmospheric CO₂ from 285 ppm in 1850 to about 940 ppm at 2100—CO₂ then continues to increase to 1962 ppm at 2300. The impacts on ocean oxygen involve a strong amplification of the pattern of change at 2100: high latitude regions show substantial oxygen declines. While there are increases in oxygen within the tropical thermocline, those regions remain below the biological thresholds of habitability for many species. The magnitude of these changes is extreme: the zonal-mean changes in oxygen concentrations at high latitudes approach and even exceed 100 mmol m⁻³; the entire deep ocean substantially deoxygenates (Figure 4.24, top right).

The changes in oxygen at 2300 are associated with a massive redistribution of nutrients. The surface ocean becomes strongly depleted in phosphate, whereas the deep ocean phosphate inventory increases; this increase is consistent with growth of the remineralized nutrient inventory and thus AOU. Stratification reduces the vertical fluxes of phosphate from depth into the surface ocean over much of the globe; however, reductions in sea ice and changes in upwelling in the Antarctic Zone of the Southern Ocean promote high productivity there, which results in a more complete transfer of nutrients from the upper ocean to deep waters (Primeau et al., 2013). The surface depletion of nutrients will drive declines in primary productivity, dramatically reducing the flow of energy into marine ecosystems. This is likely to strongly reduce potential fisheries yields (Pauly & Christensen, 1995; Stock et al., 2017) and may lead to a fundamental reorganization of ocean food webs (Hoegh-Guldberg & Bruno, 2010).

The depletion of oxygen at 2300 represents a severe contraction of viable habitat on the basis of the metabolic constraints discussed in section 4.4.4. Indeed, these changes are similar in structure to simulations conducted with CESM of ocean climate change at the end-Permian extinction event (~252 million years ago); analysis of these simulations indicates that warming and deoxygenation can account for extinction patterns (unpublished), leading to a haunting conclusion: human-induced warming is driving patterns of change that are consistent with those of the most severe crisis in the history of life on Earth.

A comparison between 2100 and 2300 confirms that the severity of deoxygenation and its consequences will grow in the absence of efforts to mitigate climate change. However, it is also important to consider that climate change is essentially irreversible on human timescales. Solomon et al. (2009) demonstrated this using an Earth System Model of Intermediate Complexity; they conducted idealized forcing scenarios, wherein emissions were instantaneously ceased following a period of increase similar to that in RCP8.5. Carbon dioxide concentrations begin to decline following the cessation of emissions, but the carbon perturbation requires several centuries to fully dissipate (Archer & Brovkin, 2008; Archer et al., 1997). Moreover, even as radiative forcing due to CO₂ begins to decline, the ocean continues to warm, but at a slower rate; thus, surface temperatures remain elevated for more than 1,000 years following an abrupt stop in emissions (Solomon et al., 2009). Few studies have explicitly examined irreversibility in the context of ocean biogeochemistry and ecology; this is an important area for further research.

The long persistence timescales of ocean deoxygenation drivers suggest that early action to mitigate climate change will maximize benefit. The benefits of mitigation can be quantified in terms of the reduced magnitude of change in some state variable (i.e. preserving oxygen content) or in delaying impacts, providing time for adaptation. Henson et al. (2017), for instance, examined the ToE of anthropogenic signals in sea surface temperature, pH, primary productivity, and interior oxygen distributions; by comparing RCP8.5 to a “mitigation scenario” (RCP4.5); they demonstrate benefits of mitigation in terms of reduced areal extent and delayed emergence of stressors. The benefits of delayed impacts can include time for organisms to adapt or migrate to avoid impacts (Henson et al., 2017). Understanding how delayed emergence will affect the

structure and function of marine ecosystems is very complicated, however; thus, it is not clear whether the difference between RCP8.5 and RCP4.5 is a meaningful one from an ecological perspective. Moreover, in cases where species are already living near the edge of their ecophysiologicaly-viable envelope, such as at high latitudes, there may be no refuge from which to avoid climate change impacts. These considerations are critical to developing better quantifications of the avoided impacts of climate change associated with mitigation efforts. A few studies have framed analyses of ESMs in this context (e.g. Krumhardt et al., 2017), but this is an area where much more research is needed.

Finally, while climate change mitigation is critical to avoiding deoxygenation, investments in observing systems and modelling capabilities may help provide adaptive capacity. There is good reason to believe, for instance, that oxygen distributions can be forecast years ahead in some regions (e.g. Pozo Buil & Di Lorenzo, 2017), possibly enabling advanced warning of especially low-oxygen periods. Humanity is changing marine ecosystems faster than we can understand them; there is a strong role for science in enabling informed decisions about managing this global-scale impact.

4.6 Conclusions

Ocean deoxygenation presents a compelling case-study demonstrating the intricate interrelationships characterizing Earth system function. The planetary energy balance is determined by the composition of the atmosphere, including, most importantly, carbon dioxide. Carbon is the primary currency of life on Earth; the flow of energy and material through the biosphere plays a role in regulating atmospheric composition and the radiative balance controlling climate. Humans, however, have released massive quantities of geologically-sequestered CO₂, disrupting this balance, trapping more heat and warming the planet. The ocean is the dominant heat reservoir in the climate system and thus absorbs most of this anomalous heat. Ocean warming drives deoxygenation by directly impacting the gas solubility: warmer waters hold less oxygen. Furthermore, warming causes the ocean to become more stratified, inhibiting vertical exchange between surface and deep waters—and thereby reducing the supply of oxygen to the ocean interior.

Ocean ecosystems are built on the energy harvested from the sun during photosynthesis—the same process

that contributes to regulation of the carbon cycle and produces most of the oxygen in the Earth system. The flow of energy contained in photosynthetically-produced organic matter and the oxygen necessary to respire it have enabled evolution of the wide diversity of animal life on the planet. The carbon cycle is coupled to the cycles of nutrients such as nitrogen and phosphorus, required building blocks of organic matter. Oxygen mediates the return of these nutrients from their organic forms to those that refuel photosynthesis. In this manner, the global biosphere consists of an interconnected metabolic network in which many of the key linkages are mediated by microbial transformations. Oxygen exerts strong control across two critical components of this network. It is a fundamental requirement for animal life and it regulates microbial metabolism, affecting which transformations take place.

Earth system models predict substantial deoxygenation over the 21st century, with a rapid acceleration in oxygen loss expected in the coming decades. These models suggest that deoxygenation will be strongest at high latitudes, where the effects of solubility and stratification are reinforcing. The loss of oxygen in the tropics, according to these models, is tempered by opposing drivers: reductions in solubility are projected to be offset somewhat by reductions in respiration, the latter caused primarily by changes in circulation. Most ESMs project increases in oxygen in the tropical thermocline over the 21st century. These increases occur in regions where oxygen is already very low in the present climate—and the models also tend to predict increases in hypoxic and suboxic water volumes, suggesting that while oxygen concentrations may increase in the core of oxygen minimum zones, these zones will still expand. However, ESMs struggle to accurately simulate present-day oxygen distributions in the tropics; thus, the future of oxygen in these regions of the ocean is somewhat uncertain. Moreover, an observationally-based relationship between oxygen loss and ocean heat content anomaly suggests that the model projections may be too conservative: the observed relationship would suggest greater rates of oxygen loss than simulated by the models.

The changes projected in dissolved oxygen over the next century are likely to force dramatic changes in marine ecosystems. Simulations of the “deep future” (out to 2300), in the absence of climate change mitigation efforts, project changes to oxygen and nutrient distributions that would yield catastrophic consequences for marine life.

More research is needed to fully quantify how climate change mitigation can benefit conservation. However, there is virtually no uncertainty that the present climate trajectory will lead to substantial oxygen loss from the oceans, resulting in profound impacts to ocean ecosystems and biogeochemistry. Animals reliant on aerobic metabolisms will experience habitat contraction as regions with oxygen below hypoxic limits expand. Ocean microbial communities will be affected, leading to altered nutrient cycles: rates of fixed nitrogen loss from the ocean will increase; N₂O production and release is likely to change, though by how much is substantially uncertain.

The scale of the deoxygenation problem is truly planetary: the ocean occupies ~70% of the Earth's surface; as anthropogenic warming proceeds, oxygen concentrations will decline—leaving a nearly ubiquitous imprint of human-activity on this vast ecosystem. The potentially profound changes in ocean habit and biogeochemical cycles associated with deoxygenation provide a dramatic illustration of the degree to which humanity is a dominant influence on Earth's ecosystems (Vitousek et al., 1997) and the need for active stewardship to maintain their vitality.

4.7 References

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“Deoxygenation is intrinsically linked to climate warming; reduction of human-driven warming is the only means of preventing widespread ocean oxygen loss.”

Chapter 4 authors

Palaeo-records of histories of deoxygenation and its ecosystem impact

5

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Summary

- Palaeo-records provide important information on relative changes in oxygen content, but quantitative reconstruction is still challenging.
- Substantial ecosystem degradation related to eutrophication and deoxygenation is recognized in fossils from sediment cores worldwide.
- More studies are needed in under-studied regions such as South America and south-eastern Asia, where symptoms of eutrophication and deoxygenation are occurring recently and rapidly. These may provide information to help make management decisions or to curtail deleterious activities.
- Given the general lack of long-term biological monitoring in oxygen minimum zones, further high-resolution sediment records using high sedimentation rate cores in pelagic settings can shed further light on biotic responses to changing oxygen minimum zone distribution or lowered oxygen concentrations in the past, present, and future.

Ocean hypoxia effect	Potential consequences
Palaeo records provide important information on relative (qualitative) changes in oxygen content.	<ul style="list-style-type: none"> • A combination of multiple proxies, influenced by low oxygen concentrations along with other environmental parameters, point to development of oxygen-deficient overlying waters. • This evidence is even more striking when compared with long-term water quality data that indicate an increase in nitrogen, phosphorus and/or organic carbon loads. • Sedimentological proxies include varved sediments formed under permanently anoxic conditions. • Palaeoecological proxies (various microscopic sized fossils known as microfossils) include crustacean Ostracoda, protozoan Foraminifera, and microalgae diatoms and dinoflagellate cysts. Their indicator species, faunal/floral composition, diversity, and abundance are sensitive to deoxygenation and eutrophication. • Geochemical proxies include redox-sensitive trace metals, biomarkers, and stable isotopes, indicating reduced and/or eutrophied conditions.
Low oxygen conditions shift biological properties.	<ul style="list-style-type: none"> • Species richness, organism abundance, and overall biomass decrease substantially in low oxygen environments. • Opportunistic species are often dominant in hypoxia conditions. • Typical community shift associated with deoxygenation is disappearance or decline of sensitive species and increase of resistant species. • These shifts in biological properties (a.k.a. ecosystem degradation) often occur at the time of industrialization and post global conflict (e.g. World War II) economic growth in association with urbanization and development.
Pelagic oxygen minimum zones show substantial variability on multi-decadal, centennial, millennial, and glacial-interglacial timescales.	<ul style="list-style-type: none"> • Oxygen minimum zones tend to be stronger/expanded during warmer periods. • Severe deoxygenation events have occurred in semi-isolated marginal seas, e.g. due to glacial sea-level fall.

5.1 Introduction

Deoxygenation induced by coastal eutrophication, open-ocean expansion of oxygen minimum zones as a result of global warming, and their consequences are some of the most serious problems in the ocean (Breitburg et al., 2018). But, awareness by the public and the scientific community of these problems has increased only recently, although coastal hypoxia has been addressed much more than open-ocean oxygen issues (Diaz & Rosenberg, 2008; Gooday et al., 2009; Levin, 2018; Levin et al., 2009; Vaquer-Sunyer & Duarte, 2008). Instrumental or biological monitoring data in coastal areas and the open ocean are at best only a few decades long and often even shorter. Although notable exceptions exist, e.g. Baltic Sea (Carstensen et al., 2014), they are seldom longer than a century. Only palaeo-records (palaeontological, sedimentological, and geochemical data from sediment cores) allow us

to reconstruct multi-decadal, centennial, millennial, and even longer time-scale histories beyond the period of monitoring. Time resolution can usually be within a few to ten years in coastal settings (embayments, deltas, and estuaries) because of higher sedimentation rates there (it can be 0.5–1 cm per year or more), than in open ocean settings that are usually characterized by much slower sedimentation rates. In most cases, there is uncertainty in age determination due to biological mixing of sediments (bioturbation), physical disturbances (lateral transport, erosion), and time variation in changes across broader geographic regions and depth ranges (Osterman et al., 2009; Platon et al., 2005; Rabalais et al., 2004; Tsujimoto et al., 2008; Turner et al., 2004; Yasuhara et al., 2007). Annual resolution is possible in the case of varved sediments deposited under anoxic conditions without bioturbation because of the inability of benthic infauna to be established. Thus palaeo-records are essential to understanding long-term dynamics of

dissolved oxygen levels and ecosystem impacts. This chapter provides a brief overview of the methods used in sediment cores to reconstruct past oxygen levels, the consequences and impacts of deoxygenation on marine ecosystems, and examples from case studies. These palaeo-data patterns reviewed here will help overcome the shifting baseline syndrome (incremental loss of our knowledge on historical “more natural” environments over generations) (Conley et al., 2009; Knowlton & Jackson, 2008; Pauly, 1995) and lead us to a better understanding of the long-term nature of cumulative human impact as well as natural baselines and long-term natural variation, aiding a better management of marine environments and ecosystems.

5.2 How to reconstruct past oxygen levels and their ecosystem impact

Past oxygen levels can be reconstructed qualitatively by using various and often coupled sedimentary, palaeoecological, and geochemical proxies from sediment cores (Gooday et al., 2009). Varved sediments (Figure 5.1) are indicative of permanent

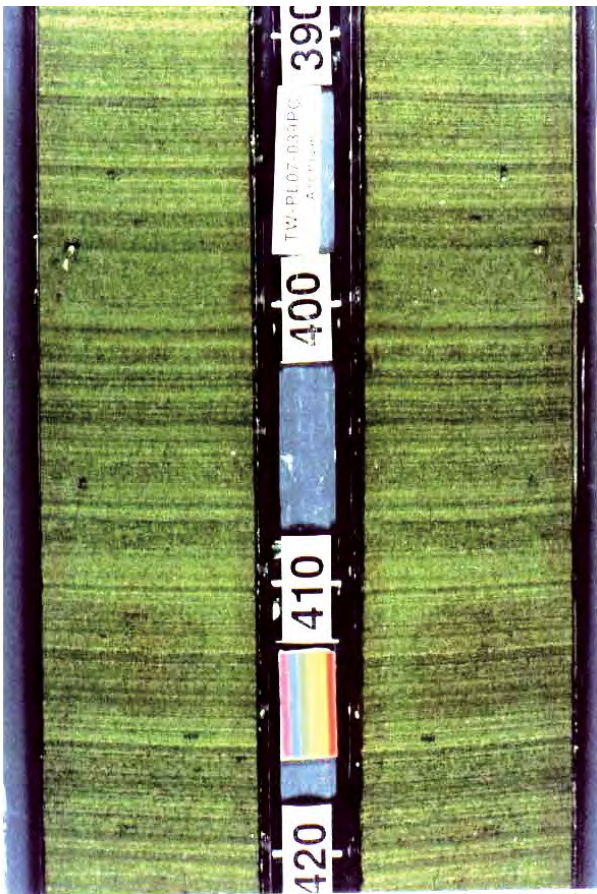


Figure 5.1 Varved sediment from Cariaco Basin on the northern margin of Venezuela. © Konrad Hughen.

anoxic conditions. Sediments from perennial, but seasonal hypoxic conditions, may not show annual layers, because seasonal normoxia allows for infaunal bioturbation. On the other hand, perennial and severe oxygen deficiency even on a seasonal basis may result in a benthic community of short-lived, opportunistic organisms restricted to surface sediments with high organic matter loading (Rabalais et al., 2001). Palaeoecological proxies (typically various microscopic sized fossils known as microfossils, e. g. crustacean Ostracoda, protozoan Foraminifera, and microalgae diatoms and dinoflagellate cysts) are important, because they tell about not only past oxygen levels but also the ecological consequences (e.g. changes in faunal composition, biodiversity and functional types) (Glover et al., 2010; Yasuhara et al., 2012, 2017). Particular species of benthic foraminiferans and ostracods can be used as hypoxia indicators (Figure 5.2). For example, ostracod species *Bicornucythere bisanensis* in north-western Pacific coastal waters and *Loxoconcha* sp. on the eastern coast of the United States are known as coastal eutrophication-hypoxia indicators (Cronin & Vann, 2003; Yasuhara et al., 2007, 2012). The ratio of abundance of *Ammonia* to that of *Elphidium* (both foraminiferan genera) is known as the A–E index and commonly used as a hypoxia proxy (Rabalais et al., 2007; Sen Gupta et al., 1996). Abundance and diversity of ostracods and foraminiferans often reflect past eutrophication and deoxygenation conditions. Organic and inorganic geochemistry, including redox-sensitive trace metals, biomarkers, and stable isotopes, can also be good proxies for past oxygen conditions (Guo et al., 2019; Rabalais et al., 2014). But it remains difficult to distinguish oxygen depletion and nutrient enrichment in some palaeo-proxies, because oxygen depletion is often caused by nutrient enrichment (Jorissen et al., 2007). A combination of multiple indicators, influenced by low oxygen concentrations along with other environmental parameters, points to development of oxygen-deficient overlying waters and its impacts on benthic ecosystems over time. Palaeo-proxies have been applied successfully to reconstruct past history of oxygen variation and its ecosystem impacts in decadal–millennial time scales (Alve, 2000; Deutsch et al., 2014; Gooday, 2003; Gooday et al., 2009; Praetorius et al., 2015; Rabalais et al., 2007; Zillén et al., 2008).

5.3 Gulf of Mexico

As emphasized by Rabalais et al. (2007), a multi-proxy approach is the key for robust and reliable reconstruction

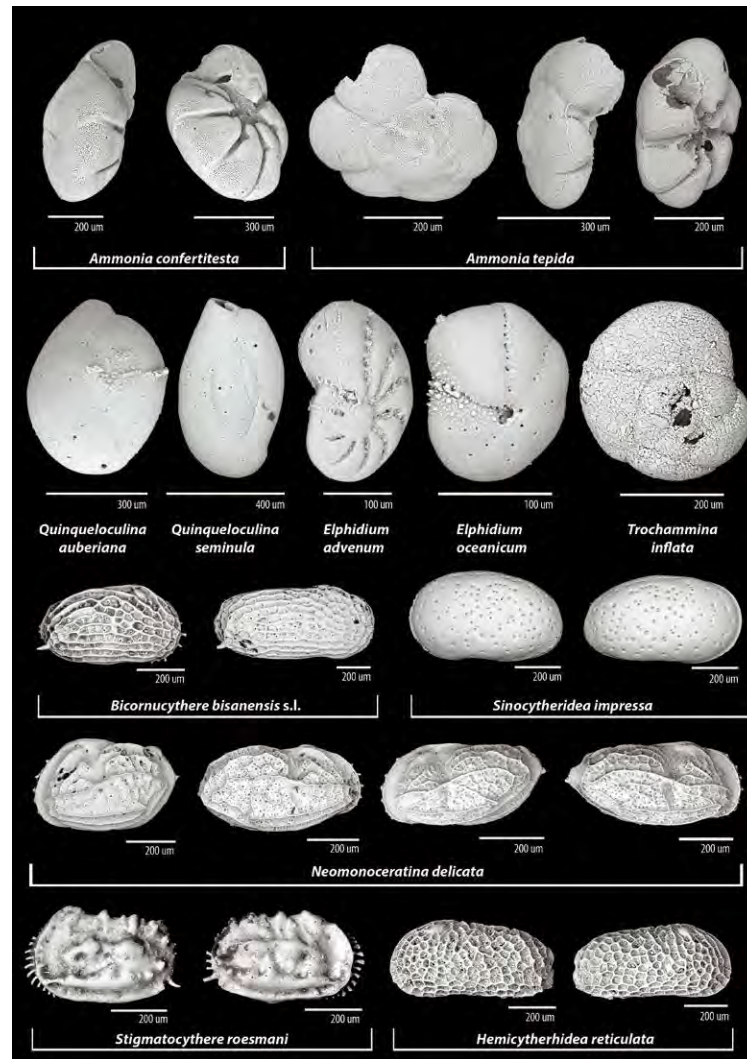


Figure 5.2 Scanning electron microscopy images of selected ostracod and foraminiferan species. All specimens are from Hong Kong. © Briony Mamo and Yuanyuan Hong.

of environmental shifts, including development of low oxygen conditions and the worsening of those conditions over time (Figure 5.3). The processes of human-caused eutrophication driven by excessive nitrogen and phosphorus results in increased production of carbon, in this case phytoplankton, and noxious and harmful algal blooms [see Section 3.2]. The flux of this organic matter to the sea bed drives increased respiration and loss of oxygen in a stratified coastal system, where oxygen re-supply is prevented by strong density gradients. Human activities lead to the increase of various forms of nitrogen and phosphorus that enter the environment with increasingly higher loads. The symptoms of eutrophication in aquatic ecosystems are noxious, and often harmful, algal blooms, and the reduction of dissolved oxygen concentrations, i.e. deoxygenation. This sequence is recorded by palaeo-indicators in

accumulating sediments in the area of the Gulf of Mexico ‘dead zone’ adjacent to the discharge of the Mississippi River. Dinoflagellate cysts are proposed by Price et al. (2018) to be good indicators of ecosystem eutrophication. Four heterotrophic taxa in particular were found to increase in the top section (1986–1997) of a core (Price et al., 2018). With an increase of nitrate-N delivered by the river, the %N, %C, and %S began to increase in the 1940s (Rabalais et al., 2014). The accompanying changes in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ indicated recent eutrophication in the form of increased marine *in situ* carbon formation, incorporation of Mississippi River nitrogen into marine *in situ* production, and increasing marine algal input and sulphide storage, respectively. Biogenic silica from diatom frustules also increased, indicating an increase in surface water phytoplankton production (Turner & Rabalais, 2004).

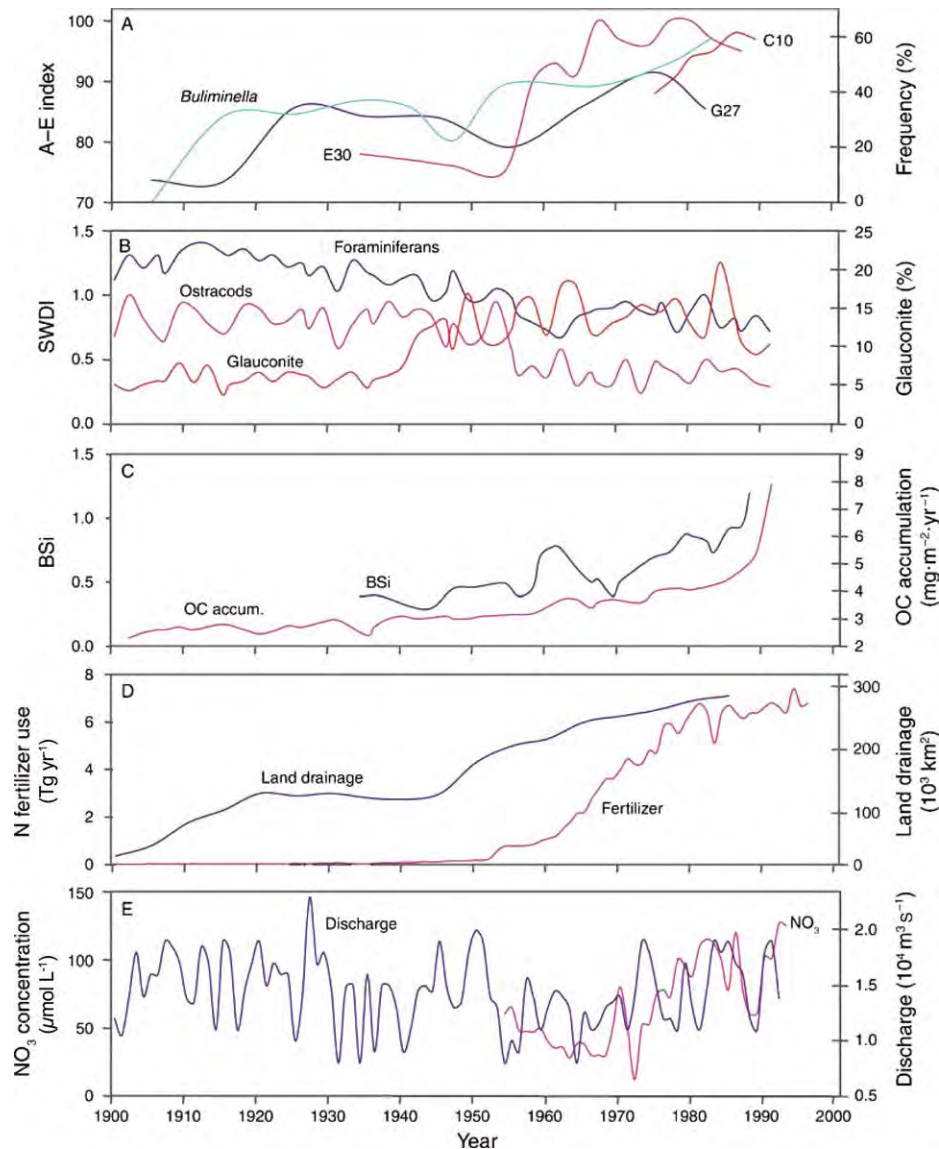


Figure 5.3 An example of multiproxy reconstruction, northern Gulf of Mexico. (A) *Ammonia–Elphidium* (A–E) index for cores C10 (3-yr running average), E30, and G27 and the percentage frequency of *Buliminella* in core G27. (B) Shannon-Wiener diversity index (SWDI) for foraminiferans and ostracods and the percentage of glauconite of coarse grains. (C) Frequency of biologically bound silica (BSi) and organic carbon (OC) accumulation. (D) Nitrogen fertilizer use in the Mississippi River basin and land drainage. (E) Nitrate concentration in the lower Mississippi River and lower Mississippi River discharge. From Rabalais et al. (2007).

A diatom genus, *Pseudo-nitzschia* (Figure 5.4), some forms of which produce the toxin domoic acid, also increased over this time (Parsons et al., 2002). With increased fluxed organic matter some foraminiferans increased (Gooday et al., 2009; Rabalais et al., 2007), but many more decreased or disappeared from the sedimentary record, indicating a worsening of oxygen levels from the 1940s (Osterman, 2003; Osterman et al., 2005, 2008; Platon et al., 2005; Sen Gupta et al., 1996). Ostracod and foraminiferan biodiversity loss paralleled an increase in glauconite (a clay mineral laid down in reducing conditions) and fertilizer use in the northern Gulf of Mexico and reflects a decrease in the

overlying oxygen concentration beginning in the 1950s (Nelsen et al., 1994). Some sensitive foraminiferans (e.g. genus *Quinqueloculina*) disappeared from the benthic community earlier than the accelerating symptoms of eutrophication (Platon et al., 2005). Some have assumed that oxygen deficiency has always been a part of the Louisiana shelf adjacent to the Mississippi River because of fresh water and temperature stratification. However, the shift in many palaeoindicators—biological, chemical, and geological—all point to worsening oxygen conditions, especially since the 1950s, when anthropogenic nutrient loads and carbon accumulation began to increase.



Figure 5.4 The diatom genus, *Pseudo-nitzschia* (not scaled) (courtesy of Oregon State University).

5.4 Combining historical records with palaeo data: Baltic Sea

Hypoxia first occurred in the Baltic Sea after its transition from fresh water to brackish water ca. 8,000 cal. yr BP and has been present intermittently throughout the Holocene (Zillén et al., 2008). Laminated sediments, indicative of hypoxic conditions, can be seen during three intervals of the Holocene sedimentary records: the Holocene Thermal Maximum (HTM), the Medieval Climate Anomaly (MCA), and the modern hypoxic interval. These intervals were also characterized by enhanced sedimentary Mo/AI (Funkey et al., 2014). This proxy tracks the intensity of reducing conditions close to the sediment–water interface, because of the conversion of seawater MoO_4^{2-} to particle-reactive thiomolybdates above a critical activity of hydrogen sulphide (Aleelson et al., 2001). Hence, the records indicate intermittent euxinic (i.e. sulphidic) conditions in the bottom waters of the deep basins during the Holocene. The hypoxic intervals are also characterized by enhanced organic carbon (C_{org}) contents, attributed to both enhanced preservation of organic matter under reducing conditions and enhanced primary productivity. Historical records of dissolved oxygen concentration show that low water-column dissolved oxygen concentrations have been observed since ca. 1900 with a 10-fold increase of hypoxia in the Baltic Sea during the last 100 years (Carstensen et al., 2014), which corresponds well with what is observed in the palaeo data (Zillén et al., 2008). Episodic reoxygenation events, associated with major inflows of oxic waters, encourage the retention of iron oxyhydroxides and iron-bound phosphorus in sediments, increasing vivianite precipitation as a result (Reed et al., 2016). However, dissolution of iron oxyhydroxides when oxygen conditions are low is significantly larger than sequestration by iron. Thus, enhancing vivianite

formation through artificial reoxygenation of deep waters is not a viable engineering solution to eutrophication in the Baltic Sea (Reed et al., 2016). Temperature and salinity changes were key drivers of past hypoxia in the Baltic Sea during the HTM and MCA (Papadomanolakia et al., 2018) and imply that ongoing climate change will delay recovery from the modern, nutrient-driven hypoxia present in the Baltic Sea today.

5.5 Chesapeake Bay

Chesapeake Bay is a region in which extensive research has been conducted to reveal ecosystem history related to human-induced eutrophication and deoxygenation. Data from sediment cores have identified a natural ecosystem, periods of landscape change, and more recent ecological degradation from human activities. Initial signs of ecological degradation were the change in diatom abundance and flora in approximately 1700 due to European settlement and deforestation that resulted in increased river discharge and initial eutrophication (Cooper, 1995; Cronin & Vann, 2003; Yasuhara et al., 2012). Diatom diversity decreased by around 1800 (Cooper, 1995) because of further deforestation (Brush, 2009; Cronin & Vann, 2003; Willard & Cronin, 2007) and perhaps industrialization (Yasuhara et al., 2012). After that, the largest ecological changes occurred at around 1960, probably because of urbanization and substantial increase in population and fertilizer use (Brush, 2009; Cronin & Vann, 2003; Willard & Cronin, 2007). The resulting eutrophication and deoxygenation, that have become much more severe and widespread since approximately 1960, have caused serious ecosystem degradation as represented by the ostracod and foraminiferan faunal and diatom floral changes (Brush, 2009; Cooper, 1995; Cronin & Vann, 2003; Karlsen et al., 2000; Willard & Cronin, 2007). The long core record covering the past 8000 years indicates that Chesapeake Bay deoxygenation is not purely a human-induced phenomenon, and natural deoxygenation existed, though to a much lesser extent, especially in deep channels during the pre-Anthropocene Holocene (Yasuhara et al., 2012).

5.6 Osaka Bay

Osaka Bay is an intensively studied region. Palaeo-ecological data indicated that initial ecological degradation was associated with the Japanese industrialization around 1900 (Tsujiimoto et al., 2008; Yasuhara & Yamazaki, 2005; Yasuhara et al., 2007).

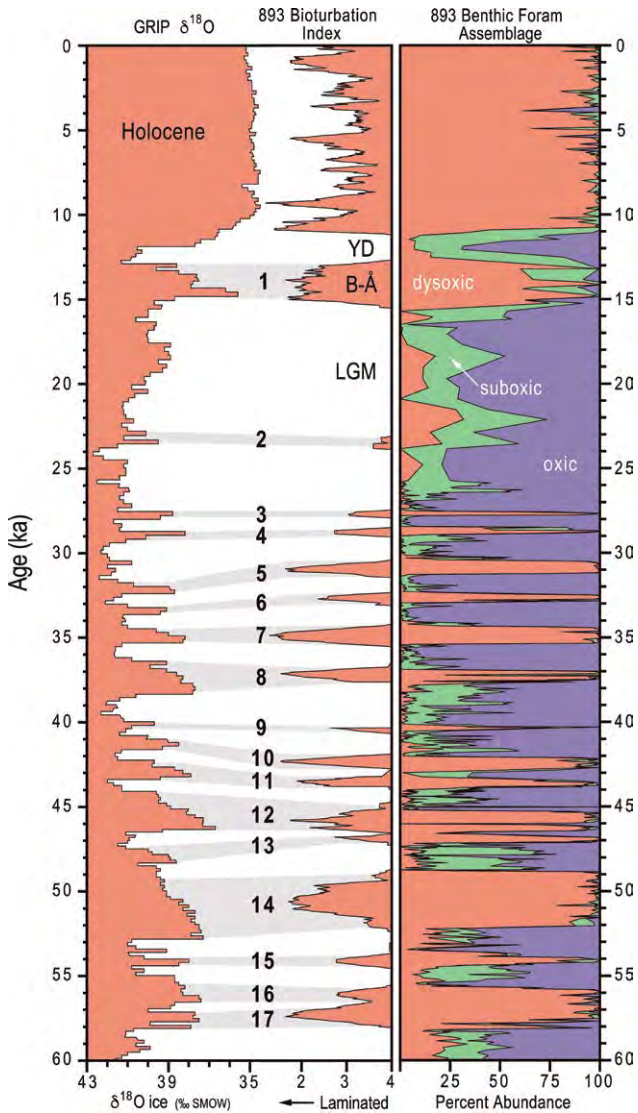


Figure 5.5 Foraminiferan community changes related to climate-induced changes in oxygen minimum zone strength, Santa Barbara Basin, USA. Relative abundance dynamics of benthic foraminiferan community (divided into dysoxic, suboxic, and oxic assemblages) are tightly linked to oxygen minimum zone strength reconstructed by laminated sediment and global abrupt climatic events recorded in a Greenland ice core GRIP. See Cannariato et al. (1999) for more details.

After this time, benthic foraminiferan diversity decreased, and the faunal composition changed (i.e. a decrease in oxygen/eutrophication sensitive species and increase in oxygen/eutrophication tolerant or opportunistic species). Simultaneously, the benthic ostracod fauna changed in a similar way. During the Japanese high economic growth period of the 1950s–1970s, these benthic faunal trends accelerated. These degradation processes of the Osaka Bay ecosystem were caused mainly by urbanization-induced eutrophication and resultant bottom-water deoxygenation since the Japanese industrialization. Since the 1970s, the abundance of the opportunistic benthic foraminiferan species has decreased and the

benthic foraminiferan species diversity has increased in the inner part of the Bay, indicating improving oxygen conditions and diversity recovery. This ecosystem recovery followed regulations that led to a reduction in organic pollution loads. However, the modern benthic foraminifera fauna is still dominated by the opportunistic species and the ostracod fauna remains impoverished (Irizuki et al., 2018; Yasuhara et al., 2012).

5.7 Open ocean systems

Dynamic palaeo-ecological changes related to oxygen content variation is known from open ocean oxygen minimum zones (OMZs) as well (Cannariato et al., 1999; Moffitt et al., 2015). OMZs are oxygen minima ($<0.5 \text{ ml L}^{-1}$ dissolved O_2) maintained at intermediate depths as a result of high biochemical oxygen consumption in the water column and weak ventilation associated with circulation patterns. Several OMZs extend over Eastern Boundary continental margins due to intense biological production and respiration (Levin, 2003; Salvatelli et al., 2016). These areas provide good records of past changes of the intensity and extent of OMZs.

A prime example is the Santa Barbara Basin, a semi-isolated area in the domain of the California Current. The millennial-scale late Quaternary abrupt climatic changes known as Dansgaard-Oeschger cycles have greatly affected the benthic ecosystem through changes in oxygen minimum zone strength (Cannariato et al., 1999; Moffitt et al., 2015). Benthic foraminiferan faunal composition categorized by their oxygen tolerance clearly track millennial-scale abrupt climate changes recorded in a Greenland ice core (Figure 5.5). Similar faunal changes are known as well from fossils other than foraminiferans (such as molluscs, ophiuroids, and ostracods) (Moffitt et al., 2015; Myhre et al., 2017). Seafloor invertebrate communities were subject to major turnover in response to relatively minor changes in oxygenation (>1.5 to $<0.5 \text{ ml L}^{-1}$) associated with abrupt (<100 years) warming (Moffitt et al., 2015).

Over the Peru-Chile margins, a suite of sediment palaeo-proxies including the presence of laminations, redox sensitive metals (U, Mo, Re, Ni and Cu), total organic carbon, nitrogen isotope ($\delta^{15}\text{N}$), and benthic foraminiferan assemblages has been used to reconstruct past changes of the Eastern Tropical South Pacific OMZ in the late Quaternary. Past oxygen levels show pronounced variability on multi-decadal, centennial, millennial, and glacial-interglacial timescales.

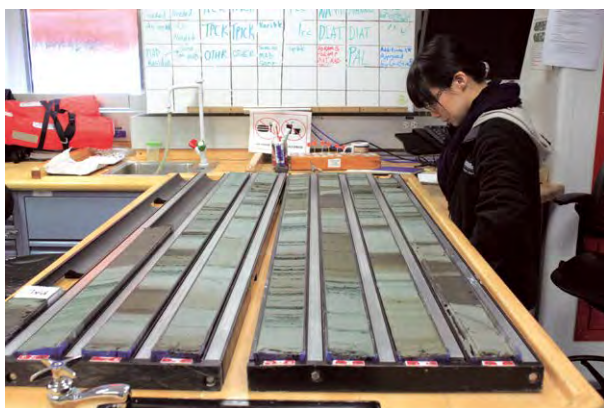


Figure 5.6 A Sea of Japan sediment core showing alternations of dark-coloured (i.e. anoxic condition) and light-coloured (oxygenated) sediment layers. © Ryuji Tada.

In general, over the margins, the OMZ was weaker/contracted during global cold periods such as the Last Glacial Maximum (23–19 kyr BP) and the Little Ice Age (1500–1850 AD). This OMZ weakening/contraction is associated with reduced export production and a weaker upwelling, as influenced by changes in the Walker circulation and the subtropical high-pressure cell. By contrast, it was stronger/expanded during warm intervals such as the last deglaciation (~17–13 kyr BP), part of the Medieval Climate Anomaly (900–1350 AD) and the last 100 years (Chazen et al., 2009; Gutiérrez et al., 2009; Salvattecchi et al., 2014, 2016; Scholz et al., 2014), associated with opposite forcing conditions. A bi-decadal period around the 1870s (associated with strong ENSO activity; Gutiérrez et al., 2011 and references therein) is characterized by diatom-rich sedimentation events from Central Peru to Northern Chile. These events were associated with a strong water column deoxygenation and bottom anoxia as inferred from $\delta^{15}\text{N}$ records in the sedimentary organic matter, enrichment of redox-sensitive metals, and changes of the benthic foraminiferan community towards a higher abundance of anoxia-tolerant species (Castillo et al., 2017; Díaz-Ochoa et al., 2011; Gutiérrez et al., 2009; Salvattecchi et al., 2014). After the mid-20th century, a slight improvement of oxygen level is recognized at lower latitudes, as the benthic foraminiferan assemblage shows higher abundance of species associated with suboxic sediment conditions. Surprisingly, this trend is decoupled from increased coastal upwelling productivity (Gutiérrez et al., 2011), suggesting it is driven by enhanced subsurface ventilation.

The Sea of Japan is a semi-enclosed marginal sea between the Asian–Russian margin of the Eurasian continent and Japanese Islands and isolated from other

oceans (Pacific Ocean, East China Sea, and Okhotsk Sea) by shallow (<130 m depth) straits. This sea is now well-oxygenated, but, during the glacial periods when the sea level was >90 m lower than the present level, this sea and its ecosystem suffered serious deep-water deoxygenation caused by the isolation of the sea and the stratification due to surface freshening (Huang et al., 2018, 2019; Kido et al., 2007; Tada et al., 2015; Watanabe et al., 2007). The variation in oxygen level is clearly recorded as centimetre- to decimetre-scale alterations of dark- and light-coloured sediment layers, indicating deoxygenated and oxygenated conditions, respectively (Tada et al., 1992; Tada, 1994) (Figure 5.6). The palaeo-ecological proxy, microfossil ostracods, clearly showed that this glacial-interglacial oxygen variability has seriously affected the deep-sea ecosystem in the Sea of Japan (Huang et al., 2018, 2019). Glacial-interglacial oxygen variability has caused faunal cyclicity with a succession from opportunistic species dominance through tolerant infauna dominance to barren zone during the deoxygenation processes and the opposite succession during the recovery processes (Huang et al., 2018).

5.8 Global ecosystem degradation and deoxygenation

Biological remains, such as microfossils preserved in sediment cores including protists (foraminiferans), microscopic algae (diatoms, dinoflagellates), and crustaceans (ostracods), allow us to reconstruct the history of marine ecological degradation. Shifts in the ecosystem can be reconstructed by using microfossils as model systems of broader marine communities. Such shifts include the loss of marine organisms (e.g. local extinction), changes in faunal communities, ecosystems (changes in dominant functional group), and biodiversity (diversity decline) related to deoxygenation. Yasuhara et al. (2012, 2017) summarized the microfossil evidence of recent marine ecosystem degradation. The start of the degradation is clearly related to industrialization, ~200 years ago in Europe and USA and ~100 years ago or less in Asia (Rabalais et al., 2010; Yasuhara et al., 2012, 2017) (Figure 5.7). Sediment cores record substantial biodiversity declines over the past 100–200 years, for example, in Chesapeake Bay and Osaka Bay (Cooper, 1995; Cronin & Vann, 2003; Tsujimoto et al., 2008; Yasuhara et al., 2012). The primary cause of this degradation is eutrophication and resulting hypoxia in coastal areas as a consequence of deforestation, population growth, urbanization, agricultural expansion,

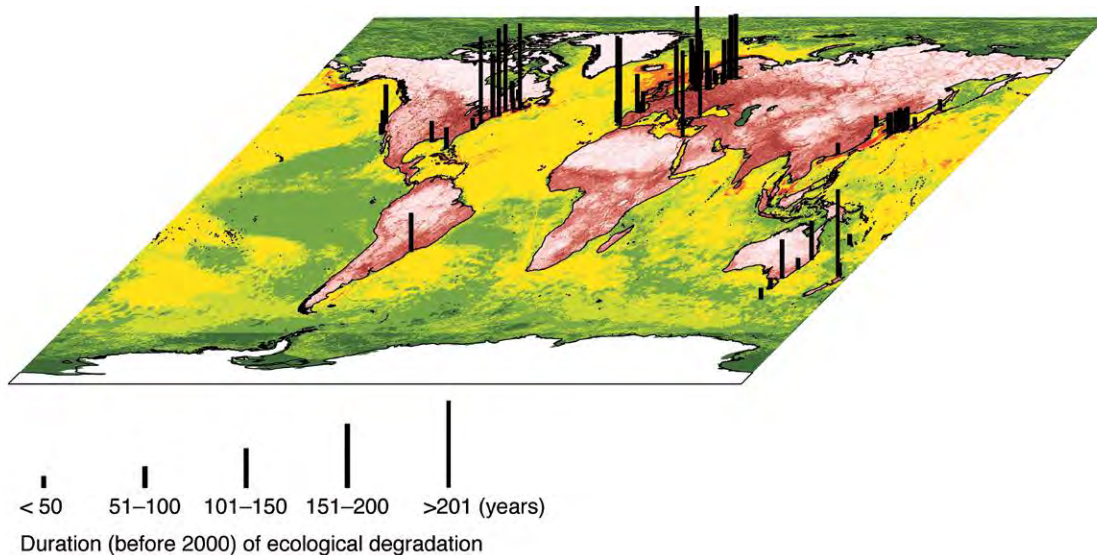


Figure 5.7 Microfossil evidence of human-induced marine ecological degradation, which is mainly related to eutrophication and resulting hypoxia. Shown is the global distribution of human footprint and historical duration of marine ecological degradation (five categories) determined from published down-core micro-palaeontological records (Yasuhara et al., 2012). Darker red colours for land and warmer colours for ocean indicate areas of higher human impact. Note that current human impact is similarly high in Europe and East Asia, but such widespread degradation occurred ~100 years earlier in Europe than in East Asia. From Yasuhara et al. (2017).

and chemical fertilizer use (Yasuhara et al., 2012); however, climate warming might also play a role in increases in hypoxia (Carstensen et al., 2014).

5.9 Societal implications

Encouraging social systems to take responsible actions to reverse eutrophication and deoxygenation is difficult. There are connections between the warming ocean with increased carbon dioxide emissions to the atmosphere from human activities and reduced solubility of dissolved oxygen. Palaeo-indicators from the coastal ocean discussed in this chapter had changed in concert with each other and are related to human-caused ecological change in the last 200 years. The palaeo-indicator correlations are not cause and effect proof, but the similarities are many and consistent and should support a “call to action” by citizens, businesses, agencies, and political bodies to reverse the negative trends. Logical conclusions leading to nutrient mitigation should be the norm rather than the opposite, which is continued and consumptive habits of an accelerating population level. The number of eutrophication-induced hypoxic zones is increasing globally, but several cases of recovery are known, mostly due to reductions in nutrient and organic matter loading. Cautiously optimistic and proactive actions are needed. The key to effective management is raised awareness of the phenomenon of deoxygenation,

as well as its causes, consequences, and remediation measures (Breitburg et al., 2018).

5.10 Conclusions

1. Palaeo records provide important information on relative changes in oxygen content. A combination of multiple indicators, influenced by low oxygen concentrations along with other environmental parameters, points to development of oxygen-deficient overlying waters. This evidence is even more striking when compared with long-term water quality data that indicate an increase in nitrogen or organic carbon loads.
2. Substantial ecosystem degradation, including loss of diversity, decreases in abundance, and changes in faunal composition often with dominance of opportunistic species, parallels palaeo-indicators indicating worsening oxygen concentrations in several coastal ocean settings. Similar faunal shifts in larger infauna (molluscs) also occur with eutrophication and oxygen decline (Kidwell, 2007).
3. Palaeo-indicator research is concentrated in Europe and North America, where most of the worsening oxygen conditions had long occurred (Diaz & Rosenberg, 2008), but symptoms of eutrophication and deoxygenation are occurring

more in under-studied regions such as South America and Southeast Asia, where similar palaeo-indicator studies are warranted. These may provide information for management decisions that would curtail deleterious activities.

- On-going global warming has caused expansion of pelagic oxygen minimum zones with further impacts on the associated marine ecosystems (Breitburg et al., 2018). Given the general lack of long-term biological monitoring in oxygen minimum zones, further fine-scale time resolution palaeo research using high sedimentation rate sediment cores in pelagic settings can shed further light on biotic responses to changing oxygen minimum zone distributions or lowered oxygen concentrations. In turn, the combination of palaeo-records collected offshore and nearshore in the continental margins may give insights on the natural and anthropogenic contributions for recent (de)oxygation trends.

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Multiple stressors – forces that combine to worsen deoxygenation and its effects

6

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Summary

- Human activities have altered not only the oxygen content of the coastal and open ocean, but also a variety of other physical, chemical and biological conditions that can have negative effects on physiological and ecological processes. As a result, marine systems are under intense and increasing pressure from multiple stressors.
- The combined effects of 'stressors' can be greater than, less than, or different from the sum of each stressor alone, and there are large uncertainties surrounding their combined effects.
- Warming, acidification, disease, and fisheries mortality are important common stressors that can have negative effects in combination with low oxygen.
- Warming, deoxygenation, and acidification commonly co-occur because they share common causes. Increasing carbon dioxide (CO₂) emissions simultaneously warm, deoxygenate, and acidify marine systems, and nutrient pollution increases the severity of deoxygenation and acidification.
- A better understanding of the effects of multiple stressors on ocean ecosystems should improve the development of effective strategies to reduce the problem of deoxygenation and aid in identifying adaptive strategies to protect species and processes threatened by oxygen decline.

Ocean hypoxia effect	Potential consequences
Oxygen decline occurs along with other changes to oceans and coastal waters caused by human activities. These changes include co-stressors such as warming, acidification, nutrient pollution and overfishing.	<ul style="list-style-type: none"> • The combined effects of multiple stressors can differ from what would be predicted from simply summing their individual effects and can be difficult to predict. • Management actions may be less effective if co-occurring stressors are not considered.
Oxygen is required by organisms to turn food into energy that can be used to escape from, adapt to, and repair damage caused by other stressors.	<ul style="list-style-type: none"> • When oxygen is insufficient, an organism may not have the necessary energy to withstand other stressors.
Increasing global temperature simultaneously worsens oxygen decline and increases oxygen requirements of organisms that rely on aerobic respiration.	<ul style="list-style-type: none"> • Some species will become more temperature-sensitive at lower oxygen levels and more oxygen sensitive at higher temperatures. • Models predict shifts in global distributions and the sizes of fishes as result of the combined effects of decreased oxygen supply and increased temperatures.
Low oxygen alone and in combination with other stressors can reduce the ability of an animal to fight pathogens and parasites.	<ul style="list-style-type: none"> • Low oxygen can lead to increased intensity and prevalence of a number of diseases of marine animals. • Energy deficiency due to low oxygen can increase morbidity and mortality from diseases.
Avoidance of low oxygen can result in altered spatial distributions.	<ul style="list-style-type: none"> • Mobile species may experience higher fishing mortality if fishers target well-oxygenated areas that serve as a refuge for animals fleeing oxygen-depleted habitat. • Well-oxygenated habitat may not be suitable as a refuge from oxygen-depleted areas because of the presence of other stressors such as high temperatures.

6.1 Introduction

Humans have wide-ranging effects on oceanic and coastal marine ecosystems that are critical to Earth's ecology, economies, and food security (Boyd et al., 2015; Breitburg et al., 2015a; Doney, 2010; Levin & Le Bris, 2015; Prichard & Granek, 2016; Wallace et al., 2014). We remove biomass through fishing; we warm, deoxygenate, and acidify waters through our release of carbon dioxide (CO₂) and other greenhouse gases into the atmosphere; we deoxygenate and acidify coastal systems by releasing nitrogen and phosphorus from agriculture, human waste, and combustion of fossil fuels; and we have increased burdens of pollutants such as trace metals, pesticides, nanomaterials, pharmaceuticals, and microplastics. We refer to these drivers (e.g. fisheries removals) as 'stressors' when they cause undesirable changes to the physical environment, or to individual organisms, food webs or ecosystems (Breitburg et al., 2015a). Only 13% of the world's

ocean can be considered wilderness with only minor anthropogenic impact; much of the remainder and even some areas considered to be wilderness are affected by multiple stressors stemming from human activities (Jones et al., 2018).

The effects of multiple stressors that co-occur, occur sequentially, or affect the same organism or water parcel as it transits among locations, are often not additive. When two or more stressors affect the same organism or ecological process, their combined effects can be greater than (synergistic effects, Folt et al., 1999), less than (antagonistic effects, Folt et al., 1999), or qualitatively different from changes that would be predicted by simply summing up the independent effects of each stressor. For example, the toxicity of mercury pollution depends on the presence of anaerobic conditions that allow methanogens (microbes using anaerobic metabolic pathways) to transform elemental mercury to methyl mercury – the form that accumulates

in individuals and food webs (Gilmour et al., 2013). Heavy rainfall causes landslides where deforestation removes the underground root structure that would otherwise hold soil in place (Glade, 2003). Malnutrition can make humans more susceptible to disease (Rice et al., 2000). The cases of greatest concern are often those in which the combined effects of multiple stressors are substantially greater than or different from their additive effects; in such cases negative effects can be most severe and difficult to predict. Important stressors that have the potential to exacerbate or alter the effects of oxygen loss in marine systems manifest at both local and global scales (Breitburg & Riedel, 2005).

There are two broad categories of stressors – (1) those that combine to worsen the decline in oxygen or to create a multi-stressor environment that includes oxygen decline, and (2) those that alter the effects of low oxygen on organisms and ecological processes. We focus on human-caused stressors because these can be mitigated through management and policy actions to ultimately reduce or reverse oxygen decline, or to reduce its ecological and economic consequences. Considering the potential for other stressors to modulate the severity and effects of deoxygenation is important for the correct identification of causes and effects of deoxygenation in complex marine ecosystems and for the development of sound policy and management strategies.

6.1.1 Suboptimal oxygen supply can limit the ability of organisms to tolerate additional stressors

The ability of an organism to tolerate stress is directly related to its ability to maintain an internally balanced physiological state (i.e. homeostasis) to counteract stressor-induced physiological perturbations (Sokolova et al., 2012, 2013). Increasing severity and duration of environmental stressors leads to elevated costs of the basal maintenance of an organism reflected in an increased basal metabolic rate (BMR) (Figure 6.1). This increase in the BMR reflects elevated energy demands of physiological mechanisms that re-establish cellular and organismal homeostasis, as well as the energy costs of cellular stress protection and damage repair. Cellular homeostasis and stress protection mechanisms are linked to an organism's immediate survival and thus typically prioritized over other energy expenditures.

In order to fuel most cellular processes, external energy (e.g. in the form of food) obtained by an organism must

be converted into adenosine triphosphate (ATP), a universal energy currency of the cell. Since the amount of energy available to an organism and its capacity to assimilate and convert energy into ATP is intrinsically limited, an increase in the BMR reduces the energy available for other fitness-related functions such as growth, reproduction, and defences against pathogens.

Oxygen is required for the production of ATP through aerobic respiration. Oxygen deficiency therefore exacerbates energy deficiency by reducing the capacity of mitochondria to produce ATP (Pamenter, 2014; Sokolova et al., 2011). As a result, the decline in oxygen in the open ocean and coastal waters is expected to increase the trade-off between basal maintenance and other functions. Exposure to low oxygen may also increase energy costs of basal maintenance due to escape behaviours, physiological adjustments to enhance oxygen delivery, or elevated expression of antioxidants that counteract hypoxia-induced oxidative stress (Bavis et al., 2007; Ivanina & Sokolova, 2016; Solaini et al., 2010). The impacts of low oxygen on energy balance may also be intensified by its negative effects on energy intake of an organism through, for example, suppressed feeding activity or food assimilation (Thibodeaux et al., 2009; Yang et al., 2013).

While the impact of each hypoxia-induced physiological and behavioural alteration on overall energy balance may be subtle, their cumulative effects exacerbate the potential mismatch between cellular ATP demand and capacity for ATP production. This can result in an earlier onset of suboptimal or bioenergetically unsustainable conditions in multiple stress exposure scenarios. As a result, declining oxygen in the open ocean and coastal waters can exacerbate the effects of other common stressors in marine and coastal environments acting as an overall 'stress enhancer' and limiting an organism's ability to deal with additional stressors.

Oxygen can be the dominant factor in multiple stressor interactions because low oxygen can limit an organism's ability to deal with additional stressors. Under optimal, well-oxygenated conditions (Figure 6.1), energy uptake and aerobic ATP production are sufficient to cover the energy costs of basal maintenance (maintaining homeostasis, cellular stress protection and damage repair), as well as the energy costs of other fitness-related functions such as growth, reproduction, immunity, locomotion, and storage of an energy buffer in the form of energy reserves (such as glycogen and

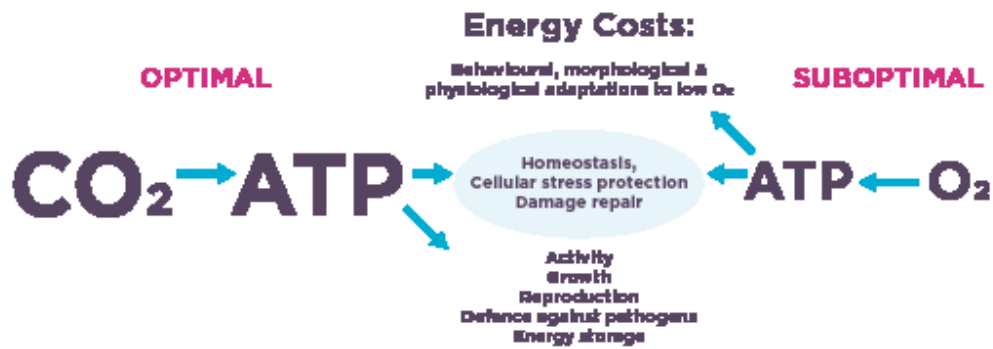


Figure 6.1 Energy-limited stress tolerance.

lipids). Under such conditions, energy is available to repair and reduce damage caused by the variety of natural and human-caused stressors that challenge an organism. As environmental oxygen conditions degrade into the suboptimal range (Figure 6.1), the energy demand for basal metabolism increases to counteract the stress-induced disturbances of homeostasis and cover the costs of stress protection and damage repair. This can result in a trade-off with other fitness-related functions such as growth, immune defence and reproduction. Furthermore energy reserves of the body may be tapped to buffer the increasing energy demand of basal maintenance. As conditions further deviate from optimal, an organism reaches a critical threshold where all available energy and metabolic capacity are used to support immediate survival. Commonly, anaerobic ATP-producing pathways become engaged to cover the elevated costs of basal maintenance. Under these conditions the organism can potentially survive a long time, but no growth or reproduction is possible and thus the population is bioenergetically non-sustainable. Some stress-adapted organisms can suppress their basal metabolic rate during suboptimal conditions; this metabolic strategy extends the survival time under stress but does not increase the energy available for other functions (Hochachka et al., 1996; Sokolova et al., 2011; Storey & Storey, 2004). Extreme stress in the lethal range occurs when the combined aerobic and anaerobic ATP production is insufficient for the basal maintenance; stress protection and damage repair mechanisms are overwhelmed, and cellular damage accumulates culminating in cell death and organ failure, and as a result, the death of the organism.

6.2 The causes of deoxygenation create a multi-stressor environment

Aerobic respiration uses O_2 and releases CO_2 and is the major driver of deoxygenation both in metabolically active coastal waters and in deeper, bathyal waters where respiration decreases the partial pressure of oxygen ($p\text{O}_2$) and elevates the partial pressure of carbon dioxide ($p\text{CO}_2$) over much longer time scales. As a result, dissolved oxygen concentrations, $p\text{CO}_2$ and pH (a measure of acidity influenced by the amount of dissolved CO_2) tend to correlate in many habitats including saltmarshes and eutrophic estuaries (Baumann et al., 2015; Cai et al., 2011; Wallace et al., 2014), oceanic oxygen minimum zones (Paulmier et al., 2011), and kelp forests (Frieder et al., 2012) (Figure 6.2). Drivers that increase respiration – especially warming and nutrient pollution – create a multi-stressor environment by simultaneously worsening oxygen depletion and acidification. In addition, the direct effects of high temperatures and nutrients, as well as the ecosystem processes that they alter, occur alongside low oxygen, leading to a complex combination of potentially stressful environmental conditions to which marine organisms are exposed. In a similar manner, harmful algal blooms, which can be caused or exacerbated by warming, nutrients and oceanographic conditions, not only lead to low oxygen, acidification and sometimes elevated $p\text{CO}_2$ as they die off, but can also release toxins and damage gills of animals in affected areas (e.g. Glibert et al., 2018; Pitcher et al., 2018).



Figure 6.2 Global warming, acidification and deoxygenation are linked. Increasing carbon dioxide in the Earth's atmosphere results in higher ocean temperatures, more acidic conditions, and deoxygenation (Gattuso et al., 2015; Gruber et al., 2012). The warming caused by greenhouse gases, including CO_2 , lowers oxygen solubility in sea water, increases respiration rates of organisms, and reduces mixing that could otherwise increase exchanges between subsurface waters and the oxygen-rich atmosphere. Respiration by microbes, plants, and animals depletes oxygen and produces CO_2 , causing further acidification. Nutrients increase total respiration (the biological demand for oxygen) in water bodies by increasing the total production of organic biomass. There are also important feedbacks not illustrated in this figure. For example, extreme low oxygen and anoxic environments can release phosphorus bound to sediment, fuelling further primary production, and are also the sites of production of potent greenhouse gases. Red = major pathways for nutrient sources and effects; blue = major pathways for warming and CO_2 enrichment; green = other stressors that can increase respiration, for example by altering food webs. (Note that the size of arrows does not indicate the relative importance of these processes.) Earth image: NASA.

6.2.1 Increased greenhouse gas emissions increase the severity of multiple interacting stressors

Increasing greenhouse gas concentrations in the atmosphere warm, deoxygenate, and acidify marine systems (Bopp et al., 2013; Gruber, 2011) (Figure 6.3). Models project a continuation of this trend, with temperature, oxygen, and acidification conditions all becoming more severe with increasing greenhouse gas (GHG) emissions to a degree that depends on future GHG emission rates (Bopp et al., 2013). Global warming reduces the oxygen content of the ocean through three primary mechanisms – by reducing ventilation (i.e. the introduction of oxygen to subsurface waters), by reducing oxygen solubility, and by altering the net balance between oxygen production and consumption (Chapters 3 and 4; Levin, 2018; Oschlies et al., 2018). As surface waters warm, the water column becomes more strongly stratified. In combination with changes in winds and ocean currents, this stratification reduces ventilation – the introduction of oxygen to subsurface waters. The solubility of oxygen in sea water declines

with rising temperature, so that the absolute amount of oxygen (e.g. mg L^{-1} dissolved oxygen) at full saturation is less in warmer water than in cooler water. Furthermore, elevated temperature increases the metabolic rates of marine bacteria and ectothermic (colloquially called cold-blooded) animals that constitute >99% of marine biodiversity and the vast majority of biomass (Pörtner, 2012). This increased respiratory demand can accelerate the rate of oxygen loss at the same time that reduced ventilation and solubility reduce oxygen re-supply.

6.2.2 High nutrients, high productivity and high temperatures combined

Coastal environments – estuaries, semi-enclosed seas and embayments – are among the most productive regions of the ocean (Cloern et al., 2016; Costanza et al., 1997). Temporal variation in ecosystem metabolism of these systems can cause large, co-occurring pH and oxygen fluctuations on diel, seasonal, and interannual timescales (Figure 6.4) (Baumann & Smith, 2018; Odum, 1961; Wootton et al., 2008). In shallow waters,

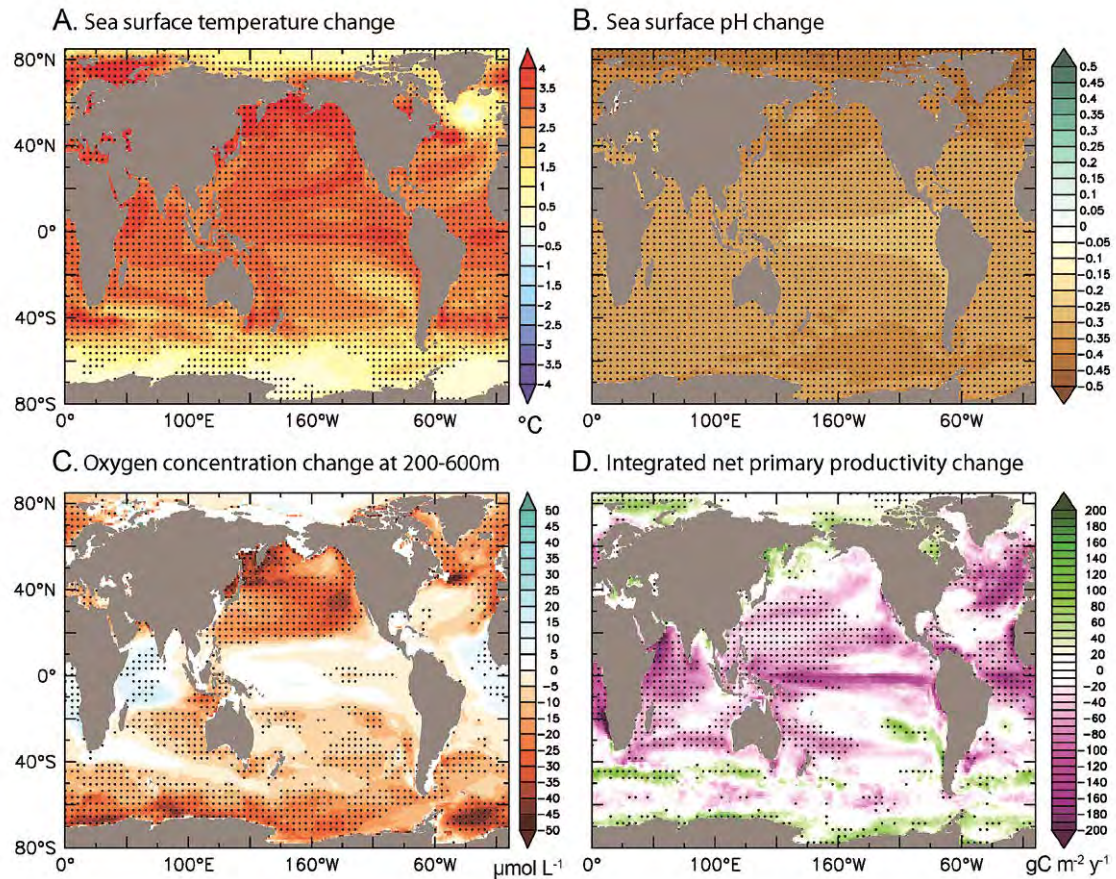


Figure 6.3 Projected changes in A) sea surface temperature, B) pH, C) dissolved oxygen concentration and D) primary production in 2090–2099 relative to 1990–1999 under the RCP8.5 “business-as-usual” model scenario (Bopp et al., 2013). Image reproduced from Bopp et al. (2013).

oxygen consumption and CO_2 production by respiration are countered by photosynthesis by phytoplankton, macroalgae, and submerged aquatic vegetation that fixes CO_2 while raising oxygen and pH levels in the water. The balance between heterotrophic (respiration) and autotrophic (photosynthesis) processes changes naturally between day and night, and between seasons of high and low productivity (e.g. summer vs. winter months), causing large correlated pH and oxygen fluctuations (Baumann et al., 2015; Baumann & Smith, 2018; Breitburg et al., 2015a; O’Boyle et al., 2013).

Human activity significantly alters and intensifies the natural dynamics of these systems. Coastal systems are warming more rapidly than average oceanic rates (Field et al., 2014). For nearshore environments, warming alone can exacerbate acidification and deoxygenation because ecosystem respiration increases more rapidly with temperature than photosynthesis (Baumann & Smith, 2018; Vaquer-Sunyer & Duarte, 2011; Yvon-Durocher et al., 2010).

Nutrient pollution (eutrophication) of coastal habitats causes or intensifies coastal hypoxia and acidification by stimulating phytoplankton production that in turn fuels high microbial respiration (Cai et al., 2011; Gobler & Baumann, 2016). Algal blooms and growth of epiphytes stimulated by nutrients can reduce light penetration, leading to altered benthic production (Cloern, 2001; Kemp et al., 2005). High nutrient loads also lead to changes in algal species composition and the efficiency of energy transfer to upper trophic levels (Cloern, 2001). As a result, hypoxia, acidification, altered benthic production, and other food web changes, as well as increasing temperatures, commonly co-occur.

Unlike many of the stressor combinations discussed above, anthropogenic nutrient loads can sometimes reduce potential negative consequences of hypoxia by enhancing productivity and food supply in coastal ecosystems (Breitburg et al., 2009; De Mutsert et al., 2016). Total fisheries landings can remain high, for example, even if demersal species in oxygen-depleted areas decline, because nutrients can stimulate prey

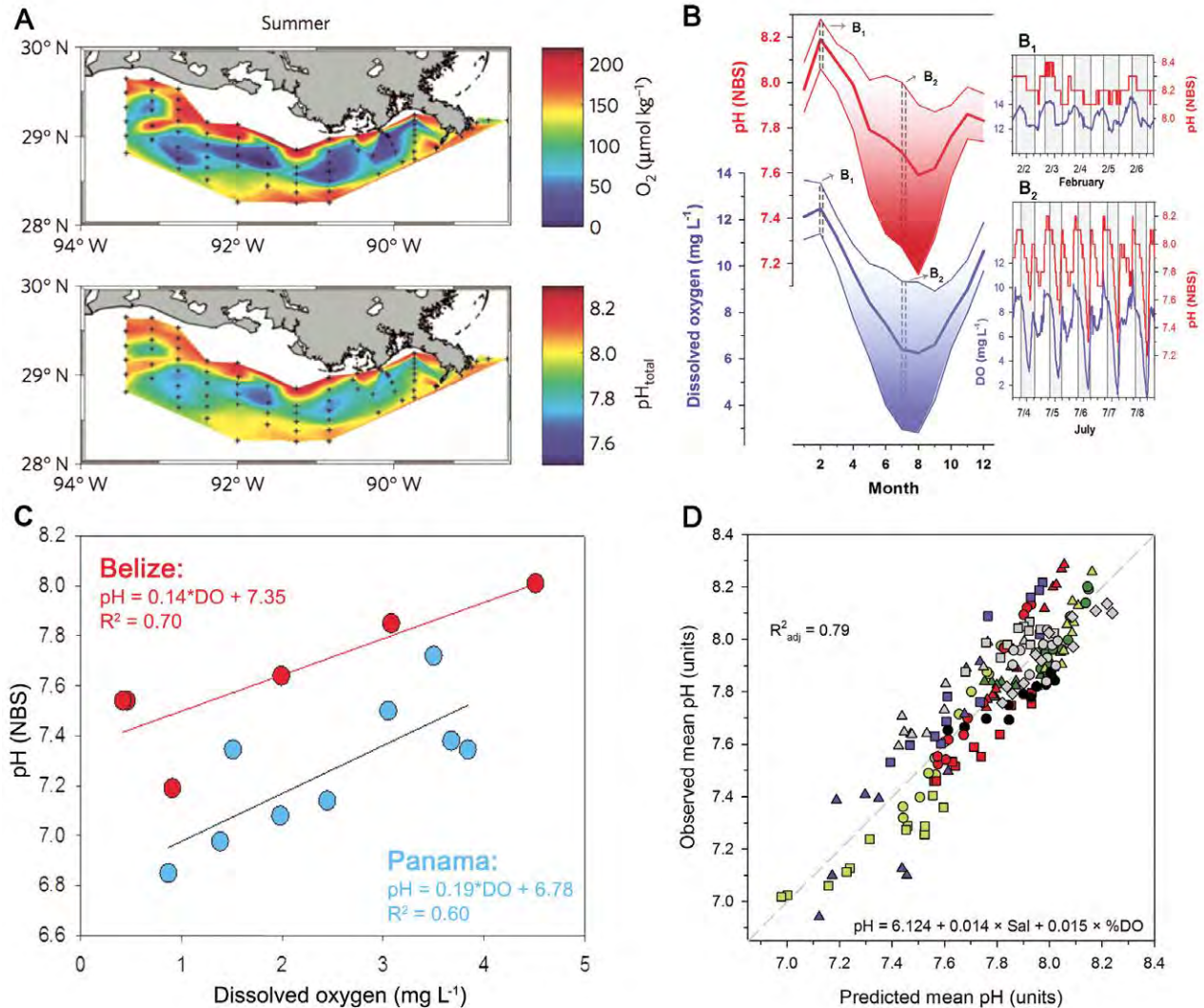


Figure 6.4 In coastal habitats, ecosystem metabolism commonly accounts for large, concurrent pH and oxygen fluctuations on diel and seasonal timescales. (A) Excessive respiration of organic material in the northern Gulf of Mexico consumes oxygen leading to hypoxia in bottom waters, while at the same time increasing CO_2 levels (decreasing pH), causing acidification (modified after Cai et al., 2011). (B) Average pH and oxygen levels decline seasonally in most coastal environments, as productivity and thus net oxygen demand increases during spring/summer months. This seasonal decline is associated with increasing diel fluctuations of pH and oxygen (B_1 , B_2 inserts) (modified after Baumann et al., 2015). (C) The correlation between minimum dissolved oxygen and pH can also be seen in saltwater ‘ponds’ that form within mangrove islands in the tropics, even in areas with minimal anthropogenic nutrient loads (modified from Gedan et al., 2017). (D) The metabolic pH-oxygen coupling is so strong in most coastal environments that average pH levels can be predicted by average oxygen and salinity conditions. Symbols in D depict predicted vs. observed monthly means of pH in 16 nearshore sites across the US Atlantic, Gulf of Mexico, and Pacific coasts (modified after Baumann & Smith 2017).

production in surface waters, shallow benthic habitats, and other well-mixed parts of a system (Breitburg et al., 2009; Nixon & Buckley, 2002). Abundant prey can also improve stress tolerance of organisms in nutrient-enriched habitats (Marigómez et al., 2017). However, system-wide compensation through enhanced productivity due to nutrient input has limits that can be reached as the volume of oxygen depleted habitat expands or critical habitats are affected (Breitburg, 2002).

6.3 Effects of multiple stressors

Synergistic negative effects have been proposed for a large number of stressors that co-occur with low oxygen. For example, the combination of low salinity in surface waters and low oxygen in bottom waters limits suitable habitat for development of cod (*Gadus morhua*) eggs in the deep basins of the Baltic Sea (Hansson et al., 2007). Avoidance of low oxygen can force aggregation of fish and mobile crustaceans in refuge habitats and increase fishing mortality where

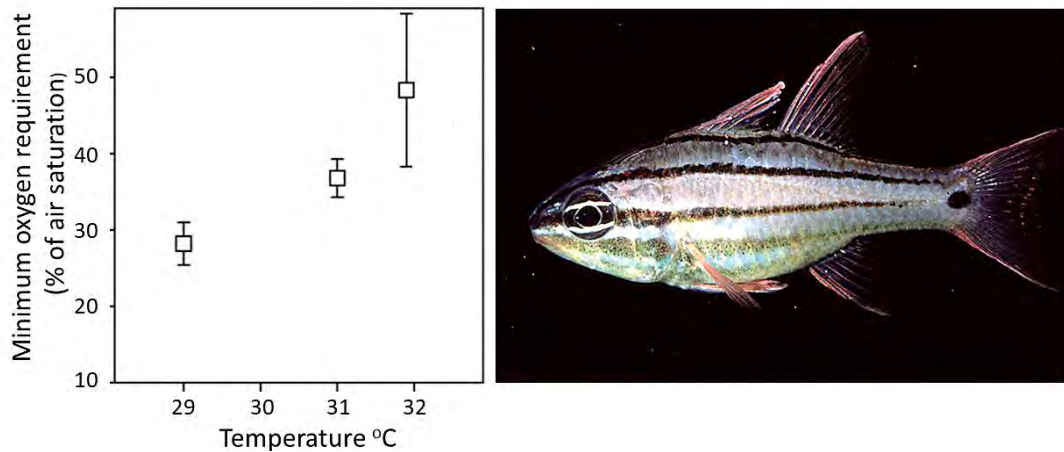


Figure 6.5 Oxygen requirements of fish increase with increasing temperatures. In the case of this coral reef cardinal fish, a 3 °C increase in temperature increased oxygen required to sustain life by 40%. Modified from Nilsson et al. (2010). Photo by JE Randall downloaded from fishbase.org.

these refuge locations are targeted, potentially increasing the likelihood of overfishing (Craig, 2012; Froehlich et al., 2017; Section 9.2). Habitat loss due to hypoxia may also make populations more susceptible to large-scale population declines due to overfishing by reducing resilience (Wainger et al., 2017). Low oxygen can sometimes increase the toxicity of contaminants, and contaminant exposure can increase sensitivity to low oxygen (Delorenzo, 2015). Here we focus on three stressors – temperature, acidification and disease – and consider the effects when they co-occur with low oxygen conditions. Warming, acidification, and disease can all increase energy requirements of organisms, while deoxygenation can limit its supply.

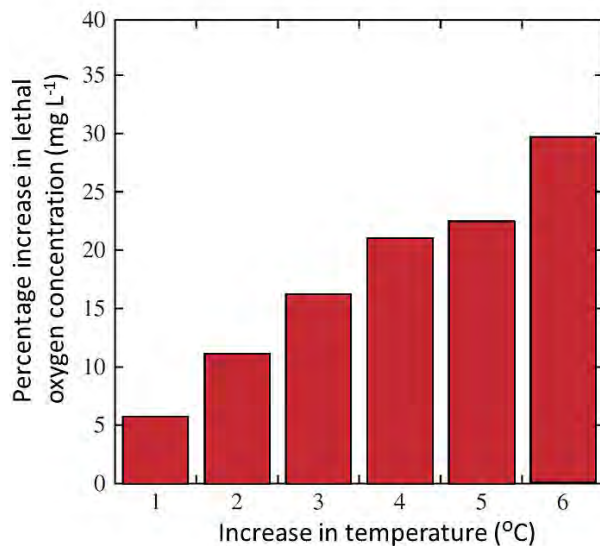


Figure 6.6 Percentage change in oxygen saturation leading to 50% mortality with temperature increases between 1 and 6 °C. Modified from Vaquer-Sunyer & Duarte (2011).

6.3.1 Deoxygenation and increasing temperature

Increasing GHG emissions, elevated anthropogenic nutrient loads (especially pronounced in coastal waters), and low ventilation rates strengthen the vertical structure of marine waters. Suitable habitat becomes limited by high temperatures in upper waters and by lower oxygen and elevated CO₂ in mid or bottom depths. This habitat compression can lead to altered distributions and reduced diversity of taxa most susceptible to these stressors in both the open ocean and in coastal waters (Coutant, 1985; Eby & Crowder, 2002; Stramma et al., 2012). Warming of surface waters can reduce the ability of vertical migrators to repay the oxygen debt (i.e. the additional energy costs of restoring homeostasis after periods of oxygen deficiency) they incur during time spent in oxygen minimum zones (OMZs; Rosa & Seibel, 2008). For species that do not migrate, the combination of warming surface waters and low oxygen in the mid or lower water column can reduce suitable habitat. High surface temperatures during summer combined with low bottom-layer oxygen conditions can limit suitable habitat in estuaries even in the absence of global warming (Coutant, 1985). In contrast to sensitive species, some hypoxia-tolerant species (e.g. some squid and jellyfish) may expand their population size and distribution areas under these conditions (Breitburg et al., 1997; Gilly et al., 2013).

Increased temperature elevates oxygen demand while simultaneously reducing oxygen supply, thus expanding the area of the ocean and coastal waters where oxygen is insufficient. Experiments on individual species often show large increases in oxygen requirements with only



Figure 6.7 European spider crab *Maja squinado* © WaterFrame / Alamy stock photo.

a few degrees centigrade increase in temperature (e.g. Figure 6.5).

An analysis of temperature effects on oxygen thresholds of benthic marine organisms (including demersal fishes), for example, found that a 4 °C increase in temperature decreased survival times for animals exposed to lethal oxygen saturation by 36% and increased the oxygen threshold leading to high mortality by 25% (Figure 6.6; Vaquer-Sunyer & Duarte, 2011). In this analysis, oxygen requirements of sessile species rose faster than those of motile species with increasing temperatures; and oxygen thresholds of crustaceans were more sensitive to temperature than other groups of animals.

In many aquatic ectotherms, thermal tolerance is limited by the capacity to meet oxygen demands of tissues as increasing temperatures lead to a progressive mismatch between the high oxygen demand for routine metabolism and supply of oxygen through gill ventilation and circulation (Pörtner, 2012; Pörtner et al., 2017). This mismatch between oxygen consumption by tissues and the capacity for oxygen delivery has been demonstrated in many fish and invertebrate species, e.g. *Maja squinado* (Figure 6.7) and *Littorina saxatilis* (Figure 6.8) (Bagwe et al., 2015; Frederich & Pörtner, 2000; Jensen et al., 2017; Sokolova & Pörtner, 2003; Sommer & Pörtner, 2004). Through this mechanism, ocean warming caused by elevated GHG emissions is predicted to result in shifts in the distribution of fishes and invertebrates poleward by 10s-100s km per decade, shifts into deeper, cooler waters, and local extinctions (Cheung et al., 2011; Deutsch et al., 2015; Nye et al., 2009). The mismatch is also predicted to reduce maximum sizes of many fish species (including those that support important fisheries), leading to a projected

14–24% reduction in assemblage-averaged body mass globally between 2000 and 2050 under a high GHG emission scenario (Cheung et al., 2013; Pauly & Cheung, 2017). Models project that warming combined with even modest deoxygenation (less than 10 $\mu\text{mol kg}^{-1}$) can cause declines in important fishery species that are sensitive to low oxygen (Stortini et al., 2017). This temperature-induced mismatch between oxygen supply and metabolic oxygen demand affects organisms at all depths including well-oxygenated surface waters but might be more pronounced at depths where the most severe deoxygenation is seen.

Some animals can, nevertheless, maintain oxygen uptake as temperatures rise by increasing heart and gill ventilation rates, or by other mechanisms (Brijs et al., 2015; Gräns et al., 2014; Verberk et al., 2016). For example, landlocked arctic char (*Salvelinus alpinus*) and Atlantic salmon (*Salmo salar*) tolerated lower oxygen saturation, and longer exposure to 13% oxygen saturation, respectively, when acclimated to 14.9 °C than when acclimated to 7.7 °C (Anttila et al., 2015). Acclimation to the higher temperature led to changes in cardiac tissue (in both studied species), capillary density within gill lamellae (in char), and lengthening of gill lamellae (in salmon) in response to hypoxia. Similarly, acclimation to elevated temperature led to increased gill lamellar surface area in mummichogs (*Fundulus heteroclitus*) (McBryan et al., 2016). All of these physiological and morphological adjustments can increase oxygen supply and delivery. This emphasizes an important role of oxygen delivery mechanisms for successful acclimation to warming and indicates that physiological plasticity of these mechanisms may provide cross-tolerance to warming and low oxygen (McBryan et al., 2016). In contrast to observed long-term temperature



Figure 6.8 Rough periwinkle *Littorina saxatilis* © Buiten-Beeld / Alamy stock photo.

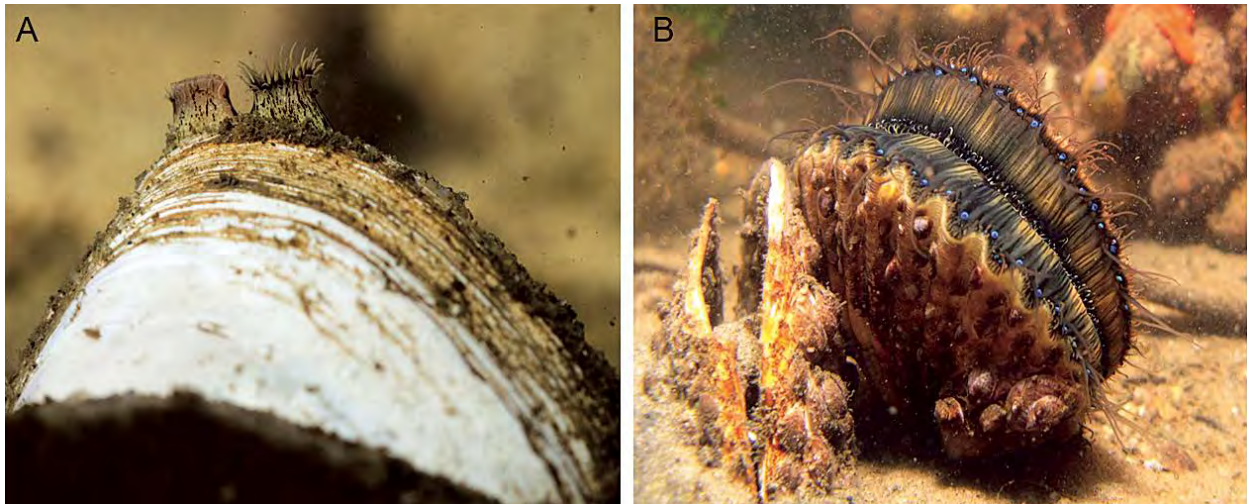


Figure 6.9 Effects of co-occurring hypoxia and acidification differ between (A) the northern quahog *Mercenaria mercenaria* and (B) bay scallop *Agropecten irradians* (Images by Christopher Paparo; provided by C. Gobler).

acclimation, acute high temperature exposure reduced hypoxia tolerance in mummichogs. McBryan et al. (2016) suggested that the magnitude of the effect indicated that the reduced hypoxia tolerance was caused by the negative effect of temperature on oxygen affinity of haemoglobin. Decreased haemoglobin affinity for oxygen with increasing temperatures has also been found for other fish species (Weber & Jensen, 1988).

Fluctuating environmental conditions sometimes modulate the combined effects of elevated temperature and low oxygen. Elevated temperature increased growth of newly settled Olympia oysters (*Ostrea lurida*) and partially offset the negative effect of diel cycling hypoxia (daily minima to 2.0 or 0.6 mg L⁻¹) on growth (Cheng et al., 2015). The authors suggested that the combination of metabolic suppression during low oxygen, and temperature-accelerated feeding during high-oxygen periods, protected oysters from the more severe effects of low oxygen that would occur under constant low oxygen conditions and resulted in an additive rather than synergistic negative interaction between the stressors. Overall, the interactive effects of fluctuating oxygen and temperature conditions may be quantitatively and qualitatively different from those of chronic, stable conditions (Dowd et al., 2015; Kingsolver & Buckley, 2017; Kingsolver et al., 2016), and future experiments should be designed to more closely mimic environmentally realistic fluctuations.

6.3.2 Deoxygenation and acidification

The combined effects of hypoxia and acidification are important to understand because of their widespread

co-occurrence, and because of increasing evidence of the ecological threat of acidification (Williamson et al., 2017). The effects of hypoxia on marine organisms have been empirically studied for decades (Breitburg et al., 2009; Diaz & Rosenberg, 1995). In isolation, hypoxia may pose a more severe threat to most marine species than acidification (Gobler & Baumann, 2016). However, the combined effects of these stressors on organisms are not well studied and thus insufficiently understood; recent studies have found that the combined effects of hypoxia and acidification can sometimes be more severe than effects of either stressor alone (Gobler & Baumann, 2016).

In general, co-occurring hypoxia and acidification can have additive, antagonistic, or synergistic effects (Gobler & Baumann, 2016). A review of the still limited empirical evidence suggested that the majority of hypoxia × acidification effects across various traits (e.g. growth, survival, calcification rate), life stages, and taxa are additive (Gobler & Baumann, 2016). However, the same review also observed that every published study to date reported at least one instance of interactive effects on a specific trait, life stage or species. Synergistic negative effects of acidification and hypoxia, which were more common than antagonistic effects, comprise the most worrisome outcome, in part because they indicate that many species may be more sensitive to low oxygen conditions in the environment than experiments conducted at high pH conditions would suggest.

Studies of molluscs such as abalone (*Haliotis rufescens*), Baltic clam (*Macoma balthica*), and northern quahog (*Mercenaria mercenaria*) (Figure 6.9A), have found



Figure 6.10 Atlantic silversides *Menidia menidia* © Jacob Snyder.

evidence for synergistic negative effects of hypoxia \times acidification on growth, but mostly additive effects for survival (Gobler et al., 2014; Jansson et al., 2015; Kim et al., 2013). In contrast, in larval bay scallops (*Argopecten irradians*) (Figure 6.9B), low dissolved oxygen conditions reduced growth but not survival, whereas low pH conditions reduced survival but not growth (Gobler et al., 2014). This suggests that potential effect interactions may be highly species-specific. In addition, sensitivity to acidification and hypoxia, alone and in combination, is likely to differ between life stages. In early northern quahog juveniles (2 months), for example, low oxygen alone reduced survival but not growth, low pH conditions reduced growth but not survival, whereas the combined low oxygen-low pH treatment elicited additive reductions in both traits. In older quahog juveniles (4 months), on the other hand, survival and growth were unaffected by acidified and low oxygen conditions individually, but their combined effect on growth was synergistically negative (Gobler et al., 2014).

For fish, the current evidence of combined hypoxia \times acidification effects is even scarcer than for molluscs. It is not clear whether this reflects the need for additional experimental work or a tolerance to acidification. As highly mobile vertebrates, fish tend to be very sensitive to reduced oxygen conditions. In contrast, acidification tested at levels that currently occur or are projected by

the end of the 21st century in marine systems primarily affect early life stages and behaviours (Baumann et al., 2012; Cattano et al., 2018; Esbaugh, 2017; Ishimatsu et al., 2008). However, experiments indicate that acidification can increase the sensitivity of adult Atlantic (Figure 6.10) and inland silversides (*Menidia menidia*, *M. beryllina*, respectively) to hypoxia - a significant synergistic effect (Miller et al., 2016). High $p\text{CO}_2$ levels (such as found in shallow estuarine waters with extreme tidal or diel-cycling conditions) inhibited the ventilatory response used by fish to acquire sufficient oxygen under low-oxygen conditions and reduced survival at higher oxygen concentrations. Under experimental low oxygen conditions, Atlantic silversides tired sooner and reached the point in which they were unable to swim against a current when $p\text{CO}_2$ was simultaneously increased (T. Targett, et al., unpublished data). Another recent study found additive negative effects on early larval survival and growth in inland silversides, but synergistically negative survival effects of low oxygen and low pH in larval Atlantic silversides (Depasquale et al., 2015).

Together, the limited empirical evidence and the likely species- and stage-specific responses to combined low oxygen and acidification preclude generalizations and do not yet afford predictions as to the occurrence of dissolved oxygen – pH interactions or their importance to marine systems. Existing bioenergetic frameworks (Pörtner, 2012; Sokolova, 2013) provide useful starting







points, because they focus on aerobic scope as the vulnerable fundamental trait (i.e. a proxy for the *surplus* energy available for growth, reproduction, predator avoidance etc.; Figure 6.11).

6.3.3 Deoxygenation and disease

Exposure to low oxygen can increase susceptibility of marine animals to disease by reducing immune responses of hosts, by increasing transmission, and by increasing the virulence of pathogens. The potential for low oxygen exposure to increase the prevalence and consequences of infections has been found for a wide range of pathogens and parasites, including viruses,

bacteria, protists, and helminths, and for host taxa ranging from molluscs to crustaceans to fish, including species that support important fisheries (Table 6.1). Correlations between disease prevalence and intensity and low oxygen conditions in the field suggest the potential for hypoxia to exacerbate disease in marine systems (Breitbart et al., 2015b). Because dissolved oxygen varies spatially, it can also influence the landscape-level pattern of the prevalence and intensity of infections in host species (Breitbart et al., 2015b) both because of increased susceptibilities to disease, and because low-oxygen areas can serve as a source of infections for better oxygenated areas (Keppel et al., 2016).

Table 6.1. Examples of effects of low oxygen exposure on diseases of marine organisms.

Host taxa	Host species	Pathogen taxa	Pathogen/disease	Additional stressor	Effect	Proposed or tested mechanism	Citation
Bivalve	eastern oyster (<i>Crassostrea virginica</i>) 	Dinoflagellate bacteria	<i>Perkinsus marinus</i> (dermo) <i>Vibrio campbelli</i>	None Elevated CO ₂	Increased acquisition and progression of infections Increased culturable bacteria in oyster tissues	Reduced ROS production; increase in granular haemocytes may provide entry point for infections Decrease in bacteriosis	Keppel et al., 2016 Breitbart et al., 2015b Macey et al., 2008
Decapod	Pacific white shrimp (<i>Litopenaeus vannamei</i>) 	virus	White spot syndrome virus	none	Increased mortality	Reduced ROS production	Lehmann et al., 2016
Fish	Atlantic salmon (<i>Salmo salar</i>) 	protist	Amoebic gill disease	none	Increased mortality	No firm conclusion	Fisk et al., 2002
Fish	European eel (<i>Anguilla anguilla</i>) 	helminth	<i>Anguilla crassus</i>	none	Increased stress (higher plasma cortisol)	Increased corticosteroid stress response and higher metabolic cost	Gollock et al., 2005
Decapod	Norway lobster (<i>Nephrops norvegicus</i>) 	bacteria	<i>Vibrio parahemolyticus</i>	Elevated CO ₂	Increased culturable bacteria in hepato-pancreas	Reduced bacteriostatic response and total haemocyte count	Hernroth et al., 2015
Fish	mummichog (<i>Fundulus heteroclitus</i>) 	bacteria	<i>Vibrio parahemolyticus</i>	Elevated CO ₂	(see mechanism)	Reduced ROS production and bactericidal activity	Boleza et al., 2001

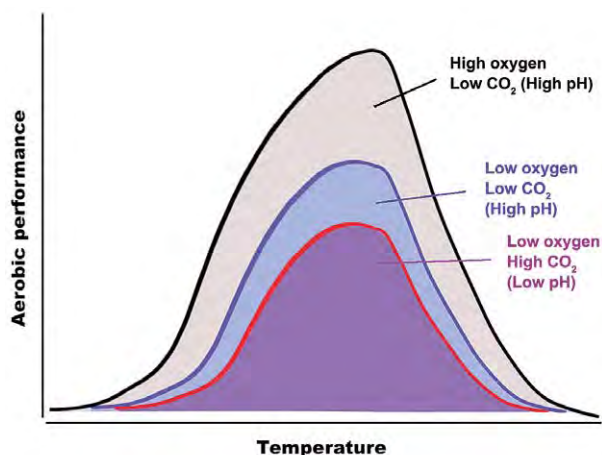


Figure 6.11 Hypothesized aerobic thermal performance curves under different O_2 and CO_2 conditions. For a given temperature, the performance curve narrows if the organism experiences hypoxic, hypercapnic (excessive CO_2) or both conditions. (Redrawn after Dam & Baumann, 2017).

Experimental evidence has shown that exposure to low oxygen can increase disease by altering immune responses that rely on phagocytosis and the production of compounds that kill or disable pathogens (Mydlarz et al., 2006). For example, the bacteriostatic response of Norway lobsters (*Nephrops norvegicus*) (Figure 6.12) to *Vibrio parahaemolyticus* was reduced by 2 weeks exposure to 23% oxygen saturation, resulting in higher pathogen loads in hypoxia-exposed infected animals (Henroth et al., 2015). Hypoxia suppresses phagocytotic activity in fish (e.g. the mummichog, *Fundulus heteroclitus*), and in combination with low pH, reduces natural defence mechanisms such as the production of reactive oxygen species (ROS) (Boleza et al., 2001). Boyd and Burnett (1999) and Keppel et al., (2015) found effects of hypoxia on ROS production by eastern oyster (*Crassostrea virginica*) haemocytes, but the direction of effects differed in these two studies, perhaps due to differences in experimental methods. Nevertheless, laboratory exposures to both diel-cycling



Figure 6.12 Norway lobster *Nephrops norvegicus* © Bernard Picton.

and constant low oxygen increased the prevalence, and sometimes, the intensity of infections of the eastern oyster by *Perkinsus marinus*, the causative agent of dermo disease. *P. marinus* has led to high mortality of oyster populations and limited the success of oyster restoration efforts (Breitburg et al., 2015b; Keppel et al., 2015).

Exposure to low oxygen that is tolerated by uninfected animals can result in high mortality of infected individuals. White shrimp (*Litopenaeus stylirostris*) infected with white spot syndrome virus suffered higher mortality when exposed to 30% or 60% oxygen saturation for 96 h than did uninfected shrimp (Lehmann et al., 2016). At 30% saturation, all infected shrimp died, as compared to about a quarter of infected shrimp maintained at 100% oxygen saturation. Eastern oysters with 100% prevalence of *P. marinus* infections suffered approximately 25% greater mortality when exposed to 3 mg L^{-1} dissolved oxygen for 6 weeks than did infected animals held at high oxygen conditions (Anderson et al., 1998). Similar-length exposures to 2.2 mg L^{-1} dissolved oxygen did not increase mortality of uninfected juvenile oysters (Keppel et al., 2016).

Distribution shifts in response to unsuitable oxygen conditions can result in crowding of mobile species (Craig, 2012). Much of the evidence of increased disease transmission due to crowding comes from studies of freshwater fishes (e.g. Ficke et al., 2007); however, this process is likely important in estuaries and other water bodies as well. Crowding can be exacerbated by the combination of high temperatures in surface waters and greater hypoxia in bottom waters, which can confine fish to narrower bands of tolerable habitat (Coutant, 1985).

Hypoxia may also sometimes increase pathogen virulence (Phippen & Oliver, 2017), although we know of only one documented example. The estuarine pathogen, *Vibrio vulnificus*, is concentrated by suspension feeding bivalves. Phippen and Oliver (2017) found that exposure to hypoxia increased expression of all three virulence-related *V. vulnificus* genes tested. This one example is particularly notable because of the potential for direct effects on human health. It is probably important to consider that the gastrointestinal tract of humans is a low oxygen environment, and that human gut microbes that can survive in brackish and marine waters might thrive in hypoxic areas where they could be concentrated by edible bivalves.

6.4 Multi-stressor considerations in three sensitive systems:

6.4.1 Coastal waters

Because of close proximity to land and to large human populations, coastal systems (such as estuaries, lagoons, and semi-enclosed seas) are strongly influenced by the human activities within their watersheds, airsheds, and waters, as well as by increased global GHG emissions (Figure 6.13). Over 500 coastal systems around the world are impacted by nutrient-related hypoxia ($<2 \text{ mg O}_2 \text{ L}^{-1}$) (Breitburg et al., 2018; Diaz & Rosenberg, 2008). The human footprint on these systems is not limited to nutrient discharges, and estuaries and other coastal waters are subject to intense multiple pressures (Mitchell et al., 2015). Both sewage-related low oxygen problems, pollution and overfishing have been reported in estuaries since at least the 19th century (Franz, 1982; Tinsley, 1992).



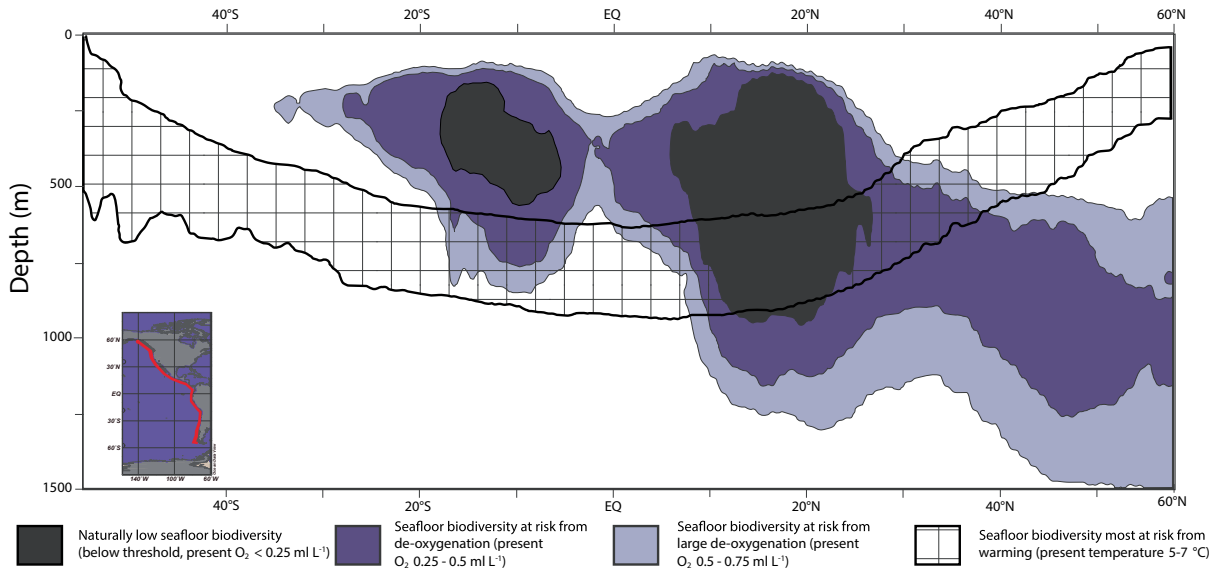
Figure 6.13 Chesapeake Bay is especially sensitive to land-based activities because of its very large watershed. © NASA.



Figure 6.14 Animals inhabiting oxygen minimum zones have evolved to reduce oxygen requirements and increase oxygen uptake – sometimes through elaborate gills as in the terebellid worm. © Greg Rouse, Scripps Institution of Oceanography.

An important characteristic of shallow coastal systems is their high temporal variability in physical and biological characteristics and processes on scales ranging from hours to years or decades (Figure 6.4). In estuaries, spatial gradients and discontinuities in salinity overlay this temporal variability. It is not surprising, therefore, that species that thrive in estuaries and similar water bodies have wide tolerances to a number of physical characteristics of the environment. That does not mean, however, that they are unaffected by multiple stressors that are common in coastal water bodies. For example, a typical estuarine species such as the eastern oyster can experience reduced growth rates, reduced reproduction and increased disease when exposed to diel-cycling hypoxia (e.g. Breitburg et al., 2015b). Nevertheless, oysters thrive in subtidal moderate-salinity waters because their tolerance to reduced salinity is sufficient for survival, and their echinoderm predators are excluded by reduced salinities in estuaries.

A. Eastern Pacific Ocean



B. Arabian Sea

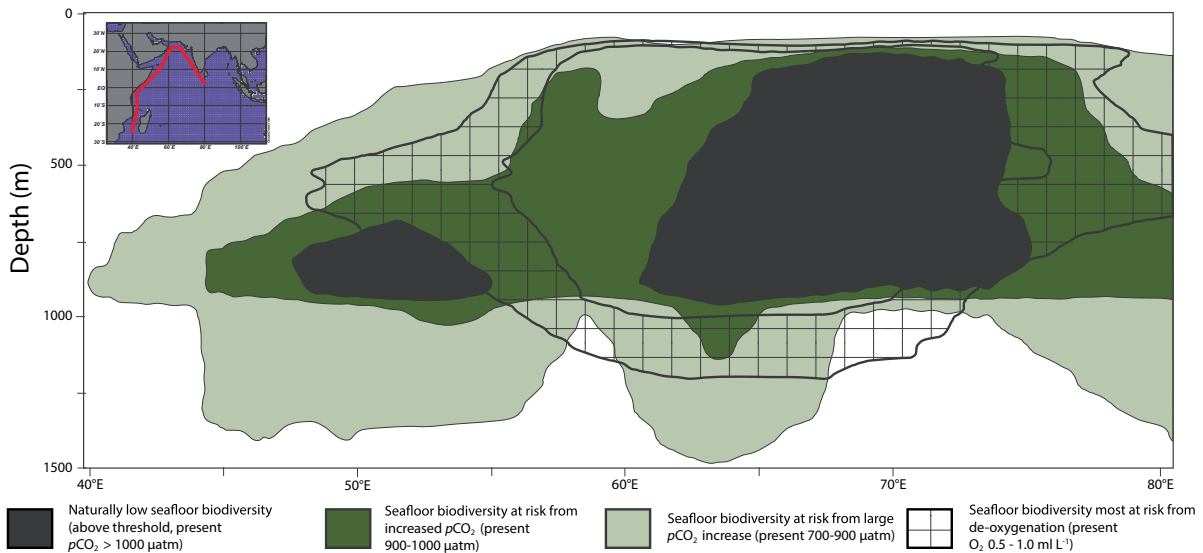


Figure 6.15 Ocean seafloor depths along (A) the eastern Pacific and (B) Arabian Sea (red transect line in inset figures) that are most likely to experience macrofaunal biodiversity loss due to further deoxygenation and increasing temperature. Locations where shading and cross-hatching overlap indicate areas of sea floor where multi-stressor effects of low oxygen and temperature could be strongest. Reproduced from Sperling et al. (2016).

6.4.2 Oxygen minimum zones

Oxygen minimum zones are naturally occurring low-oxygen areas that cover vast regions of the ocean at midwater depths (200 to 1,000 m). OMZs impinge on more than a million km² of sea floor (Helly & Levin, 2004), and are most prominent below the more productive regions of the world's surface ocean, where organic matter sinks and is degraded by microbial activity. As in shallow coastal waters, microbial degradation of organic matter in the open ocean consumes oxygen while producing CO₂, so that OMZs are regions where

acidification co-occurs with low oxygen (Paulmier et al., 2011). Conditions within OMZs can be established over millions of years (Jacobs et al., 2004), but can be dynamic on glacial/interglacial (10,000 years) as well as much shorter time scales (Moffitt et al., 2015a, b).

The deep sea is not isolated from anthropogenic climate change (Mora et al., 2013). Surface waters hold less oxygen at full saturation because of increased sea-surface temperatures. As these waters travel to depth, they contain less oxygen than they otherwise would (Keeling et al., 2010). In addition, acidification at depth



Figure 6.16 Massive 'walk-out' of rock lobsters in Eland Bay, South Africa. Rock lobsters attempting to escape low oxygen and high levels of hydrogen sulphide crawl out of the ocean and become stranded on the shore. © G. Pitcher.

can be enhanced by anthropogenic CO_2 (Keeling et al., 2010). The amount of anthropogenic CO_2 in deep waters is dependent on the age of that water (i.e. the time elapsed since water was last at the sea surface) because anthropogenic CO_2 enters the ocean at the surface. As a result, for example, waters that are decades old that upwell along the U.S. West Coast contain anthropogenic CO_2 at levels reflecting atmospheric concentrations that were already elevated by the mid 20th century (Feely et al., 2008).

The upper and lower boundaries of OMZs are characterized by strong zonation in community structure, with rapid shifts in biological diversity that are responding to hydrographic changes, often in a threshold-like manner (Gooday et al., 2010; Levin, 2003). The combination of upward-expanding midwater deoxygenation with the warming and acidification of surface water reduces the vertical extent of suitable habitat for sensitive species (Gilly et al., 2013). Oxygen exerts tremendous control on marine biodiversity (Figure 6.14) through effects on evolution, physiology, reproduction, behaviour, and species interactions (Gooday et al., 2010; Stramma et al., 2010, 2012). Temperature, acidification, and food availability can act individually and in combination with low oxygen to further alter biological diversity patterns (Sperling et al., 2016; Figure 6.15).

Regional differences among OMZs reflect differences in hydrography and lead to differing combinations and intensities of multi-stressor effects. Deep-sea mining is an additional stressor proposed within some of the

ocean's low-oxygen regions. For example, phosphorites (phosphorus-containing solid particles) are targets for mining for use as an industrial fertilizer and are found along continental margins with low oxygen. Mining removes seabed sediments, including the organisms living on and in the sediment. Some nations – New Zealand and Mexico – have rejected marine phosphate mining proposals because of the associated environmental risks. Other nations, like Namibia, are still considering such projects. The combined effects of expanding low oxygen in the ocean and mining are unknown.

6.4.3 Upwelling margins and open coastline

Along coastal upwelling margins, cold and nutrient-rich waters are brought to the surface through the action of wind-driven currents that move surface water away from the coast to be replaced by deeper waters. Coastal upwelling supports some of the most productive fisheries in the world (Jennings et al., 2009). Upwelled water masses are, however, low in oxygen content and enriched with CO_2 (that leads to low pH) due to decomposition of organic matter originating in surface waters. In some upwelling regions, such as the coasts of Peru and Namibia, extreme oxygen depletion leads to production of toxic hydrogen sulphide plumes, which can erupt and affect thousands of km^2 of the ocean surface (Ohde & Dadou, 2018; Schunck et al., 2013; Weeks et al., 2004). Decomposition of harmful algal blooms in nearshore portions of upwelling regions further deplete oxygen, can fuel production of toxic hydrogen sulphides, and can result in large-scale mortality of important fishery

species (Cockcroft et al., 2001; Pitcher & Probyn, 2011) (Figure 6.16). The combined effects of GHG emissions and nutrient enrichment are projected to further reduce oxygen content, increase $p\text{CO}_2$ and warm upwelled waters along some coasts (Doney, 2010).

Habitat diversity is a characteristic of coastal upwelling margins. Canyons, reefs, methane seeps, kelp forests, rocky subtidal, and intertidal ecosystems are thus periodically subjected to deoxygenation and co-occurring stressors (Levin & Dayton 2009). Some habitats, such as kelp forests (Figure 6.17), may mediate the effects of hypoxia and acidification through productivity. Kelps exhibit exceedingly fast growth rates that can moderate local water conditions (Frieder et al., 2012). The co-occurrence of expanding hypoxia and acidification on coastal upwelling margins might also result in less biogenic (i.e. produced by the organisms) heterogeneity (Levin, 2003). For example, cold-water corals are structure-forming species that provide shelter from predation and can act as nursery grounds for commercially important species (Koslow et al., 2000). Cold-water corals and other calcifying taxa (e.g. bivalves and echinoderms) may be susceptible to co-occurring hypoxia and acidification leading to reduced survival and growth, brittle structures and loss of habitat.

6.5 Conclusions

Reducing, and where possible, reversing deoxygenation, and conserving species and ecosystem services where oxygen has declined, require an understanding of the

causes and effects of deoxygenation in the real-world environmental context in which it occurs. That context includes the presence of additional stressors, many of which are caused by human activities, and some of which can have non-additive negative effects on species or ecological processes when they co-occur with low oxygen. Although the combined effects of individual stressors can sometimes be predicted by summing their individual effects, this simple approach can yield misleading results. Mitigation efforts focusing on a single stressor may not yield the desired relief, and adaptation strategies may provide less protection than desired. Because different sectors of civil society and different governmental jurisdictions can be responsible for causing or mitigating different stressors, fair assignment of responsibility is difficult without considering and evaluating the roles of multiple, potentially interacting stressors. This complexity also means that cross-disciplinary science is critical, and that management actions that cross boundaries of different agencies and jurisdictions are often required.

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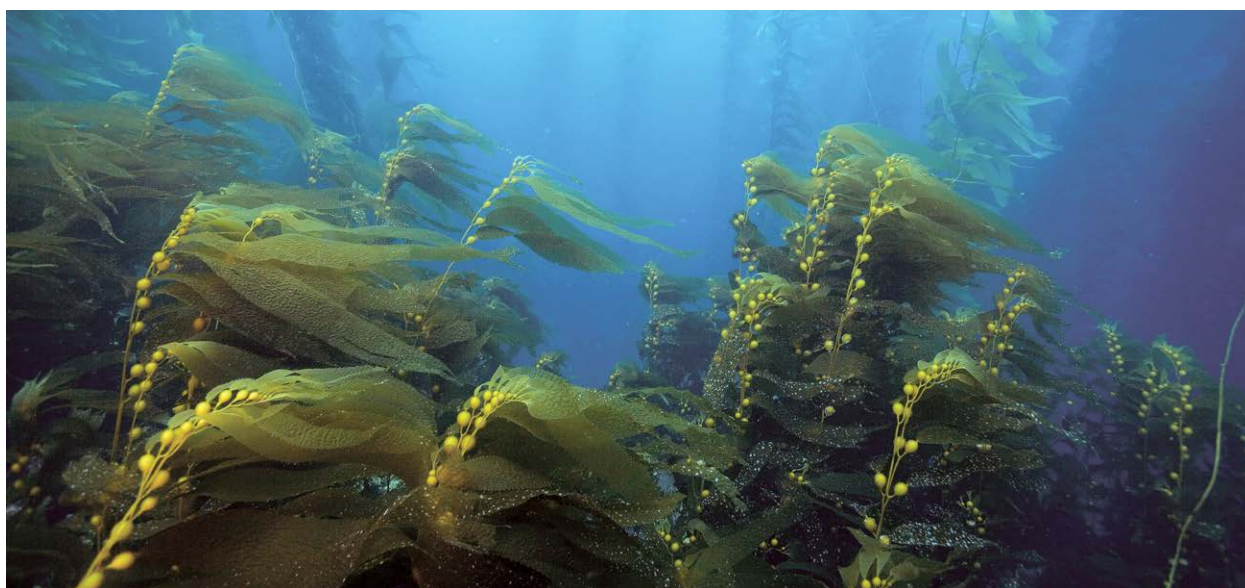


Figure 6.17 Upwelled nutrients stimulate growth of macroalgae, like this giant kelp *Macrocyctis pyrifera* along the eastern boundaries of continents. Where upwelled waters are not severely oxygen depleted, highly productive ecosystems can thrive. © Minden Pictures / Alamy stock photo.

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"Increasing carbon dioxide emissions simultaneously warm, deoxygenate, and acidify marine systems, and nutrient pollution increases the severity of deoxygenation and acidification."

Chapter 6 authors

Ocean deoxygenation 7 impacts on microbial processes, biogeochemistry and feedbacks

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Summary

- Ocean deoxygenation strongly impacts the rates and pathways of the breakdown of organic matter. The associated reactions dramatically change the sources, sinks and cycling of a range of important elements in the environment. This occurs especially for the biologically important elements such as nitrogen (N), phosphorus (P) and iron (Fe), but also for the production of carbon (C) and gases that contribute to Earth's warming by the greenhouse effect such as nitrous oxide (N₂O) and methane (CH₄).
- Increased oxygen loss in coastal waters is mostly caused by enhanced nutrient inputs from fertilizer and wastewater from land, which stimulate phytoplankton blooms. At the end of such blooms, phytoplankton sink to the sea floor where they degrade and thereby remove oxygen. The degradation of organic matter can increase the acidity of coastal waters and may enhance the release of methane from the sea floor. Global warming may exacerbate loss of oxygen from and methane release to coastal waters.
- Oxygen minimum zones (OMZs) in the ocean are well known for playing an essential role in the global nitrogen cycle, in which various chemical species such as ammonium, nitrite, nitrate, nitrous oxide, and nitrogen gas participate, and different bacterial processes are involved in transformations from one chemical species to another. Substantial nitrogen losses are observed in OMZs and they account for approximately 10% of global denitrification. OMZs also are responsible for a large fraction of the oceanic nitrous oxide emission to the atmosphere, which is a powerful greenhouse gas. With global warming, OMZs are projected to significantly expand, leading to alterations in the oceanic nitrogen balance and enhanced oceanic nitrous oxide emissions, further exacerbating warming of the Earth.
- The recycling of phosphorus (P) in marine systems is enhanced when oxygen in sea water is low. The resulting increased availability of phosphorous can further enhance productivity and, upon sinking of the organic matter, enhance the oxygen demand in deeper waters. This positive feedback-loop between productivity, oxygen loss and increased P availability can contribute to further deoxygenation.

- Sediments of continental margins can act as a source of the trace nutrient iron (Fe) to waters in adjacent open ocean areas. This sediment release of iron responds non-linearly to ocean deoxygenation and is at a maximum when oxygen concentrations near the sea floor are low and sulphide is not present. This implies that ocean deoxygenation may initially enhance iron availability for primary producers, followed by a decline in iron availability when waters become sulphidic.
- The Baltic Sea and Black Sea are the world's largest enclosed low oxygen marine ecosystems. While the deep basin of the Black Sea is naturally anoxic, the low oxygen conditions currently observed in the Baltic Sea have been caused by human activities and are the result of enhanced nutrient inputs from land, exacerbated by global warming.
- Understanding coupled element cycles and their links to oxygen can strengthen our ability to predict and manage the impacts of climate change.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen concentrations will change biogeochemical cycles that alter the productivity of coastal and ocean ecosystems.	<ul style="list-style-type: none"> • Changes the cycling of different elements. • Enhanced P recycling. • Reduced N losses. • Enhanced Fe availability (initially).
Decreasing oxygen concentrations will increase greenhouse gas emission.	<ul style="list-style-type: none"> • Increased methane release. • Increased N₂O release.
Enhanced sequestration of organic matter under low oxygen conditions will leave a legacy of carbon and nutrients in the sediments.	<ul style="list-style-type: none"> • Organic matter degradation in sediments continues to consume oxygen. • Nutrients (N, P) can be recycled. • Creates delays in recovery of ecosystems.

7.1 Introduction

Ocean deoxygenation not only impacts bottom-living organisms (Levin, 2017; Vaquer-Sunyer & Duarte, 2008) and fish communities but also alters the biogeochemical cycles of many elements. The concentrations of oxygen affect the rates and pathways of the breakdown of organic matter and the associated reactions dramatically change the sources, sinks and cycling of a range of important elements in the environment. This is true especially for the biologically important elements such as nitrogen (N), phosphorus (P) and iron (Fe), but also for the production of carbon (C) and N-bearing gases that contribute to Earth's warming by the greenhouse effect such as nitrous oxide (N₂O), and methane (CH₄). Here, we identify some of the most important biogeochemical changes in the cycling of elements with deoxygenation, how biogeochemical processes have changed through time, and the consequences for ecosystems and society. Finally, we evaluate how continued deoxygenation will influence internal ecosystem feedbacks that enhance the production of new organic matter contributing to further deoxygenation.

7.2 Definition of the issue

Biogeochemistry is the scientific discipline that involves the study of the chemical, physical, geological, and biological processes and reactions that govern the composition of the environment. Oxygen forms chemical bonds with almost all of the other elements to give corresponding oxides. These oxides, in turn, can bind elements through processes such as sorption. As a consequence, there is a wide range of elements that are affected by oxygen concentrations, including:

- *Carbon* forms a vast number of biologically relevant compounds more than any other element and is the basis for all known life on Earth. The carbon cycle involves both organic compounds such as cellulose and inorganic carbon compounds such as carbon dioxide, carbonate ions, and bicarbonate ions. The rate and extent of breakdown of organic compounds containing carbon varies tremendously depending on whether it occurs in an oxic or an anoxic environment. Aerobic remineralization of organic matter is generally greater than anaerobic remineralization in the absence of oxygen with the processes of decomposition producing different end products.

- *Methane* is produced in sediments during the breakdown of organic matter without oxygen and is a potent greenhouse gas. Eutrophication can accelerate the production of methane gas from the sea bed because enhanced organic matter deposition favours anaerobic remineralization.
- *Ocean acidification* is the decrease in the pH of the Earth's ocean that is primarily associated with the build up of carbon dioxide (CO₂) in the atmosphere from the burning of fossil fuels. When CO₂ is dissolved in ocean waters the pH decreases. In addition, the CO₂ produced during organic matter degradation increases acidity. Because deoxygenation occurs in poorly mixed waters, both hypoxia and decreases in pH can co-occur in many coastal and open ocean environments.
- *Nitrogen* gas (N₂) constitutes about 78% of the Earth's atmosphere, making it the most abundant uncombined element. Nitrogen occurs in all organisms, primarily in amino acids, proteins, nucleic acids (DNA and RNA) and in the energy transfer molecule adenosine triphosphate (ATP). Nitrogen can be limiting to growth in aquatic systems. Major perturbations have occurred in the global nitrogen cycle especially through the production of nitrogen as a fertilizer. Oxygen is a strong regulator of the remineralization of nitrogen compounds with end-products including nitrate, ammonium, dinitrogen gas from denitrification, and nitrous oxide.
- *Phosphorus* is essential for life. Phosphates (compounds containing phosphate (PO₄³⁻)) are a component of DNA, RNA, ATP, and the phospholipids. Phosphate can be limiting to growth in aquatic systems. Humans have caused major changes to the global phosphorus cycle through the use of phosphorus as fertilizer. Deoxygenation greatly influences the biogeochemical cycling of P and oxygen levels regulate the form of P buried in sediments.
- *Sulphur* chemically reacts with most elements and usually occurs as sulphide or sulphate. Hydrogen sulphide (H₂S) is produced in bottom sediments through anaerobic oxidation of methane and microbial breakdown of organic matter in the absence of oxygen, which is a globally important organic carbon oxidation pathway (Jørgensen & Kasten, 2006). It is a

colourless gas with the characteristic odour of rotten eggs and is poisonous to most organisms.

- *Trace metals* are a subset of elements that are normally present in small but measurable amounts in sea water, animals and plants and are a necessary part of nutrition and physiology. Many trace metals are redox-sensitive. Key examples are manganese and iron, which undergo reduction upon the transition from oxic to anoxic conditions and are characterized by strong cycling at redox-interfaces in the water column and sediment. Reducing sediments are the ultimate repository for a large proportion of the trace metals in the oceanic dissolved pool (Little et al., 2015).

Historically, biogeochemical cycles have been studied individually, element by element. However, element cycles in the environment are intimately tied to one another, and a change in one cycle thus impacts multiple cycles. Ocean deoxygenation thus involves the alteration of a large number of interacting element cycles. In the biogeochemical nitrogen cycle, for example, low oxygen leads to changes in processes involving sulphur and carbon compounds besides oxygen and nitrogen. A mechanistic and quantitative understanding of all these processes and their rates is critical if we wish to predict and mitigate the impacts of continued ocean deoxygenation.

The *nitrogen cycle* has been profoundly affected by the activities of humans through the increased combustion of fossil fuels and the growing demand for nitrogen in agriculture (Galloway et al., 2008). As a consequence, concentrations of nitrogen compounds in aquatic ecosystems have increased greatly. Most loss of nitrogen compounds from aquatic ecosystems takes place through microbially facilitated processes, which ultimately transform dissolved inorganic nitrogen to nitrogen gas. Nitrogen gas is not chemically reactive and is not a form of nitrogen that is available to most organisms. Nitrifying microbes aerobically convert ammonium (NH₄⁺) to nitrite (NO₂⁻) and nitrate (NO₃⁻). Denitrifying microbes convert nitrite to nitrogen gas and require a very low oxygen concentration as well as organic C for energy. Anammox bacteria convert nitrite and ammonium ions directly to nitrogen gas and water. Globally, this latter process may be responsible for 30-50% of the nitrogen gas produced in the ocean (Dalsgaard et al., 2003; Kuypers et al., 2003). Both denitrification and anammox are performed by

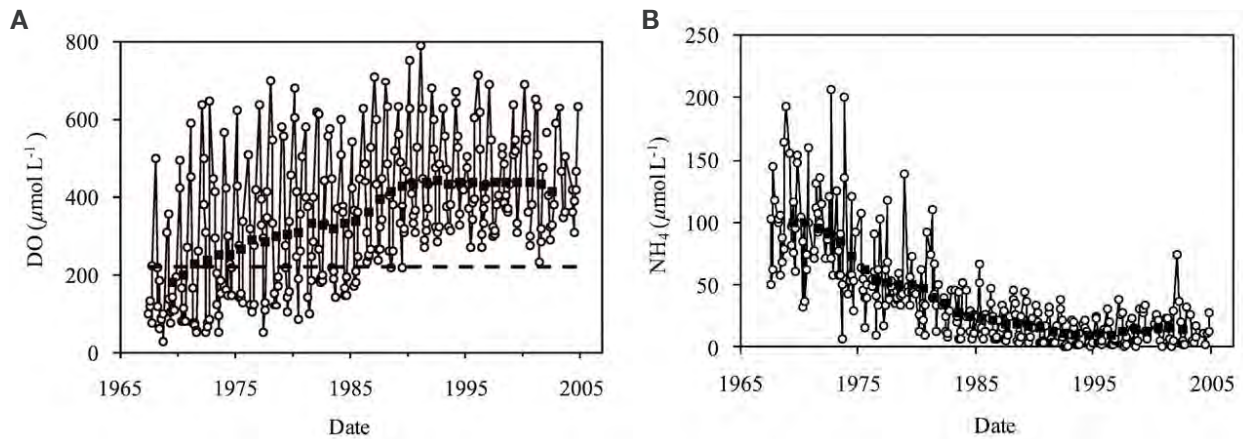


Figure 7.1 Examples of A) dissolved oxygen (DO) and B) ammonium (NH_4) in the Delaware River estuary, USA, in the urban river region (Sharp, 2009).

anaerobic microbes near oxic /anoxic interfaces. Some nitrogen gas can also be produced through reduction of nitrite coupled to methane oxidation (Z. He et al., 2015).

Nitrous oxide (N_2O) a potent greenhouse gas, is a by-product of both nitrification and denitrification (Bange et al., 2010). The amount of nitrous oxide produced is strongly dependent on prevailing oxygen conditions. Production of nitrous oxide is enhanced at the oxic / suboxic boundaries of low-oxygen waters such as found in OMZs, but nitrous oxide is further reduced to nitrogen gas in anoxic conditions, so small differences in oxygen concentration determine whether there is net production or consumption of this gas. Low-oxygen zones (including shelf and coastal areas) contribute a

large fraction of the oceanic nitrous oxide emission to the atmosphere and expansion of low-oxygen zones with global warming may significantly enhance oceanic nitrous oxide emissions. Record air-sea nitrous oxide fluxes have recently been observed above the OMZ in the eastern tropical South Pacific (Arévalo-Martínez et al., 2015) suggesting that hotspots of nitrous oxide emissions occur in high-productivity upwelling ecosystems.

7.3 Trends and impacts

Over the past century, an increase in hypoxia has been observed around the world in hundreds of coastal areas and the open ocean oxygen minimum zones have



Figure 7.2 Thames estuary ©Terry Kent / Shutterstock.com.

expanded by several million km² (Breitburg et al., 2018). Hypoxia in coastal and shelf waters has increased largely because of increases in nutrient availability, but it also is affected by global warming. Warming reduces the amount of oxygen that can saturate in the water, increases rates of respiration and the degradation of organic matter, and strengthens the density difference between surface waters and bottom waters (stratification) decreasing the ventilation of near bottom waters. In turn, deoxygenation has a large influence on nutrient biogeochemical cycles especially elements that are redox sensitive. Below we examine trends of oxygen in a number of different marine environments where hypoxia occurs and its impact on biogeochemical cycles. This is not meant to be an exhaustive list but provide examples of marine systems that are impacted by low oxygen concentrations.

7.3.1 Upper reaches of estuaries

The upper reaches of estuaries are amongst the most heavily populated areas of the world and also suffer from degradation of water quality due to excessive nutrients from sewage, agriculture and animal wastes as well as pollutants including heavy metals, PCBs, oestrogens, etc. Deoxygenation occurs in the upper reaches of estuaries primarily due to inputs of oxygen demanding substances especially from poor wastewater treatment. There are a number of important examples of cities that have accomplished reductions in the organic pollution that consume oxygen during their degradation. This is termed biochemical oxygen demand (BOD) and is a measure of organic pollution. By instituting advanced sewage treatment this has resulted in remarkable improvements in water quality in recent decades (Figure 7.1). Reductions in nutrient loads from advanced wastewater treatment plants with both phosphorus and nitrogen removal have been clearly demonstrated to lead to increases in oxygen concentrations in diverse locations. Estuaries that have exhibited improved water quality from advanced wastewater treatment include Boston Harbour, MA, USA (Tucker et al., 2014), the Scheldt River estuary, The Netherlands/Belgian border (Soetaert et al., 2006), the urban region of the Delaware estuary, USA (Sharp, 2010), and the Mersey River Estuary (Jones, 2006) and Thames River Estuary in the UK (Figure 7.2) (Tinsley, 1998).

A global estimate by the United Nations Environment Programme (UNEP) and UN-HABITAT determined that 90% of all wastewater generated is released into

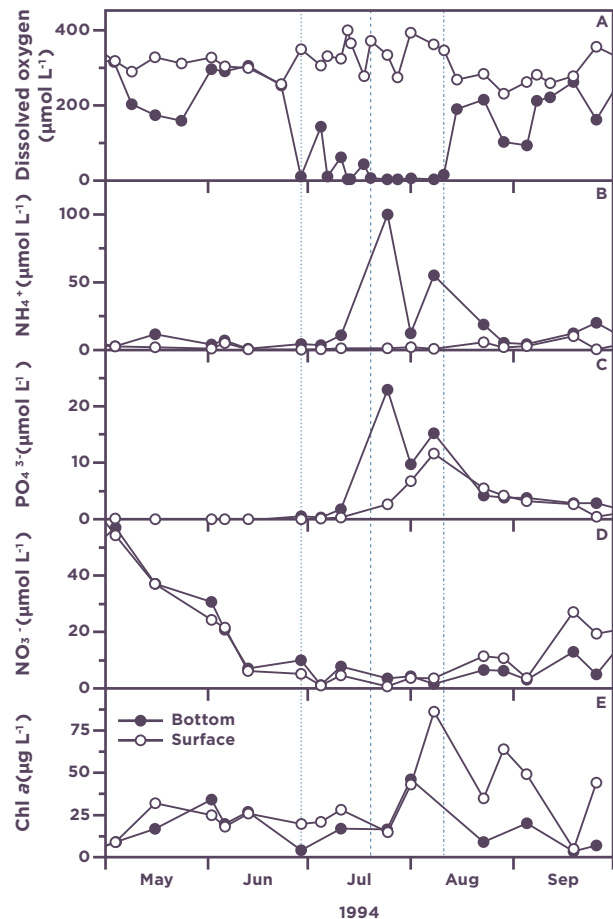


Figure 7.3 Time trend of the impact of deoxygenation on the biogeochemical cycles of nitrogen and phosphorus. Concentrations of (A) dissolved oxygen, (B) ammonia (NH₄⁺), (C) phosphate (PO₄³⁻), (D) nitrate (NO₃⁻) plus nitrite (NO₂⁻), and (E) chlorophyll a (Chl a) in bottom water and surface water in the central part of Skive Fjord, Denmark. Vertical lines indicate onset of hypoxia with intermittent re-oxygenation (dotted line), onset of the period with oxygen deficiency (dashed line), and the end of hypoxia (dashed and dotted line), respectively (Conley et al., 2007).

the environment untreated (Corcoran et al., 2010). The input of organic material not only depletes oxygen, but these hypoxic and anoxic environments lead to large concentrations of reduced species such as ammonium and the production of toxic hydrogen sulphide. In addition to aerobic respiration, processes such as nitrification substantially contribute to the consumption of oxygen, and may have a significant impact on carbonate equilibria and pH in coastal waters. For example, in the heavily impacted Pearl River Estuary (Dai et al., 2006; B. He et al., 2014), China, the oxygen depleted water is concentrated in the low salinity regions between 1 and ~5 and is accompanied by high pCO₂ (up to 7000 µatm) and nutrients (ammonium-N > 600 µM and nitrate N > 200 µM). Recent studies have confirmed that serious oxygen depletion occurred year-round throughout the water column in the upper reaches of the Pearl River Estuary primarily from sewage.

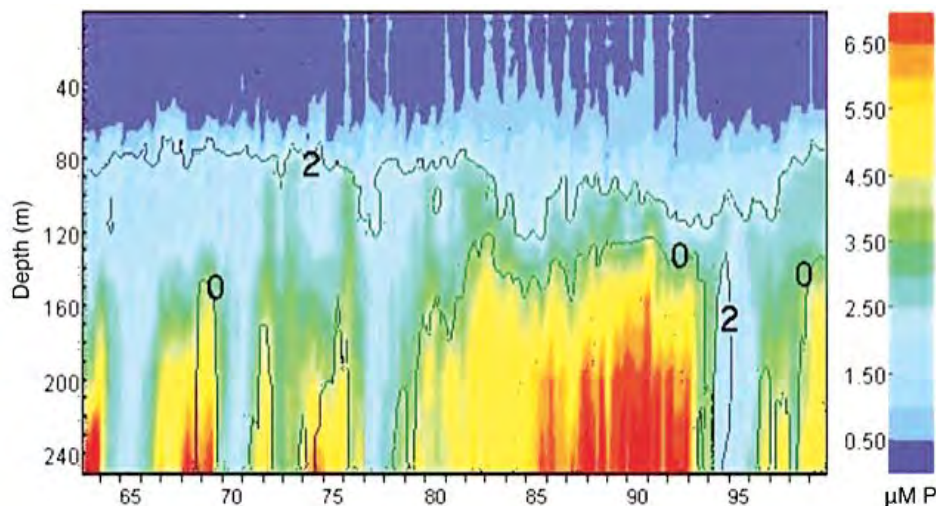


Figure 7.4 Time trends of dissolved inorganic phosphate (PO_4^{3-}) and dissolved oxygen (ml L^{-1}) isopleths from vertical profiles in the Gotland Deep, Baltic Sea from 1963-2000.

7.3.2 Estuarine systems

Estuaries form a transition zone between rivers and marine environments. The inflows of fresh water often provide high levels of nutrients making estuaries among the most productive natural habitats in the world. However, excessive nutrient inputs have increased the rate of deoxygenation with hundreds of estuaries experiencing hypoxia and anoxia (Breitburg et al., 2018). A classic example of time trends in nutrient biogeochemical cycles with deoxygenation is seen from Skive Fjord, Denmark (Figure 7.3). With decreasing bottom water oxygen concentrations, phosphate fluxes from sediments increase, less nitrogen is denitrified and more nitrogen is anaerobically reduced to ammonium (Conley et al., 2007). The accumulation of nutrients in the bottom water can accelerate the rate of growth of algae in surface waters as nutrients are mixed upwards during wind events. Many estuarine systems have high bottom water concentrations of nutrients during periods of hypoxia (Caballero-Alfonso et al., 2015; Kemp et al., 2009).

7.3.3 Enclosed large marine ecosystems

The Baltic Sea is the largest anthropogenically-induced zone of hypoxia in the world (Diaz & Rosenberg, 2008). Carstensen et al. (2014) reported a 10-fold increase of hypoxia in the Baltic Sea from the period 1898 to 2012 and showed that deoxygenation is primarily linked to increased inputs of nutrients from land, although increased respiration due to higher temperatures during the last two decades has contributed to worsening oxygen conditions. Conley et al. (2002) showed that annual changes in dissolved inorganic phosphate in the

water column were positively correlated to the area of bottom covered by hypoxic water, but not to changes in total phosphorus load (Figure 7.4). The variations in phosphorus pools that have occurred during the past decades do not reflect any human activities to reduce nutrient inputs but are instead regulated by variations in vertical stratification of the water column and variations in phosphorus retention in the surface sediment. Denitrification is the dominant pathway for nitrogen loss in the water column and thus is of the same order of magnitude as sediment denitrification (Dalsgaard et al., 2013). The amount of dissolved inorganic nitrogen in the Baltic Proper is negatively correlated with the volume of hypoxic water suggesting that denitrification is enhanced when oxygen is low (Conley et al., 2009a). The expansion of hypoxia in the Baltic Sea has led to major changes in iron dynamics: while initially release of Fe from shelf sediments and the transfer to adjacent deep basins was enhanced, prolonged hypoxia has led to strong retention of Fe in shelf sediments, likely in the form of iron sulphides. This shelf iron, released in a “window of opportunity” when bottom waters were neither oxic nor sulphidic may have helped to initially buffer sulphide concentrations in the deep basins (Lenz et al., 2015). Changes in pathways of organic matter degradation associated with eutrophication and hypoxia can lead to an enhanced release of methane, ammonium and sulphide from sediments into the water column (Thang et al., 2013).

The Black Sea is the world's largest naturally occurring anoxic basin and is characterized by a strong salinity stratification with well-mixed, oxic surface waters overlying nearly stagnant, anoxic and sulphide-rich

deeper water. Human-induced eutrophication and coastal hypoxia have been reported for the continental shelves surrounding the deep basin, especially in the vicinity of major rivers (Friedrich et al., 2014). The most prominent example is the coastal hypoxia observed on the north-western shelf where the fresh water and nutrient input from the Danube and other rivers contribute to thermohaline stratification and stimulate primary productivity in summer. The areal extent and intensity of the seasonal hypoxia on the north-western shelf increased from the 1960s to the 1990s, followed by a partial recovery, related to a strong reduction in nutrient input in the 1990s (Capet et al., 2013; Friedrich et al., 2014). Physical processes contribute strongly to the temporal and spatial variability of the coastal hypoxia on the shelf (Capet et al., 2013). The coastal hypoxia likely contributes to strong nutrient recycling from the sediments, which for phosphate and ammonium was equal in size to half of the yearly input from the Danube river in the late 1990s (Friedrich et al., 2002).

A major difference between the Black Sea and Baltic Sea is that in the latter system, the shallow, shelf areas surrounding the deep basin(s) are highly eutrophic (e.g. Jilbert et al., 2011), leading to one nearly uninterrupted area of anoxia in summer that extends from the deep basins into shallower waters (Carstensen et al., 2014). This clearly differs from the Black Sea where there is a distinct spatial separation between the coastal zone hypoxia and that of the deep basin (Friedrich et al., 2014).

7.3.4 Shelf ecosystems

Bottom-water hypoxia has occurred during summer in the northern Gulf of Mexico for more than three decades largely driven by nutrient inputs from the Mississippi River (Rabalais et al., 2014). Low oxygen concentrations on the Mississippi River shelf enhance denitrification and the sediment removal of nitrogen (McCarthy et al., 2015). Hu et al. (2017) reported that benthic (both aerobic and anaerobic) respiration-produced CO_2 flux could be responsible for acidifying hypoxic bottom water in addition to water column aerobic respiration.

The Changjiang (Yangtze River) is one of the largest rivers in the world and strongly influences its estuary and adjacent shelf forming stratified and turbid plumes, especially during summer (Zhang et al., 1999). Like many other rivers in the world, the Changjiang has been suffering from eutrophication and oxygen depletion for the past few decades (Figure 7.5) (Zhu et al., 2011). Coupled variation in particulate organic carbon (POC), dissolved inorganic phosphorus (DIP), dissolved inorganic nitrogen (DIN) and apparent oxygen utilization (AOU) occurs in near-bottom waters suggesting hypoxia is driven by the degradation of organic matter produced during intense phytoplankton blooms (Qian et al., 2017).

The Namibian shelf and Oregon shelf are examples of ecosystems where upwelling of nutrient-rich low oxygen waters is the main cause of shelf hypoxia. On the

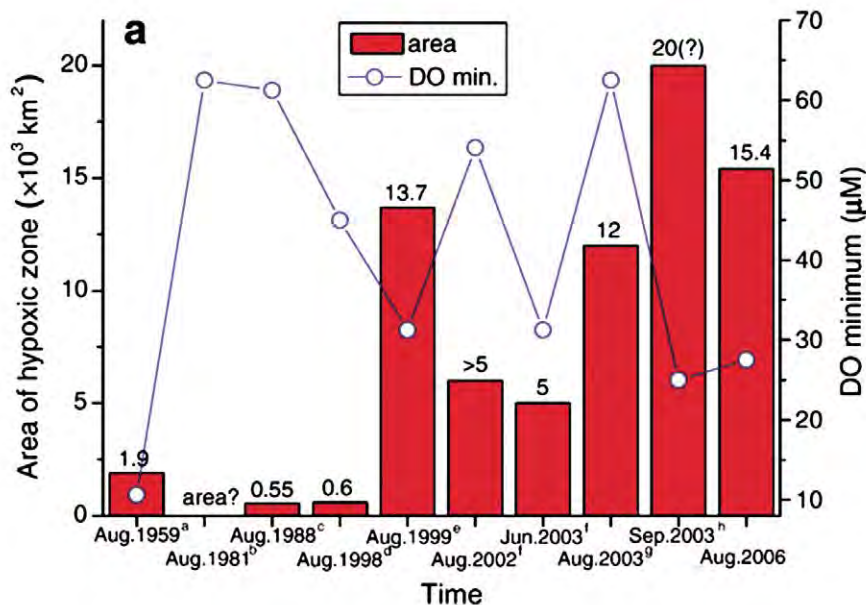


Figure 7.5 The long-term pattern of hypoxia off the Changjiang (Yangtze River) Estuary, China (Zhu et al., 2014).

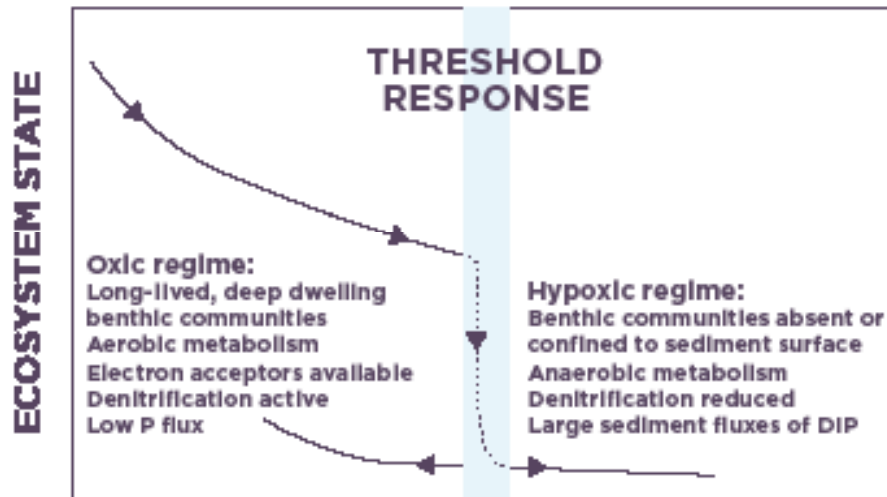


Figure 7.6 Hypothetical diagram showing change in ecosystem state as represented by bottom water oxygen concentrations versus nutrient concentrations. An ecosystem is believed to reach a threshold when bottom-living organisms are killed and the system switches to one dominated by anaerobic processes (Conley et al., 2009a).

Namibian shelf, seasonal and interannual variations in oxygen are primarily the result of variability in advective oxygen supply. On the Oregon shelf, advective flows are also key, but local respiration also accounts for a major proportion of the observed oxygen loss (Fennel & Testa, 2019; and references therein)

7.3.5 Oxygen minimum zones (OMZ) in the open ocean

Total loss of bioavailable nitrogen from the open ocean is currently estimated to be 65-80 Tg N y^{-1} from the water column and 130-270 Tg N y^{-1} from sediments (Somes et al., 2013). Analysis and modelling of global benthic data also indicate that denitrification in sediments underlying high nutrient-low oxygen areas such as OMZs remove around three times as much N per unit of carbon deposited as sediments underlying highly oxygenated water, and account for approximately 10% (i.e. 15 Tg N y^{-1}) of global benthic denitrification (Bohlen et al., 2012).

Deoxygenation of OMZ waters is expected to increase the volume of water where denitrification and anammox occur and may lead to increased marine nitrogen loss (Bristow et al., 2017). This could alter the ocean's nitrogen inventory and, eventually, biological production on millennial timescales if nitrogen losses are not compensated for by increases in nitrogen fixation (Gruber, 2016).

The direction and magnitude of change in the nitrous oxide budget and air-sea nitrous oxide flux are also

unclear because increased stratification could reduce the amount of nitrous oxide that reaches the surface ocean and escapes to the atmosphere (Martinez-Rey et al., 2015).

Where OMZs impinge on continental margins, low oxygen in bottom waters may enhance the benthic release of dissolved iron (Scholz et al., 2014) and phosphate (e.g. Kraal et al., 2012). When these nutrients subsequently reach the surface water, they may increase productivity and contribute to a further expansion of OMZs. While for iron, the release occurs in a narrow redox window where neither oxygen nor sulphide is present (Scholz et al., 2014), for phosphate, the benthic release generally increases when conditions are more reducing (Algeo & Ingall, 2007). In some areas, phosphorite formation, which may be mediated by microbes, can partly counteract the enhanced benthic release of phosphorus (e.g. Schulz & Schulz, 2005).

Through a combination of molecular techniques and biogeochemical analyses, a hidden ("cryptic") cycle of sulphur was recently revealed to be active in the water column of the OMZ offshore Chile (Canfield et al., 2010). In such a cryptic cycle, sulphide produced through sulphate reduction can drive enhanced nitrate reduction thereby contributing to a coupling of the sulphur and nitrogen cycles in the water column. Other recent work points towards a link between the cycles of nitrogen and methane in OMZs, with methane from sediments potentially fuelling nitrite-dependent anaerobic oxidation of methane in the water column (Chronopoulou et al., 2017). Increased ocean deoxygenation is expected to

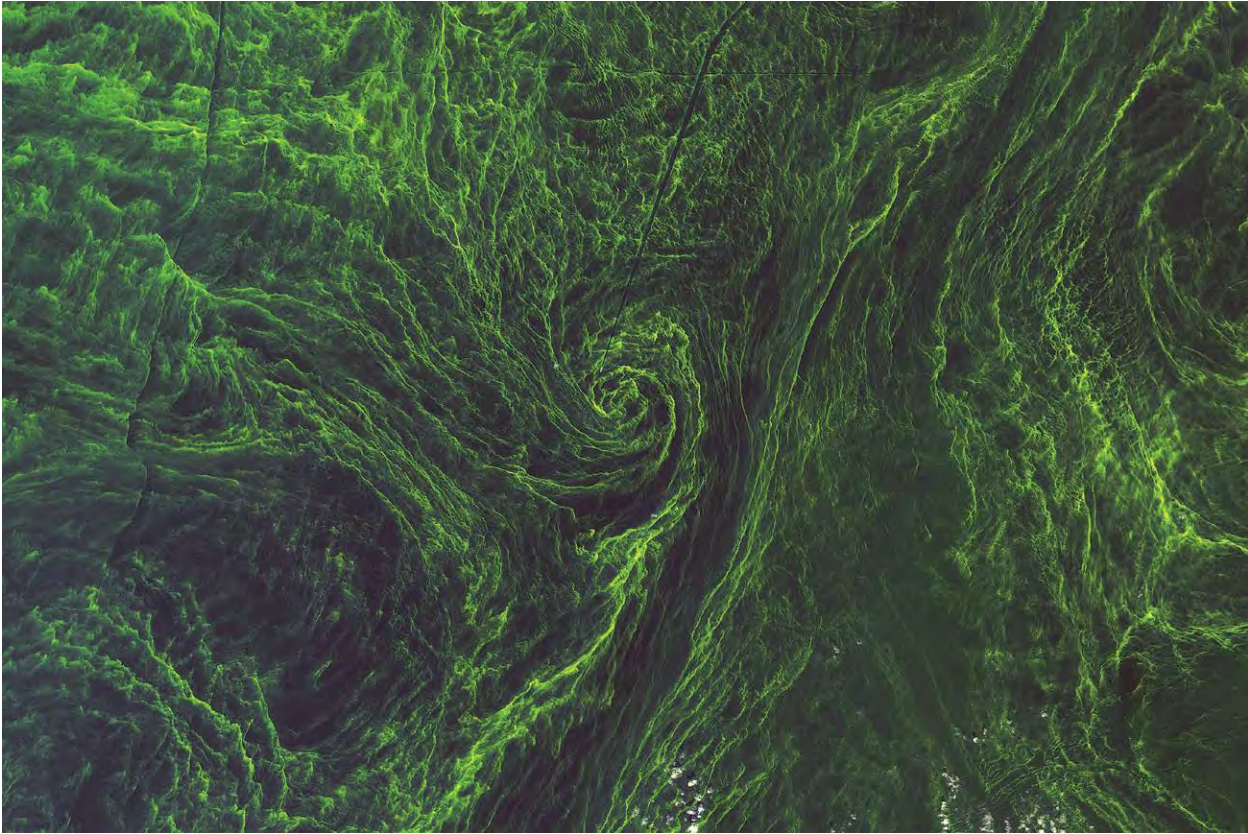


Figure 7.7 Cyanobacteria bloom in Baltic Sea © lavizzara / Shutterstock.com.

increase the importance of these anaerobic pathways in the coupled S-C-N-O cycles.

7.4 Ecosystem consequences

7.4.1 Nutrients are not buried, but recycled

It is being increasingly recognized that there is a legacy of excess carbon and external nutrient loading from the last century in the sediments of many coastal and shelf ecosystems that contributes to continued eutrophication despite large-scale nutrient reductions. Labile organic carbon and associated nutrients buried in sediments can be remobilized during periods of low oxygen, especially phosphorus. Nitrogen cycling processes, especially denitrification is strongly regulated by oxygen concentrations with decreases in denitrification when oxygen becomes low, shifting nitrogen cycling towards the regeneration of nitrogen as a reduced compound such as ammonium instead of being lost from the system as nitrogen gas. The legacy of a higher sediment respiratory demand following eutrophication has been shown for a number of coastal systems (Kemp et al., 2009; Turner et al., 2008) whereby repeated hypoxic events lead to an increased susceptibility of further

hypoxia and accelerated eutrophication (Figure 7.6) (Conley et al., 2009a).

Phosphorus previously buried in the sediments can be returned to the water column causing an increase in eutrophication. The supply of phosphorus released from the sediments is generally enhanced under anoxic conditions (Ingall & Jahnke, 1994; Scholz et al., 2014) and has the potential to further stimulate biological production if phosphorus and nitrogen reach well-lit surface waters, such as above the OMZs associated with coastal upwelling regions and the surface layer of coastal waters. Elevated dissolved inorganic phosphorus and chlorophyll are found in surface waters when anoxia occurs in fjords and estuaries (Conley et al., 2007) and in some systems, deep waters supply as much phosphorus to productive surface layers as do watershed discharges. Increased productivity will tend to increase oxygen consumption, may increase the sediment area in contact with low-oxygen waters, and may eventually lead to further release of phosphorus from the sediment. There is evidence for this positive feedback in enclosed seas like the Baltic Sea, where enhanced nitrogen fixation in response to deoxygenation has led to the recent proliferation of

undesirable cyanobacteria blooms (Figure 7.7) that can be toxic and have adverse impacts on ecosystems and society. Enhanced phosphate levels may generally favour nitrogen fixation by diazotrophs, especially in the presence of nitrogen loss when ordinary plankton are driven towards nitrogen limitation.

7.4.2 Changing nutrient limitation with deoxygenation

The availability of nutrients in the ocean frequently limits the activity and abundance of phytoplankton primary producers. Nitrogen availability tends to limit productivity throughout much of the surface low-latitude ocean, where the supply of nutrients from the subsurface is relatively slow. Iron often limits productivity where subsurface nutrient supply is enhanced, including within the main oceanic upwelling regions, and phosphorus and micronutrients may also (co-)limit marine phytoplankton (Moore et al., 2013). By contrast, coastal and shelf systems can be limited by both, or either, nitrogen and phosphorus and can vary both temporally and spatially (Conley et al., 2009b). The biogeochemical cycles of nitrogen and phosphorus are strongly governed by oxygen concentrations (Figure 7.8); thus, deoxygenation can have significant effects on primary productivity.

Marine nitrogen fixation occurs in close spatial association with the major regions of marine denitrification, such as the eastern tropical North and South Pacific (Gruber & Deutsch, 2015) and is related to the generation of nitrogen-deficient waters by denitrification in OMZs. The loss of fixed nitrogen through the microbial processes of denitrification and/or anammox thus creates a niche for cyanobacteria, through effectively generating an excess of phosphorus (Moore et al., 2013). Increases in phosphorus supply with enhanced biogeochemical cycling in OMZs lead to higher ocean productivity and oxygen demand in subsurface water (Watson et al., 2017) although sometimes nitrogen fixation is displaced downstream due to the availability of iron concentrations (Bonnet et al., 2017).

Low oxygen may affect the global distribution of trace metals, some of which serve as micronutrients for plankton growth, but the significance of such controls is yet to be fully evaluated. Nitrogen–iron co-limitation is pervasive in the ocean, with other micronutrients

also approaching co-deficiency (Browning et al., 2017). Major questions remain regarding the long-term impact on primary productivity depending on changes in N-P-Fe cycling with continued ocean deoxygenation.

7.5 Societal consequences

As outlined by Rose et al. (Chapter 10) deoxygenation can kill fish, especially with the production of toxic hydrogen sulphide (Vaquer-Sunyer & Duarte, 2008). Trophic efficiency (landings per unit nitrogen loadings) are lower in systems with extensive hypoxia with reduced recruitment and population abundance. There are likely abiotic effects of hypoxia on egg survival and hatch success. All of these aspects reduce the quantity of fish available for fisheries. These aspects can affect food security making uncertain the availability of nutritionally and safe foods from marine environments and can affect the livelihood of fishermen.

Low oxygen enhances the biogeochemical cycling of phosphorus and can affect the cycling of nitrogen in different ways depending upon the times scales of hypoxia and circulation. These processes associated with deoxygenation leads to the rapid recycling of nutrients, reductions in the long-term sediment sink of nutrients, with excess nutrients cycling in the water column. For example, cyanobacteria blooms are closely linked with the appearance of hypoxia in the Baltic Sea (Funkey et al., 2014). Algal blooms create poor water quality conditions reducing the quality of life for those living near coastal areas. Algal blooms also reduce the opportunities for recreation by covering beaches with algae washed up on shore. In addition, some species of cyanobacteria are toxic.

It is being increasingly recognized that there is a legacy of excess external nutrient loading from the last century in the sediments of many coastal and shelf ecosystems that contributes to continued eutrophication despite large-scale nutrient reductions. The legacy of a higher sediment respiratory demand following eutrophication has been shown for other coastal systems (Turner et al., 2008) whereby repeated hypoxic events lead to an increased susceptibility of further hypoxia and accelerated eutrophication. Phosphorus previously buried in the sediments can be returned to the water column and the regeneration of nitrogen to ammonium can cause an increase in eutrophication (Conley et al., 2009a).

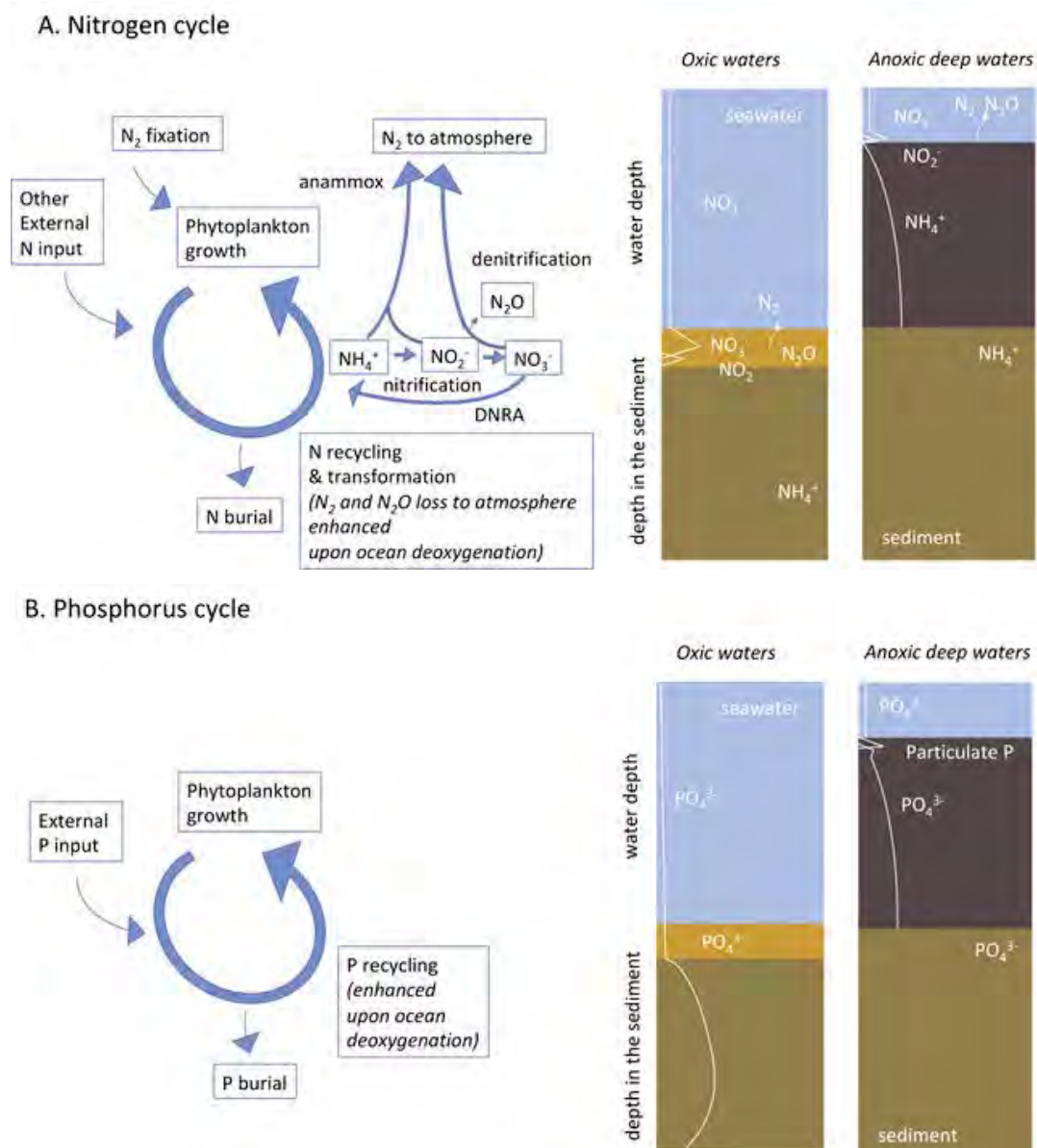


Figure 7.8 Conceptual figure of nutrient pathways for (A) the nitrogen cycle and (B) the phosphorous cycle. Differences in the cycles of nitrogen and phosphorous are depicted between oxic waters and in anoxic deep waters. For the nitrogen pathways N_2 and N_2O loss to the atmosphere are enhanced upon ocean deoxygenation. For phosphorous, enhanced recycling occurs upon ocean deoxygenation.

There are unequal capacities for adaptation throughout the world. Developing countries, who often have not significantly contributed to the amount of greenhouse gases in the atmosphere, will now be at an even greater disadvantage when it comes to dealing with the effects of ocean deoxygenation with climate change. In addition, many large cities in developing countries have limited capacity to reduce the input of sewage derived nutrients into adjacent waters fuelling eutrophication, and if the conditions are suitable, algal blooms with subsequent deoxygenation.

7.6 Implications of continuing ocean deoxygenation

Ocean deoxygenation is becoming an increasingly widespread phenomenon throughout the world (Breitburg et al., 2018). Despite nutrient reductions that have reduced the deleterious effects of eutrophication, it remains difficult to improve bottom water oxygen conditions (Anderson et al., 2017; Reimann et al., 2016). This does not mean that nutrient reductions are not important for improving oxygen concentrations;

deoxygenation would have been even worse if nutrient inputs had not been reduced. Failure to reduce nutrient inputs may lead to cascading effects of increasing hypoxia with the return to an ecosystem with less hypoxia becoming more and more unlikely. Nutrient reduction and efforts to reduce the effects of global warming are the only realistic management measures for improving oxygen conditions.

The time scales for improvement in oxygen conditions depend greatly on residence time and circulation. Changes in oceanic temperature with global warming leading to more deoxygenation in the OMZs are likely to lead to an expansion of OMZs with a decline in the extent of at least 10,000 years (Shaffer et al., 1989). In contrast the prospect of reducing the effects of deoxygenation on coastal areas and open shelf systems is much greater due to the shorter residence time allowing the ecosystems to more easily recover if nutrient reductions are implemented.

7.7 Conclusions / Recommendations

Ocean deoxygenation is leading to major changes in elemental cycling in the coastal zone and in oxygen minimum zones in the open ocean. Recycling of nutrients and burial of organic matter is enhanced (Figure 7.8). Deoxygenation increases the risk of enhanced release of the greenhouse gases nitrous oxide and methane to the atmosphere. While in the coastal zone anthropogenic nutrient inputs from land are the main driver of low oxygen, global warming plays an increasingly important role in modulating water column mixing and lowering oxygen solubility in both coastal and open ocean waters, thereby decreasing oxygen supply. Worldwide reductions in nutrient loss from land to the sea and measures to restrict global warming are essential to improve oxygen conditions in the ocean and avoid further harmful impacts on ecosystems.

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The significance of ocean deoxygenation for species and assemblages 8

Oxygen is required by marine organisms to turn food into energy that can be used to grow and reproduce, as well as escape, adapt to, and repair damage caused by other stressors. When ocean oxygen levels are insufficient, an organism may not have the necessary energy to withstand other stressors. Increasing global temperature simultaneously worsens oxygen decline and increases oxygen requirements of organisms that rely on aerobic respiration. In this chapter the impacts and effects of ocean deoxygenation on a variety of key habitats and species are explored.

The consequences of continuous loss of global oceanic dissolved oxygen content are predicted to result in changed ecosystems, compression of currently biologically available habitats, and large-scale changes in ecosystem services. At the scale of an individual animal, low oxygen alone and/or in combination with other stressors can reduce its ability to fight pathogens and parasites, which can lead to an increase in intensity and prevalence of a number of diseases, and higher morbidity and mortality. For more mobile species the avoidance of low oxygen can result in altered spatial and temporal distributions. Such species may experience higher fishing mortality if fishers target the better-oxygenated surface waters that serve as a refuge for animals fleeing deeper oxygen-depleted habitats. Well-oxygenated habitat may also not be suitable as a refuge for species from oxygen-depleted areas because of the presence of other stressors such as high temperatures and predators.

The consequences for species will vary and include range shifts, changes to vertical and across-shelf movement patterns, losses in spawning habitats, altered ecological interaction rates among consumers and prey, and species that compete for resources, and altered ecological interactions as invasive hypoxia-tolerant species increase in abundance.

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8.1 The significance of ocean deoxygenation for mesopelagic communities

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Summary

- Mesopelagic community structure is directly dependent on the availability of oxygen for aerobic metabolism. Diversity, abundance, distribution and composition of mesopelagic species are all influenced by variations in oxygen at both large and small scales.
- Ocean deoxygenation will decrease the minimum oxygen content in the mesopelagic zone and cause oxyclines to shift vertically (i.e. expansion of the oxygen minimum zone (OMZ) core) in the water column.
- A species' ability to extract oxygen from sea water has evolved to meet specific oxygen demand. As a result, species do not have excess capacity, nor do they live in environments with excess oxygen relative to their evolved capacity; thus, they are susceptible to reductions in oxygen partial pressure and increasing temperature (which elevates metabolic demand).
- Changes in temperature and oxygen profiles within the water column may therefore decouple or enhance competition among different mesopelagic zooplankton species and the larger predators that forage on them at depth by changing zooplankton abundances, distributions, and the depth of layers, and altering species composition and diversity. The biogeochemical cycles (i.e. the biological pump and microbial assemblages) that rely on the mesopelagic zooplankton community will be substantially altered.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen partial pressure (PO_2) in any habitat will reduce aerobic metabolic performance of all species living there (but PO_2 will not decrease in surface waters that are in equilibrium with the atmosphere).	<ul style="list-style-type: none"> • Reduced capacity for prey capture and predator evasion. • Depending on extent of deoxygenation and interacting effects of rising temperature, may lead to species-specific reductions in survival, growth and reproduction.
Shallower upper oxycline and hypoxic layers may result in species-specific suppression of vertical movements and compression of aerobic vertical habitat towards the surface.	<ul style="list-style-type: none"> • May alter the ecological relationships between species living in different depth strata. • May reduce abundance of species as they are forced into shallower, well-lit waters with higher predation pressure. • May reduce diversity in OMZ core and alter species composition of the ecosystem. • May alter biogeochemical cycles and efficiency of biological carbon pump.
Expansion of OMZ will force the lower oxycline community into deeper waters.	<ul style="list-style-type: none"> • May alter life histories (diapause and reproduction) of seasonal inhabitants. • Will alter predator-prey interactions with deeper bathypelagic species. • May alter biogeochemical cycles and efficiency of biological pump.

8.1.1 Introduction

Oceanic oxygen minimum zones (OMZs) refer to sections of the water column at intermediate depths where oxygen concentrations are depleted relative to over- and under-lying waters. OMZs form in subsurface waters, usually between 100 and 1000 m depth, due to a mismatch between heterotrophic oxygen consumption (by microbes and animals) and oxygen input by photosynthetic production, atmospheric diffusion and deep-water ventilation (Figure 8.1.1). OMZs are most pronounced in upwelling regions along the eastern edges of oceans because of high productivity in surface waters and enhanced heterotrophic activity at depth, especially in the Eastern Tropical Pacific (ETP) where deep waters have been out of contact with the atmosphere and oxygen consumption has been occurring for hundreds or thousands of years (Figure 8.1.2). The horizontal and vertical extent of the OMZ, as well as the intensity of the hypoxia (low oxygen) found there, varies considerably between ocean basins and, to a lesser extent, over many spatial and temporal scales within ocean basins (Figure 8.1.2). Dissolved oxygen has declined and hypoxic zones have expanded and shoaled (ocean deoxygenation) throughout much of the ocean as a result of reduced solubility of oxygen in warming waters and enhanced stratification (reduced mixing) that impacts surface

productivity and deep-water oxygen content and utilization (Bograd et al., 2008; Brietburg et al., 2018; Deutsch et al., 2011; Keeling et al., 2010; Paulmier & Ruiz-Pino, 2009; Stramma et al., 2008; Whitney et al., 2007). The variation in oxygen and temperature throughout the mesopelagic zones of the ocean has important implications for organismal performance as well as community structure and composition (Maas et al., 2014; Robinson et al., 2010; Smith & Madhupratap, 2005; Saltzman & Wishner, 1997; Wishner et al., 2013, 2018).

8.1.2 Oxygen concentration, partial pressure and tolerance thresholds

the term 'hypoxia' is most appropriately used to denote an oxygen (O_2) concentration less than some arbitrary value perceived as normal. Within the oceanographic community, hypoxia is typically defined by O_2 concentration, usually without knowledge of the effect of that particular O_2 level on organism or ecosystem function. For example, Kamykowski and Zentara (1990) define hypoxia as a concentration less than 0.2 ml L^{-1} ($\sim 9 \mu\text{M}$) while Diaz and Rosenberg (1995) define it as less than 2.0 ml L^{-1} ($90 \mu\text{M}$). Among all marine animals, a median lethal concentration of $60 \mu\text{M}$ was identified by Vacquer-Sunyer and Duarte (2008). However, this reported threshold concentration exerts a partial

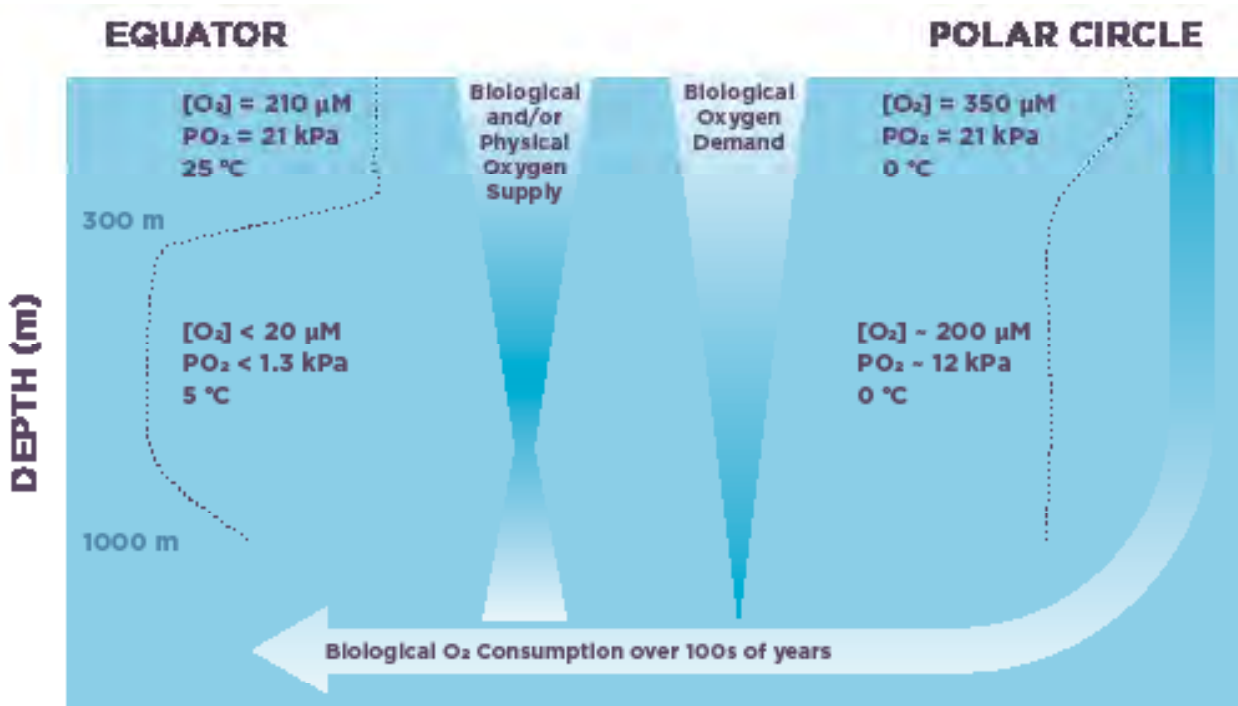


Figure 8.1.1 Schematic showing the processes involved in oxygen minimum zone formation and the resulting oxygen profiles with depth. Biological oxygen supply results from photosynthetic production in shallow waters along with physical diffusion from the atmosphere. The biomass of microbes and animals declines with depth resulting in reduced oxygen consumption (respiration associated with decomposition and metabolism). Deep bottom water formed in polar regions supplies additional oxygen to depths below the oxygen minimum. However, organismal oxygen consumption over 100s of years results in oxygen depletion of deep water by the time it reaches the Eastern Pacific. Approximate oxygen concentrations ($[O_2]$), partial pressure (PO_2) and temperatures across a 1000 m depth range are shown in tropical and polar regions.

pressure ranging from ~ 4 kPa at 0°C to more than 7 kPa at 30°C because oxygen concentration is driven by oxygen solubility, which declines with increasing temperature. The concentration of oxygen in air-saturated sea water varies across the range of ocean temperatures from less ~ 180 μM in the tropics to over 350 μM at the poles. Thus, defining hypoxia by O_2 concentration is problematic because a concentration

that is lethal at one temperature may not be at another and is species-specific. Moreover, it is the partial pressure (PO_2), not the O_2 concentration, that drives O_2 across gill membranes into organismal tissues and determines the effect of hypoxia on organism function. Sea water in equilibrium with the atmosphere has an oxygen partial pressure of 21 kPa (21% of atmospheric pressure) regardless of temperature. For a parcel of water that

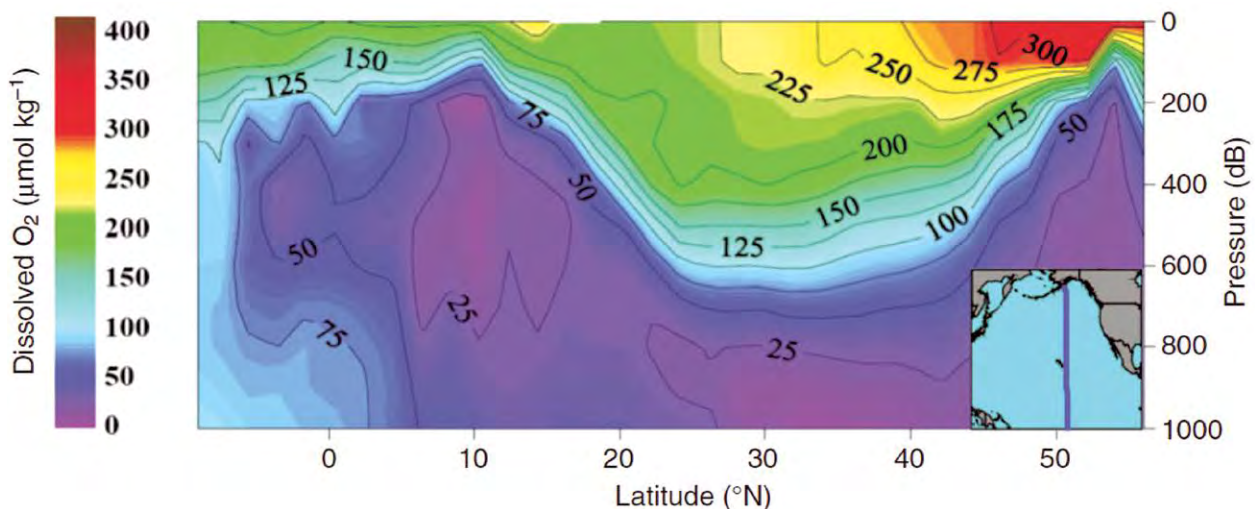


Figure 8.1.2 Oxygen concentration (μM) as a function of depth along a transect from north to south in the Eastern Pacific. A map of the transect line is inset (Seibel, 2011).

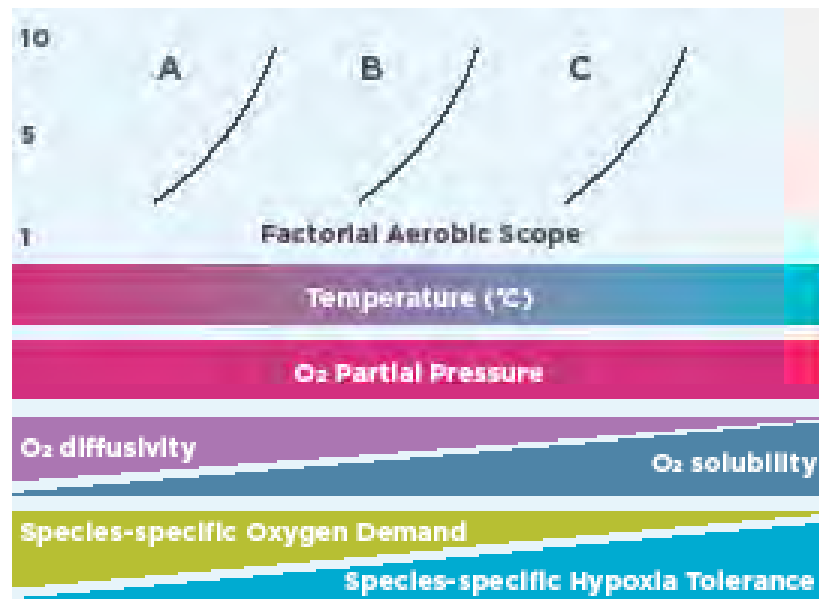


Figure 8.1.3 Temperature influences oxygen availability for organismal metabolism via the counter-acting effects of diffusivity, solubility, metabolic demand and physiological capacity for oxygen extraction and transport (hypoxia tolerance). Oxygen partial pressure in air-saturated water is constant across a temperature range. The result is that oxygen availability is slightly higher in warm water despite reduced solubility, but that physiological hypoxia tolerance compensates for increased demand. Factorial Aerobic Scope (FAS) is the species-specific ratio of maximum to resting oxygen demand and is quantitatively equivalent to the ratio of environmental PO_2 (The Metabolic Index; Deutsch et al., 2015). The FAS in most species (shown for hypothetical species A, B and C) ranges from ~6 to 2 and typically declines with increasing temperature toward a value that characterizes a species' evolved upper temperature limit.

is isolated from the atmosphere, the concentration of oxygen in that parcel will exert a lower pressure at cooler temperatures. Moreover, oxygen diffusivity increases with temperature, which more than offsets temperature-induced reductions in solubility (Figure 8.1.3). Thus oxygen availability at a given concentration is improved in warm waters (Verberk et al., 2011). Regardless, organismal oxygen demand increases with temperature while the capacity for physiological gas exchange has evolved to meet demand within their primary habitat (Figure 8.1.3). Thus, any definition of hypoxia related to the survival or performance of organisms is necessarily species-specific and will depend on the particular physiological requirements of the species and on the environment to which the species is adapted.

The median lethal oxygen concentration reported by Vacquer-Sunyer and Duarte (2008) ($60 \mu\text{M}$); did not include animals evolved to persist in OMZs. An oxygen content above that threshold is found only in the mixed layer above pronounced OMZs suggesting that half of all marine species would not survive for long at depths below ~50 m in the ETP or below ~300 m in the California Current. However, virtually all zooplankton living in these regions can actually tolerate $60 \mu\text{M}$ oxygen ($PO_2 \sim 5 \text{ kPa}$ at 5°C) and many can tolerate a PO_2 less than 1 kPa ($15 \mu\text{M}$ at 5°C ; Childress & Seibel, 1998; Seibel, 2011). More recent studies show some species have critical PO_2 thresholds as low as 0.2 kPa (Wishner et al., 2018).

Such extreme hypoxia tolerance permits movement and habitation across the entire water column in the California Current and expanded movements in the upper few hundred metres in the ETP. Even so, most species are precluded from the core of the most pronounced OMZs. The lack of ability to extract sufficient oxygen from such an oxygen-depleted environment explains the reduction in biomass, abundance and diversity in the core of the ETP OMZ and also why most remaining biomass undergoes diel vertical migration, returning to more oxygenated waters at night in these regions (Maas et al., 2014; Wishner et al., 2013).

8.1.3 Mesopelagic community structure and composition

Mesopelagic communities are structured by trade-offs in food availability, predator avoidance (associated with light level), and species-specific responses to hydrographic features including tolerance to the strong gradients in temperature and oxygen with depth. In regions with intense OMZs, the epipelagic habitat is distinctly separated from deeper water by the strong thermocline and oxycline at the base of the mixed layer (coinciding with the upper boundary of the OMZ; Figure 8.1.4). While this constrains vertical distributions of many taxa, some zooplankton and nekton, such as krill and pelagic crabs (Figure 8.1.5) show strong diel and ontogenetic vertical migration hundreds of metres

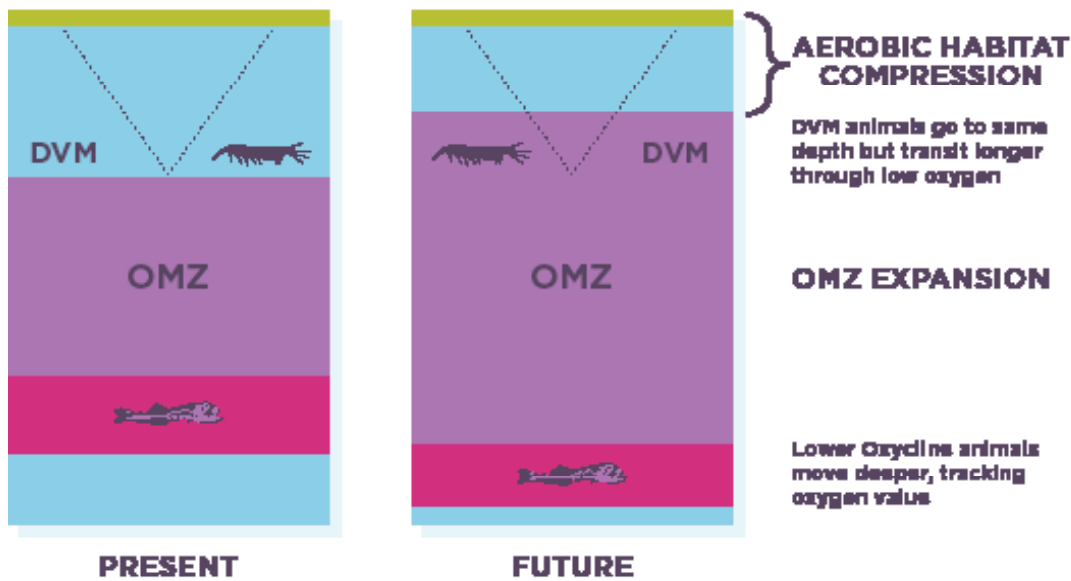


Figure 8.1.4 Schematic showing simplified community structure in oxygen minimum zones and possible consequences of OMZ expansion due to climate change. Diel vertical migrators, such as euphausiids (e.g. krill), migrate to similar depths regardless of oxygen. This is driven primarily by light and the resulting risk of predation during daytime migration. In pronounced OMZs, many vertically migrating animals suppress metabolism during the daytime. The deep lower oxycline community does not migrate but alters depth to persist at a particular oxygen partial pressure.

into hypoxic water (e.g. Ambriz-Arreola et al., 2016; Maas et al., 2014; Seibel, 2016; Wishner et al., 1998, 2013, 2018). The lower boundary of the OMZ, where oxygen increases with depth, has more gradual physical gradients, although there are associations of organism layers with particular oxygen concentrations (Wishner et al., 2013, 2018). Epipelagic and mesopelagic communities also interact as part of the biological pump via the vertical flux and processing of sinking particles (Steinberg & Landry, 2017), a phenomenon that may be influenced in OMZs by effects of low oxygen on distributions and metabolic processes of microbes, zooplankton, and nekton. Additionally, both the upper and lower OMZ oxyclines, as well as the low oxygen core of the OMZ, provide specialized habitats for microbes that may provide novel food resources for mesopelagic zooplankton (Gowing & Wishner, 1992, 1998).

Within strong OMZs, the steep oxygen gradients (oxyclines) at the upper and lower OMZ boundaries create microhabitats of differing oxygen concentration (and temperature regime related to their depth) that are characterized by layers of high zooplankton biomass and abundance, with distinct species zonation (Maas et al., 2014; Wishner et al., 1995, 1998, 2013). For some zooplankton species, including the copepod *Lucicutia hulsemannae* and the shrimp *Gennades* spp. (Figure 8.1.5), oxyclines at the upper and lower OMZ boundaries are loci of distributional peaks in the water column. These characteristics contrast notably

with the OMZ core, where oxygen is extremely low but relatively stable, and where resident zooplankton biomass, abundance and diversity are much reduced (Koppelman et al., 2005; Longhurst, 1967; Smith & Madhupratap, 2005; Wishner et al., 1998, 2008). Responses of the mesopelagic zooplankton community to the OMZ vary geographically. For example, the zooplankton community in the very hypoxic ETP is dominated by population peaks at the upper and lower oxyclines and by diel vertical migrators that inhabit the OMZ core for hours each day. In the California Current, slightly higher oxygen levels and colder temperatures also play a role in structuring the community, however, a diverse midwater assemblage lives permanently in the OMZ core (Gilly et al., 2013).

Under continuing ocean deoxygenation, mesopelagic communities, including those at oxycline boundaries, and the processes they support, may be displaced vertically and horizontally. Boundary-related effects could include altering the depth of zooplankton biomass layers and species distributions and impacting diel vertical migration patterns and life history strategies. In a recent study (Wishner et al., 2013), comparison of two ETP locations differing in the depths of their upper and lower oxyclines served as a natural experiment demonstrating the sort of shifts in faunal distributions that may occur in the future with deoxygenation and OMZ expansion. A large zooplankton biomass peak at the lower OMZ boundary appeared to be strongly locked

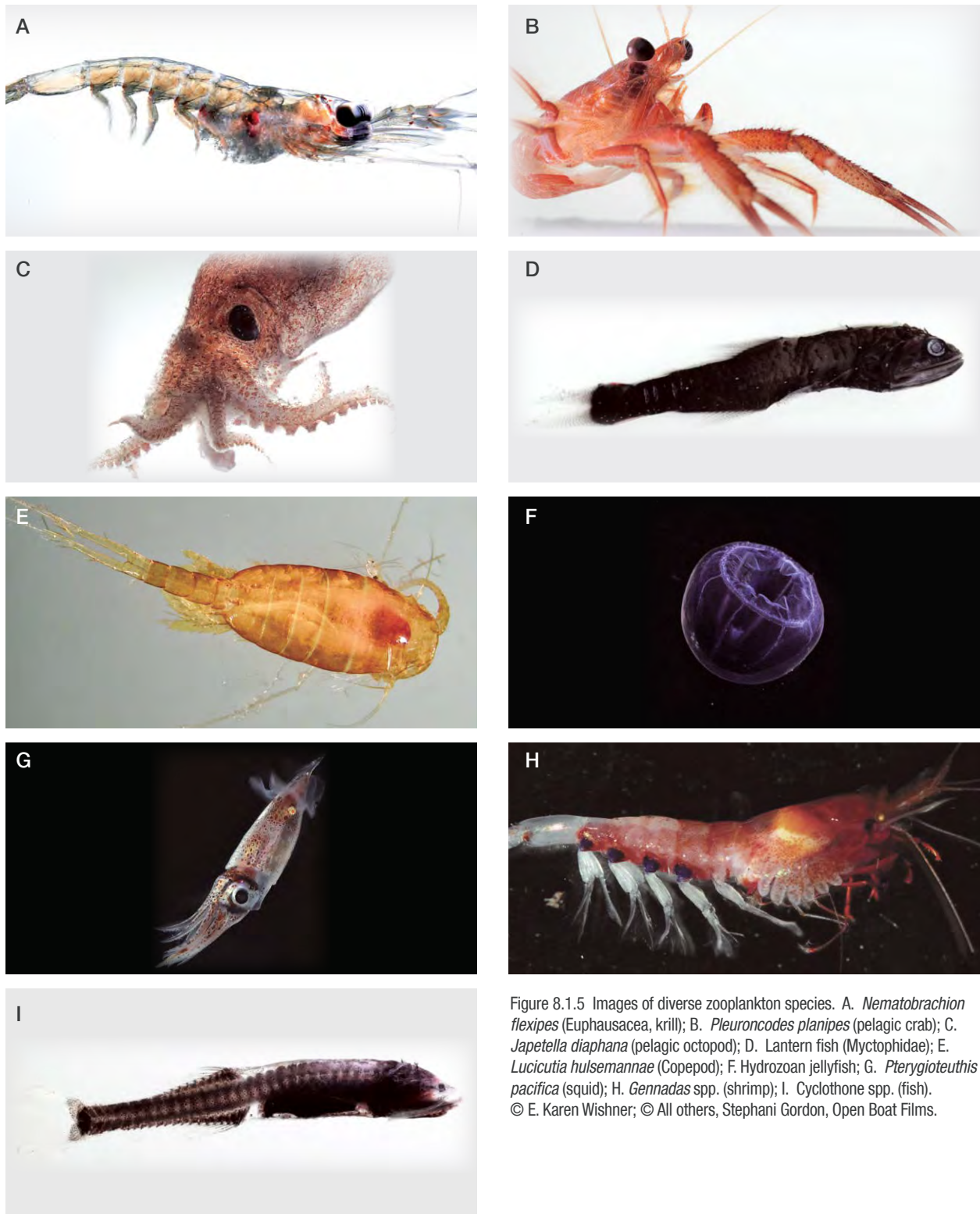


Figure 8.1.5 Images of diverse zooplankton species. A. *Nematobrachion flexipes* (Euphausacea, krill); B. *Pleuroncodes planipes* (pelagic crab); C. *Japetella diaphana* (pelagic octopod); D. Lantern fish (Myctophidae); E. *Lucicutia hulsemannae* (Copepod); F. Hydrozoan jellyfish; G. *Pterygioteuthis pacifica* (squid); H. *Gennadas* spp. (shrimp); I. *Cyclothone* spp. (fish). © E. Karen Wishner; © All others, Stephani Gordon, Open Boat Films.

into position by oxygen concentration. It changed in depth by over 200 m between the two locations, with a depth-associated change in temperature. However, the oxygen concentration at the two depths where this layer was located was virtually identical at both stations ($\sim 2\text{--}8 \mu\text{M}$). In contrast, for animals within the upper

oxycline, the depth (and temperature at that depth) of the daytime diel migration peak was similar at the two stations (200 – 300 m, $11.0\text{--}1.9\text{ }^\circ\text{C}$), even though oxygen concentration at that depth varied between the two regions. Thus, on a daily basis, animals (total biomass) at these two stations migrated to a nearly

constant depth that appeared to be set by light even though the animals at one station had to transit through a broader hypoxic habitat. On a more global scale, however, the depth of diel migration of sound scatterers does appear to be influenced by oxygen concentration (Bianchi et al., 2013; Netburn & Koslow, 2015). In the California Current, even a small future decline in oxygen could result in a shift of this ecosystem and midwater community towards a more highly oxygen-structured system similar to the more sparsely populated Eastern Tropical Pacific OMZ.

Long-term deoxygenation trends (Brietburg et al., 2018) reportedly play a role in declines in abundance of mesopelagic fishes (Koslow et al., 2011), shifts in zooplankton diel migration depths (Bianchi et al., 2013), potential threats to fisheries (Townhill et al., 2016), and alterations in diving depths of top predators (Mislán et al., 2017; Prince & Goodyear, 2006; Stramma et al., 2011). These community changes likely reflect complex interactions of multiple variables including deoxygenation, over-fishing, long- and short-term climate cycles and change, and cascading ecological shifts. Known with much more certainty is that interactions between temperature and oxygen availability on aerobic metabolism will have strong direct effects on oceanic species distributions and performance (Deutsch et al., 2015; Pierson et al., 2017; Seibel, 2016).

8.1.4 Deoxygenation and organismal physiology

The ability of organisms to cope with long-term hypoxia depends on their metabolic rate, which is dependent on temperature and physiological state (activity level, feeding history, reproductive state, etc.), and the ability to extract oxygen from the sea water and transport it to the tissues. Permanent zooplankton residents of oxygen minimum zones tend to have oxygen-binding proteins (haemoglobin or haemocyanin) with a high affinity for oxygen, high ventilatory and circulatory capacity, and enlarged gas-exchange surfaces (i.e. gills) with thin membranes that reduce diffusion distances (Childress & Seibel, 1998; Seibel, 2011). These integrated physiological characteristics set a critical oxygen partial pressure (P_{crit} ; Figure 8.1.6), below which aerobic metabolism can no longer be maintained. The P_{crit} correlates strongly with historical long-term hypoxia exposure (Figure 8.1.7) but may respond to short-term changes via acclimation and, in species with short generation times, adaptation. P_{crit} is species-specific,

and no strong phylogenetic, temperature or size-related trends in hypoxia tolerance appear to exist across marine animals more broadly (see Table S4 in Wishner et al. (2018) for a compilation of all measured P_{crit} values to date for marine crustaceans).

Species without complex oxygen transport systems, such as gelatinous zooplankton, are often reported as oxyconformers, meaning that the rate of oxygen consumption declines with environmental oxygen. However, oxyconformation must merely describe the metabolic response of organisms to O_2 levels below their P_{crit} . This is because there must always be a species-specific upper limit to resting metabolism above which additional O_2 will have no influence. The appearance of oxyconformation may result from 1) a very high P_{crit} (low hypoxia tolerance) most often found in species with limited metabolic scope (low capacity for activity), 2) experimental methods that fail to distinguish a true baseline level of metabolism, or 3) a complex response to declining oxygen that includes multiple processes with distinct oxygen limits. The latter case implies that a baseline level of metabolism that supports all maintenance processes must exist with a higher organismal P_{crit} and that oxygen-dependent metabolic rates are not sustainable in the long-term. Nevertheless, several studies on gelatinous zooplankton demonstrate a clear ability to regulate a constant rate of oxygen consumption as PO_2 falls (Rutherford & Thuesen, 2005; Thuesen et al., 2005). In gelatinous species, which typically have low metabolic rates and short diffusion distances, the P_{crit} may result from simple diffusion limitation as opposed to a limitation in heart or ventilation rate or oxygen carrying capacity as may be seen in fishes, crustaceans and cephalopods.

The evolutionary adjustments in oxygen extraction and transport in individual species have compensated for variations in oxygen demand and availability in their specific habitats such that all species are living similarly near their ultimate limits (P_{crit} , where environmental oxygen supply equals resting demand; Figure 8.1.3). Thus, any decrease in oxygen partial pressure or increase in temperature will reduce the scope for metabolic activity toward critical levels for all species (i.e. Metabolic Index) (Deutsch et al., 2015; Wishner et al., 2018). Because PO_2 is near 21 kPa in surface waters in equilibrium with the atmosphere regardless of temperature, ocean deoxygenation will not impair organismal performance in shallow oceanic waters (but will in coastal regions where PO_2 declines due to eutrophication or upwelling; Chan

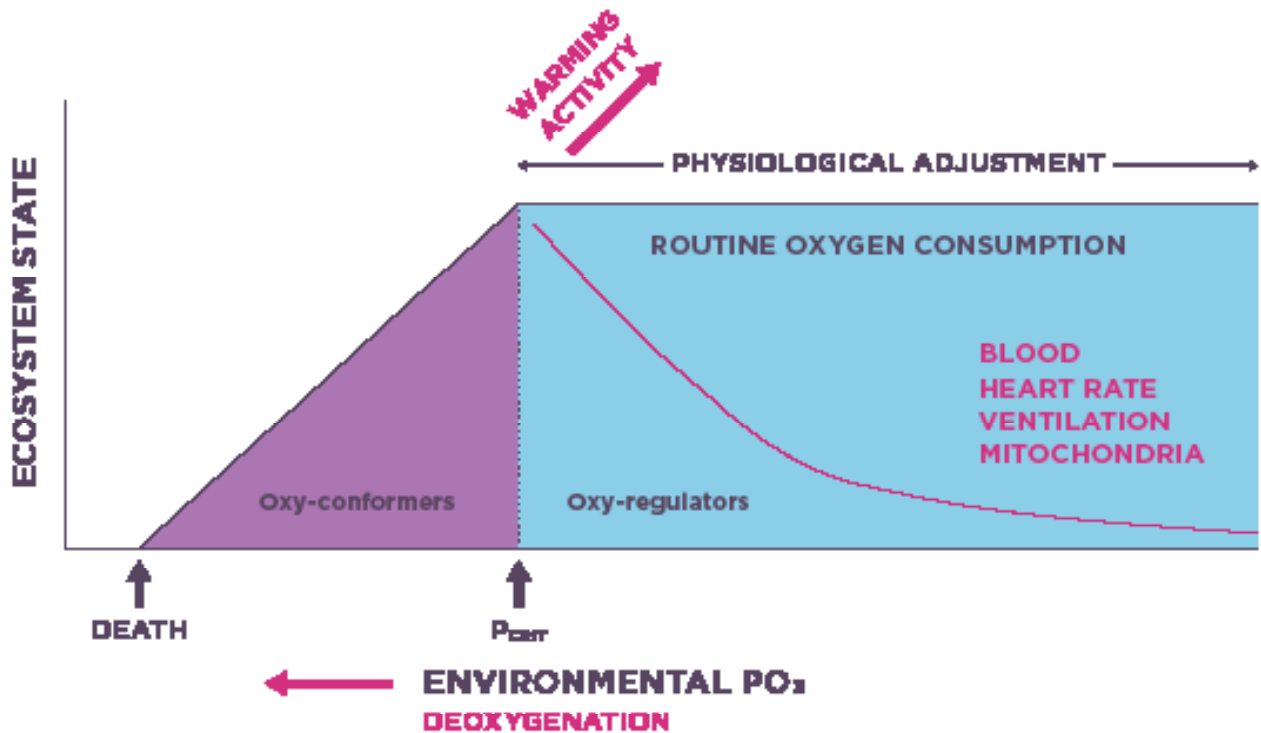


Figure 8.1.6 Schematic of the metabolic response of organisms to declining oxygen partial pressure. Most organisms maintain a constant resting rate of oxygen consumption until a critical PO (P_{crit}) is reached, below which supply fails to meet demand. The red curve represents the physiological adjustments that permit regulation of the metabolic rate at PO above P_{crit} . Ocean warming or increased activity will result in an elevated oxygen consumption rate and higher P_{crit} (reduced hypoxia tolerance). Ocean deoxygenation will reduce PO toward the critical level for any species.

et al., 2008; Rabalais et al., 2002). Thus, organismal oxygen limitation in surface waters may result only from temperature-driven increases in oxygen demand and consequent reductions in the scope for aerobically-fuelled activities such as growth, reproduction and locomotion (Deutsch et al., 2015; Pörtner et al., 2017). However, the transport of waters with reduced $[O_2]$ to deeper layers and alterations in oxygen utilization there will lead to expansion of oxygen minimum zones and reductions in the PO_2 , pushing organisms beyond their evolved tolerance. Thus, all zooplankton are susceptible to warming and deoxygenation.

Species living in cold, well-oxygenated regions, such as the mesopelagic zone of the Southern Ocean, have low metabolic oxygen demand, while oxygen concentration is high in cold water. This has led to a belief that polar waters contain “excess oxygen” and that species living there will not be strongly impacted by deoxygenation (Chapelle & Peck, 1999). However, polar animals have evolved relatively limited oxygen uptake systems and have correspondingly high P_{crits} (i.e. low hypoxia tolerance, Torres et al., 1994). For example, the Antarctic krill, *Euphausia superba*, has a P_{crit} of ~5 kPa at 0 °C, substantially higher than related species living

in pronounced OMZs in the Eastern Tropical Pacific. The krill, *Nematobrachion flexipes*, for example, has a metabolic rate at 10 °C that is similar to that of *E. superba* at 0 °C. However, its P_{crit} is ~10x lower (0.68 kPa; Wishner et al., 2018; Figure 8.1.5). *Euphausia superba* routinely experience oxygen values of ~10 kPa at depths below 200 m. This provides a potential aerobic scope for activity (i.e. Metabolic Index) of only 2, a value known to delineate metabolically suitable habitat for many species (Deutsch et al., 2015). The ocean deoxygenation and warming that have already occurred in the Southern Ocean are substantial and are likely to continue (Schmidtko et al., 2017). Any further decline in PO_2 or increase in temperature will restrict the habitable depth range of polar zooplankton with likely consequences for their growth, reproduction and survival. Thus, excess oxygen does not exist anywhere.

In regions with pronounced OMZs, species that undergo diel vertical migration are capable of short-term survival at sub-critical oxygen levels via metabolic suppression. Some additional energy is acquired through anaerobic metabolic pathways. However, anaerobic metabolism typically accounts for a small fraction of the total energy demand and does not fully compensate for the energy

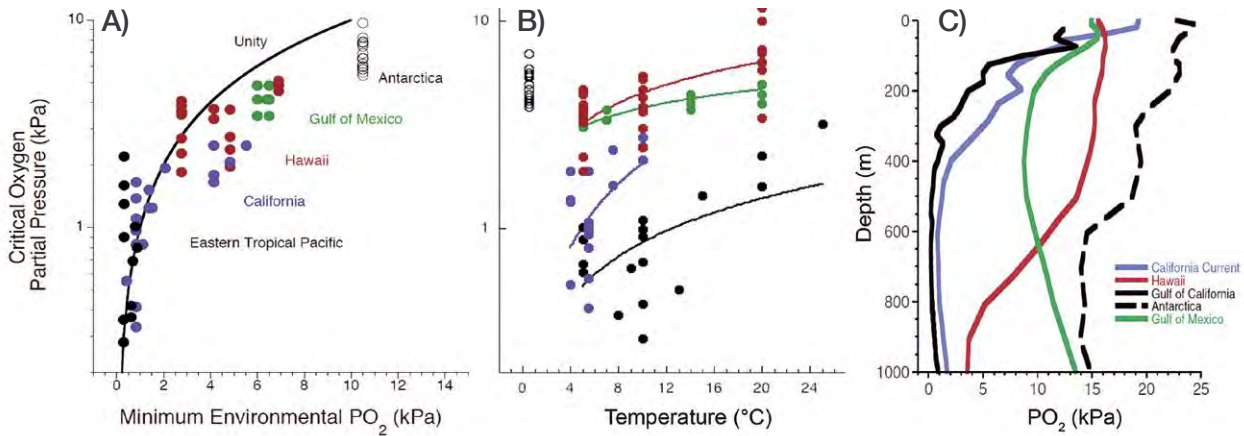


Figure 8.1.7 Critical oxygen partial pressures (P_{crit}) for diverse zooplankton species, including fishes, crustaceans and cephalopods, living in different oceanic regions. Each point is a unique species. A) P_{crit} plotted as a function of the minimum oxygen partial pressure experienced by each species indicates that all species are living similarly near their oxygen limits (unity line). Some vertical migrators experience oxygen levels below their P_{crit} (left of the unity line) during the daytime and must migrate to surface waters at night. B) P_{crit} of each species as a function of temperature demonstrating that species in relatively hypoxic regions (Eastern Tropical Pacific and California Current) have evolved greater physiological capacity for oxygen uptake and transport compared to species in relatively well-oxygenated regions (Antarctica, Hawaii and Gulf of Mexico). C) Oxygen depth profiles from each region investigated (Gulf of California profile represents the Eastern Tropical Pacific species).

deficit due to oxygen limitation. Metabolic suppression is achieved by limiting energetically expensive processes such as ion transport, transcription and translation. Reductions in total metabolism of 40-80% have been demonstrated in mesopelagic squids, pteropods, krill, crabs, copepods and amphipods (Childress, 1977; Elder & Seibel, 2015; Kiko et al., 2015, 2016; Maas et al., 2012; Seibel, 2011, 2016; Seibel et al., 2014, 2016, 2018; Figure 8.1.5). Such reductions in oxygen consumption are accompanied by reduced carbon dioxide and ammonia excretion, with consequences for biogeochemical cycles. Below critical oxygen levels, some energy is still acquired from aerobic metabolism. Thus, continued deoxygenation may restrict the distributions and abundances of key vertically migrating species and their predators.

As the ocean warms and oxygen declines, the metabolically viable habitat of the upper ocean will shoal (aerobic habitat compression). Oxygen limitation is, of course, not the only potential limitation on habitat depth. Light, temperature, pH and food availability may impose independent limits and selective pressures. Figure 8.1.3 illustrates that all species live within a similar range of metabolically available habitat. A PO_2 near 1 kPa appears to be a lower limit for meso-zooplankton diversity and abundance (Childress & Seibel, 1998). The OMZ core of the California Current is near this limit. Further deoxygenation may cause an ecosystem shift there from a diverse mesopelagic community to one largely devoid of permanent mesopelagic inhabitants and dominated by vertical migrators that return to

oxygenated waters night. That said, some species are known to permanently occupy the lower oxycline despite lower oxygen values there. For example, persistent (non-migrating) layers of several copepod species occur at about 2 – 8 μM (~0.2 to 0.8 kPa at 5 $^{\circ}C$) at the lower oxycline of the ETP and Arabian Sea OMZs where they are actively feeding and reproducing (Wishner et al., 1998, 2000, 2013). Some copepod species have life history stages that undergo diapause (a type of hibernation) and form layers, presumably lasting months, at these same low oxygen depths in OMZs around the world; these species are not feeding at depth and are probably inactive (Hidalgo et al., 2005; Wishner, 2013). Recent measurements for Eastern Tropical Pacific lower oxycline species reveal the greatest hypoxia tolerance reported for any species ($P_{crit} \sim 0.3$ kPa; Wishner et al., 2018). Interestingly, they display a reverse temperature effect where hypoxia tolerance is improved at higher temperatures despite higher oxygen demand. This trait is adaptive in the lower oxycline where temperature and oxygen are inversely correlated (Wishner et al., 2018).

Future research must address, with greater precision, the vertical and horizontal distribution and physiology of organisms, the mesoscale variability of oxygen and temperature, and the rate and magnitude of future changes in these parameters. These goals can be accomplished utilizing a greater diversity of techniques and new technologies including acoustics, camera systems, towed measurement systems and more precise net sampling. Hypoxia tolerance is species- and temperature-specific and can only be determined

through measured response of live animals to a range of oxygen partial pressures. There are as yet no proxies for simple estimation of hypoxia tolerance. However, a variety of metrics have been used, including P_{crit} , loss of equilibrium, anaerobic metabolite accumulation (e.g. lactate), and lethal concentrations (LC_{50}) at specified temperatures that provide useful measures of hypoxia tolerance. Modelling efforts, such as the Metabolic Index (Deutsch et al., 2015), may incorporate these metrics to assess metabolically available habitat across latitudinal and depth gradients.

8.1.5 References

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8.2 The significance of ocean deoxygenation for open ocean tunas and billfishes

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Summary

- Tunas and billfishes should be especially sensitive to low ambient oxygen conditions given their high metabolic rates as well as the large differences between their resting and maximum metabolic rates. Although there are many behavioural similarities among the different species, there are also clear and demonstrable differences in growth rates, maximum adult size, physiological abilities, low-oxygen tolerances, and preferred environmental conditions.
- Climate change is projected to alter oxygen concentrations throughout the open ocean, with most regions undergoing decreases due to a slowdown in ocean ventilation and a decline in surface oxygen solubility. Between 200 and 700 m depth (a vertical range including depths to which tunas and billfishes commonly descend to forage), the greatest and most certain decreases in oxygen concentrations are projected to occur in the North Pacific and much of the Southern Ocean, while the smallest and least certain changes are projected to occur within the tropical Pacific Ocean. Along a north-south line through the middle of the Pacific Ocean (160°W longitude), projected oxygen concentration decreases are most pronounced from 15°N to 50°N between 250 and 750 m depth and south of 50°S between 50 and 300 m depth.
- The depth at which oxygen concentrations drop below 3.5 ml L⁻¹ (a threshold hypoxic concentration for several tuna and billfish species including yellowfin and skipjack tunas, marlins, and sailfish) is projected to shoal throughout the global oceans, which may lead to widespread vertical habitat compression and changes in vertical movement patterns. Projected shoaling of the 3.5 ml L⁻¹ threshold depth is especially pronounced within subtropical and mid-latitude Pacific Ocean regions. Oxycline depth is also projected to shoal by over 150 m in these same Pacific Ocean regions and throughout much of the Southern Ocean. Species residing in the temperate North Pacific, such as swordfish and yellowfin, bigeye, Pacific bluefin, and albacore tunas, may therefore be impacted by future oxygen changes more greatly than other species, as projected decreases in oxygen concentrations are greatest within their present-day ranges.
- Changes in temperature and oxygen content have the potential to alter the distribution and catchability of tunas and billfishes in three dimensions. Because they are highly mobile, tunas and billfishes can exhibit complex shifts in their distributions in response to changing environmental conditions. Where surface layer temperatures become too warm, they may spend more time at depth (assuming oxygen concentrations are sufficient); where low-oxygen layers shoal or expand, they may spend more time near the oxygenated surface (assuming temperatures are not too warm), increasing their vulnerability to surface fishing gears. If no vertical refuge from unsuitable conditions is available, they may shift their distributions horizontally. Because temperature and hypoxia tolerances of tunas and billfishes are species-specific, any changes in temperature and oxygen content within the water column may modify competition among different species as their vertical and horizontal habitats shift in different ways, potentially altering established food web dynamics, ecosystem structures, and bycatch rates. Differential responses of prey species to changes in environmental conditions could also affect food web structures, the ability of tunas and billfishes to find food, age at first reproduction, and mean body sizes.

- Future changes in the distributions of tunas and billfishes are likely to complicate stock assessments and to have important socio-economic effects. As spatial habitats of targeted tuna and billfish species shift, the ability of fishery-dependent, catch per unit effort (CPUE)-based abundance indices to capture stock dynamics accurately will be compromised, unless CPUE-standardization methods can adapt. Where populations of targeted tuna and billfish species decrease in abundance or move away from traditional fishing grounds, fishers will have to spend more resources to locate and catch these species or reconfigure their gear to target new ones. Economic, political, and regulatory constraints can, however, hinder the ability of fishers to effectively adapt, particularly if species move across management boundaries. Smaller-scale fisheries in developing nations and fisheries relying on vessels with limited range and low technological capabilities are likely to be most vulnerable to shifts in range or migratory patterns.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen concentrations in current habitats may result in species-specific shifts in range and migratory patterns.	<ul style="list-style-type: none"> • Alters the ecological relationships between some tuna and billfish species and their prey. • Geographically redistributes catches and societal benefits from fisheries. • Complicates stock assessment and management, as changes in environmental conditions alter fish availability and subsequent fishery data-derived estimates of abundance.
Shallower oxyclines and hypoxic layers may result in species-specific changes in vertical movement patterns and compression of vertical habitat.	<ul style="list-style-type: none"> • Decreases vertical separation among tuna species, resulting in future increases in the frequency of competitive species interactions. • Alters coupling between predator and prey and thus foraging success. • Increases vulnerability to capture by surface fishing gears.
Changing oxygen concentrations may lead to changes in locations of spawning grounds.	<ul style="list-style-type: none"> • Alters spawning success and year class strength, which could modify the ability of tuna and billfish populations to withstand high rates of fishing mortality. • Albacore tuna in the South Pacific may be negatively affected by oxygen concentration decreases on their spawning grounds; other species may be either negatively or positively affected.
The temperate North Pacific Ocean is projected to undergo large decreases in oxygen content within the upper water column (above 1000 m).	<ul style="list-style-type: none"> • Species currently residing in this region (which include swordfish and yellowfin, bigeye, Pacific bluefin, and albacore tunas) are expected to experience the most dramatic decreases in oxygen concentrations and shoaling of hypoxic layers within their habitat.

8.2.1 Introduction

The effects of temperature and ambient oxygen on the behaviours and physiology of tunas (members of the family Scombridae, tribe Thunnini) and billfishes (members of the family Istiophoridae and Xiphiidae) (Figure 8.2.1) have been actively investigated over five decades (e.g. Barkley et al., 1978; Blackburn, 1965; Bushnell & Brill, 1991, 1992; Bushnell et al., 1990; Dizon, 1977; Dizon et al., 1974, 1976; Gooding et al., 1981; Sharp, 1975, 1978, 1983; Stevens, 1972; Stevens &

Fry, 1972; Sund et al., 1981). Variations in temperature and ambient oxygen with depth have long been known to influence species-specific vertical movement patterns which, in turn, affect vulnerability to different types of fishing gear (Figure 8.2.2). Understanding changes in the vulnerability of fish to specific gear types under different oceanographic conditions defined by temperature and oxygen content is important for standardizing catch-per-unit effort (CPUE) indices used in stock assessments and management decisions (e.g. Bigelow et al., 2002; Bigelow & Maunder, 2006; Brill,

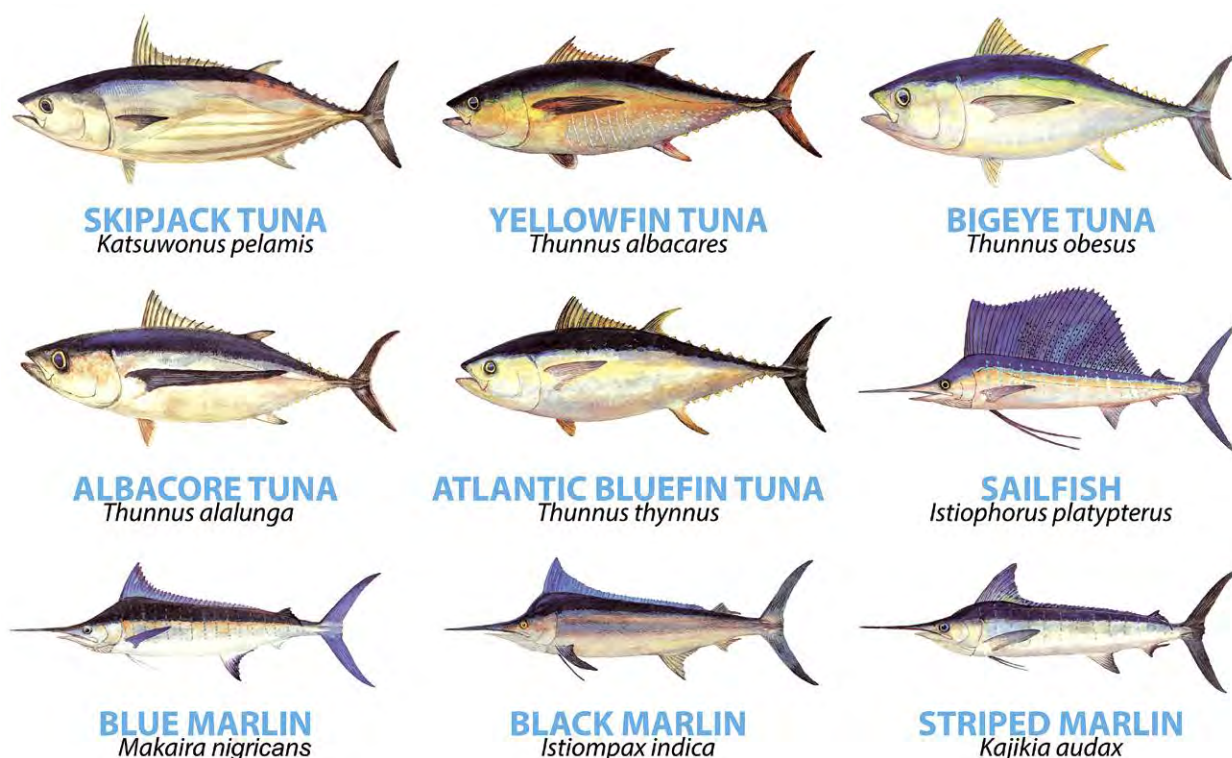


Figure 8.2.1 Tuna and billfish species. (Paintings by George Mattson).

1994; Hinton & Deriso, 1998; Hinton & Nakano, 1996; Sharp, 1995, 2001). Horizontal migrations away from traditional habitats and fishing grounds can also result from changes in environmental conditions (Block et al., 2011; Pinsky et al., 2013), with important downstream effects on the food security and economic development of regions dependent on tuna and billfish fisheries.

On theoretical grounds alone, tunas and billfishes should be especially sensitive to low oxygen concentrations given their unique anatomical and physiological characteristics, which permit high routine and maximum metabolic rates and large absolute metabolic scopes (e.g. Bernal et al., 2009; Brill & Bushnell, 1991, 2001; Brill & Chin Lai, 2016; Bushnell & Jones, 1994; Deutsch et al., 2015; Killen et al., 2016; Korsmeyer & Dewar, 2001; Stoffels, 2015; Wegner et al., 2013). Metabolic rates of billfishes have never been measured but are assumed to be similar to those of tunas because of the high degree of convergent evolution (Bernal et al., 2001, 2009; Wegner et al., 2013). The limiting effects of hypoxia in the marine environment appear, however, to be highly species-specific (e.g. Childress & Seibel, 1998; Deutsch et al., 2015; Seibel, 2011, 2013). An understanding of basic mechanistic principles (i.e. species-specific physiological abilities and tolerances and the resultant behavioural responses to environmental conditions)

is therefore needed to better predict species-specific movement patterns (e.g. Hobday et al., 2013; Horodysky et al., 2015, 2016; McKenzie et al., 2016). The ability to predict the effects of environmental conditions on the movements of large and economically important fish species is becoming even more critical as the effects of directional global climate change become increasingly apparent in the pelagic environment – including but not limited to increasing upper ocean temperature¹, expansion of oxygen minimum zones, and the resultant interaction of these two factors (e.g. Breitburg et al., 2018; Deutsch et al., 2015; Gilly et al., 2013; Mislan et al., 2017; Muhling et al., 2017a; Prince & Goodyear, 2006, 2007; Prince et al., 2010; Stramma et al., 2010a, 2012).

This section aims to summarize the main effects of projected changes in ocean oxygen content on species-specific tuna and billfish habitats and populations, as well as the resulting ecosystem and societal consequences. We begin by defining the tuna and billfish species of interest and comparing limits of hypoxia tolerance and

¹ The effects of ocean warming *per se* on the geographic distributions and vertical movement patterns of large pelagic tunas have been extensively investigated and the conclusions reviewed elsewhere (e.g. Gilman et al., 2016; Hobday et al., 2013, 2017; Lehodey et al., 2011) and therefore have not been extensively discussed here.

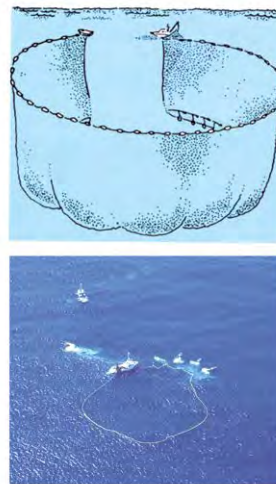
Table 8.2.1 Relative importance of the principal market species of tunas based on annual landings (FAO. Fishery Statistical Collections. Global Tuna Catches by Stock. 2014; Available at: <http://www.fao.org/fishery/statistics/tuna-catches/en>. Accessed: 30/12/2014.)

Species	Percentage of Total Tuna Catch
Skipjack tuna	58.1%
Yellowfin tuna	26.8%
Bigeye tuna	8.2%
Albacore	5.9%
Atlantic bluefin tuna	less than 1%
Pacific bluefin tuna	less than 1%
Southern bluefin tuna	less than 1%

resultant movement behaviours among these species. We then analyse projected changes in oxygen content within current habitat spaces and summarize projected oxygen-induced habitat suitability changes calculated from four different types of models. Lastly, we highlight the potential effects of these oxygen-induced habitat suitability changes on ecosystems and human society.

Throughout this section, we will discuss oxygen content and conditions in terms of either dissolved concentrations (units of ml L^{-1} or mg L^{-1}) or partial pressures (units of kPa), depending on the context. Oxygen content within the ocean has historically been expressed in terms of dissolved concentrations rather than partial pressures because unlike partial pressures, dissolved concentrations do not depend on temperature, salinity, or depth in the water column and are thus useful for mass balance calculations and numerical models. The driving force for molecular oxygen transfer (both from water to blood in the gills and from blood through tissues to the mitochondria) is, however, controlled by the partial pressure of oxygen (Hofmann et al., 2011). To characterize the oxygen environment experienced by

Purse Seine



Longline



Figure 8.2.2 Common types of fishing gear used to commercially capture tuna and billfish. (Conceptual drawings from Joseph et al. (1980). Left photograph © Jessica Farley. Right photograph © Alistair Hobday).

tunas and billfishes more completely, we therefore also report oxygen conditions in terms of partial pressures whenever possible. Because partial pressures depend on both dissolved oxygen concentrations and oxygen solubility (which in turn depends on temperature, salinity, and depth), we will avoid conversion to partial pressures when comparing results with historical thresholds or measurements expressed in dissolved concentration units and lacking simultaneous temperature, salinity, and depth data.

8.2.2 Definition of species group

Various species of billfish and tuna are discussed, but emphasis is placed on the seven principal market species of tunas (Table 8.2.1) both because of their importance and the availability of data. Tunas in aggregate support the world's largest fisheries with an economic value of ~US\$9 billion, landing $\sim 6.5 \times 10^6$



Figure 8.2.3 (A) Yellowfin tuna *Thunnus albacares* © Juniors Bildarchiw / Alamy stock photo; (B) Skipjack tuna *Katsuwonus pelamis* © Paulo Oliveira / Alamy stock photo.



Figure 8.2.4 Atlantic blue fin tuna (*Thunnus thynnus*) shoal © Paulo Oliveira / Alamy stock photo.

metric tons annually. The seven principal market species collectively account for ~66% of the global tuna landings (FAO, 2014; Guillotreau et al., 2017; Sumaila et al., 2007) (Table 8.2.1). Yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas (Figure 8.2.3) collectively account for ~85% of the landings of the seven principal market species. Albacore (*Thunnus alalunga*), bigeye (*Thunnus obesus*), and bluefin tunas collectively account for >10% of the landings, but the latter two have high economic value because they dominate the fresh fish (i.e. sashimi-grade) market (Guillotreau et al., 2017). Because of the especially high political profile of Atlantic (*Thunnus thynnus*) (Figure 8.2.4), Pacific (*Thunnus orientalis*), and Southern (*Thunnus maccoyii*) bluefin tunas (e.g. Safina, 2001), these three species have received significant scientific attention, especially with regard to the effects of climate change on their movements, distributions and spawning areas (e.g. Hazen et al., 2013; Kitagawa & Kimura, 2015; Muhling et al., 2015, 2017a, b). The aggregate landings of billfishes (~136 x 10³ metric tons in 2015) (FAO, 2017) are approximately three orders of magnitude less than



Figure 8.2.5 Swordfish (*Xiphias gladius*) © Paulo Oliveira / Alamy stock photo.

those of the primary market species of tunas, with swordfish (*Xiphias gladius*) (Figure 8.2.5) constituting most of the billfish catch. Other billfishes are, however, highly prized by recreational anglers because of their acrobatic ability and because some species (e.g. blue and black marlin, *Makaira nigricans* and *Istiompax indica*, respectively) achieve extraordinary body sizes.

Tunas and billfishes are highly mobile, top-level carnivores (though trophic level varies with age class) that live predominately in the energy-depauperate pelagic environment, where rates of primary productivity (per unit area) are approximately one-tenth of those in coastal areas (e.g. Antoine et al., 1996; Westberry et al., 2008) and where forage-species are highly aggregated (such as at fronts) and these aggregations are heterogeneously distributed (e.g. Lehodey et al., 1998; Polovina et al., 2001). Though several tuna species also inhabit coastal waters where productivity is higher overall, it is tunas' unique anatomical, biological, and physiological attributes (e.g. Block & Stevens, 2001; Brill, 1996; Brill & Hobday, 2017) that allow their now well-documented

Table 8.2.2 (From Lehodey et al. (2011)): Lower lethal oxygen levels for four of the seven principal market species of tunas based on the ratio of minimum speed needed to sustain hydrostatic equilibrium (i.e. to keep these negatively buoyant fish from sinking) (Magnuson, 1978; Magnuson & Weininger, 1978). Values are shown for a 50 cm and 75 cm skipjack, yellowfin, bigeye, and albacore tuna. Percentage saturation data for skipjack, yellowfin, and bigeye tunas were calculated using oxygen solubility in sea water at 25 °C and data for albacore using oxygen solubility in sea water at 15 °C.

	Fork length (cm)	Lower lethal oxygen levels		
		mg L ⁻¹	ml L ⁻¹	% saturation
Skipjack tuna	50	2.45	1.87	37
	75	2.83	2.16	43
Yellowfin tuna	50	1.49	1.14	23
	75	2.32	1.77	35
Bigeye tuna	50	0.52	0.40	8
	75	0.65	0.50	10
Albacore	50	1.67	1.23	21
	75	1.39	1.03	18

extraordinary growth and reproductive rates (Gaertner et al., 2008; Gaikov et al., 1980; Schaefer, 2001; Wild, 1986). These extraordinary growth and reproductive rates in turn permit simultaneous high rates of natural (Murphy & Sakagawa, 1977) and fisheries mortality. Less is known about the physiological abilities of billfishes because, in contrast to tunas (Farwell, 2001), they have never been maintained in shore-side facilities and therefore have never been available for laboratory

studies involving whole animals. There is, however, considerable evidence for rapid somatic and gonadal growth rates and high fecundity in billfishes (e.g. Hopper, 1990; Prince & Pulos, 1983).

Although there are many behavioural similarities among the principal market species of tunas, there are also clear and demonstrable species-specific differences in growth rates (Fromentin & Fonteneau, 2001; Murua et

Table 8.2.3 Summary of oxygen conditions encountered in present-day, species-specific tuna and billfish habitats. For simplicity, we assumed a constant, frequently-visited vertical range throughout each species' horizontal extent to delineate present-day, three-dimensional habitat. Species-specific horizontal ranges were taken directly from the IUCN Red List (IUCN, 2011, 2014), while depth ranges were taken from the IUCN Red List (IUCN, 2011, 2014) with six modifications as follows: (1) IUCN lists 10 m as the lower depth limit for longtail tuna, but the minimum depth interval for our analysis was 25 m depth, which is therefore the frequently-visited lower depth used here; (2) IUCN lists 2743 m as the absolute lower depth limit for Southern bluefin tuna, but we deemed 600 m to be a more reasonable frequently-visited lower depth based on tagging data (Patterson et al., 2008); (3) IUCN lists 50 m as the upper depth limit for Southern bluefin tuna, but there is evidence that they spend large amounts of time much closer to the surface (Patterson et al., 2008); we therefore used 0 m as the frequently-visited upper depth here; (4) IUCN lists 1500 m as the absolute lower depth limit for bigeye tuna but mention that they are mostly found above 500 m, which is therefore the frequently-visited lower depth used here; (5) IUCN lists 1000 m as the absolute lower depth limit for blue marlin but mention that they remain mostly within the upper 40 m, which is therefore the frequently-visited lower depth used here; (6) IUCN lists 2878 m as the absolute lower depth limit for swordfish but mention that its typical range is from the surface to 550 m, which is therefore the frequently-visited lower depth used here. Next, we computed present-day annual mean oxygen partial pressure (PO_2) values over the entire ocean using data from World Ocean Atlas 2013 (WOA, 2013) on a $1^\circ \times 1^\circ$ horizontal grid at 25-m depth intervals. From these gridded PO_2 values analysed over each species' assumed three-dimensional range, we then calculated the spatial means and standard deviations of minimum PO_2 values in the water column encountered by each species and the depths at which these minimum PO_2 values occur. Lastly, we also calculated the spatial mean and standard deviation of the oxycline depth within each species' assumed habitat. For reference, 1 kPa = 7.5 mmHg.

Common Name	Scientific Name	Frequented Depth Range (m)	Minimum PO_2 (kPa)	Depth of Minimum PO_2 (m)	Depth of Oxycline (m)
Skipjack tuna	<i>Katsuwonus pelamis</i>	0 - 260	12±6	236±37	117±94
Albacore tuna	<i>Thunnus alalunga</i>	0 - 600	9±5	533±107	128±95
Yellowfin tuna	<i>Thunnus albacares</i>	0 - 464	9±5	407±82	121±95
Blackfin tuna	<i>Thunnus atlanticus</i>	0 - 200	15±3	185±46	99±39
Southern bluefin tuna	<i>Thunnus maccoyii</i>	0 - 600	15±2	575±90	106±97
Bigeye tuna	<i>Thunnus obesus</i>	0 - 500	9±5	454±82	122±93
Pacific bluefin tuna	<i>Thunnus orientalis</i>	0 - 550	7±4	522±75	178±146
Atlantic bluefin tuna	<i>Thunnus thynnus</i>	0 - 500	13±4	460±109	80±31
Longtail tuna	<i>Thunnus tonggol</i>	0 - 25	21±1	20±8	77±50
Black marlin	<i>Istiompax indica</i>	0 - 100	17±5	98±12	127±102
Sailfish	<i>Istiophorus platypterus</i>	0 - 40	21±2	29±15	118±92
White marlin	<i>Kajikia albida</i>	0 - 150	16±4	146±18	88±42
Striped marlin	<i>Kajikia audax</i>	0 - 289	11±6	255±45	126±101
Blue marlin	<i>Makaira nigricans</i>	0 - 40	21±2	28±15	124±94
Shortbill spearfish	<i>Tetrapturus angustirostris</i>	0 - 200	12±6	196±13	133±104
Roundscale spearfish	<i>Tetrapturus georgii</i>	0 - 200	14±4	195±23	93±44
Longbill spearfish	<i>Tetrapturus pfluegeri</i>	0 - 240	13±5	218±30	93±44
Swordfish	<i>Xiphias gladius</i>	0 - 550	10±6	494±98	117±93

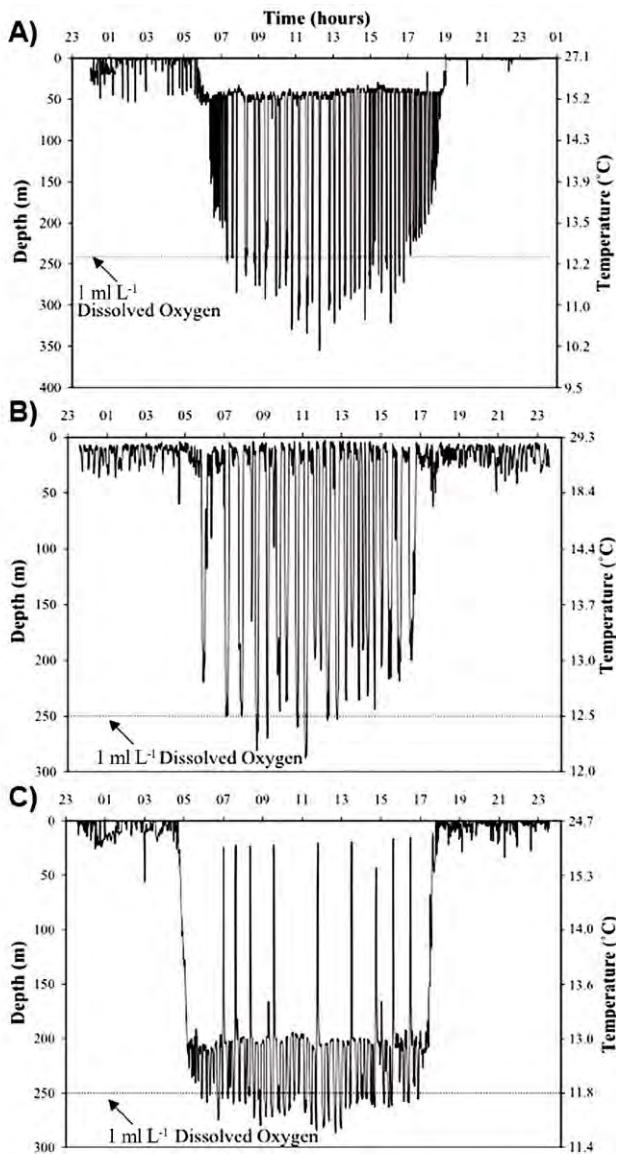


Figure 8.2.6 Representative daily vertical movement patterns of (A) skipjack tuna (66-cm), (B) yellowfin tuna (52-cm), (C) bigeye (88-cm) tunas. Tuna dive to deep depths during the day to forage for prey in the deep sound scattering layer. Skipjack and yellowfin tunas stay for short periods <15 minutes whereas bigeye tuna remain for much longer periods (>2 hours). The 1 ml L⁻¹ oxygen line indicates a tuna hypoxic threshold. At 12 °C, 1 ml L⁻¹ = 1.3 mg L⁻¹. Adapted from Schaefer et al. (2009a).

al., 2017), maximum adult size, physiological abilities, and tolerances of temperature and oxygen reductions that occur with increasing depth (e.g. Bernal et al., 2009, 2017; Blank et al., 2004; Galli et al., 2009, 2011; Lowe et al., 2000; Shiels et al., 1999, 2015; Sibert et al., 2006) (Tables 8.2.2 & 8.2.3). It is primarily differences in adult body size, thermoregulatory ability, and cardio-respiratory function that determine species-specific thermal and hypoxic tolerances, which in turn account for documented differences in daily vertical mobility patterns (Figures 8.2.6 & 8.2.7), spatial distributions

(Figure 8.2.8), migratory patterns (which take some species from temperate feeding areas to tropical spawning areas), and apparent resource partitioning (e.g. Bernal et al., 2009, 2017; Block et al., 2001; Boustany et al., 2010; Carey, 1990; Carey & Robison, 1981; Muhling et al., 2017b; Musyl et al., 2003; Schaefer & Fuller, 2002; Schaefer et al., 2009a; Wilson et al., 2005, 2015). These species-specific movements have been reviewed extensively for tunas, billfishes and sharks by Bernal et al. (2009), and more recently and specifically for tunas and billfishes by Horodysky et al. (2016) and Bernal et al. (2017). These reviews show that tuna species can be categorized into groups exhibiting distinct vertical movement behaviours (Figure 8.2.7). For example, the extensive vertical movements of bigeye tuna (and other species in Group 3, Figure 8.2.7) and their ability to remain at depth for extended periods are in stark contrast to the vertical movement patterns of skipjack and yellowfin tunas (Schaefer & Fuller, 2002, 2007, 2010; Schaefer et al., 2007, 2009a, b, 2014). The latter species also make forays to depths of ~500 m, but times spent in these cold and hypoxic waters are brief compared to time spent at depth by bigeye tuna, which include long periods (~45-60 minutes) below the thermocline (~500 m depth) during daylight hours, where water temperatures may be below 6 °C and oxygen levels ~1 mg L⁻¹ (~0.7 ml L⁻¹, assuming 5 °C) (Figure 8.2.6) (Evans et al., 2008; Fuller et al., 2015; Hanamoto, 1987; Musyl et al., 2003; Schaefer & Fuller, 2002, 2010). Albacore also exhibit vertical movements to depths below 400 m, but their vertical forays are generally brief (<32 minutes), like those of skipjack and yellowfin tunas (Childers et al., 2011; Williams et al., 2015). Tracking data show that albacore usually experience oxygen levels >5 mg L⁻¹ (> ~3.7 ml L⁻¹, assuming 15 °C) (Laurs & Lynn, 1977) and shipboard experiments on swimming showed that aerobic metabolism declined below this oxygen level, all of which imply that albacore are relatively hypoxia-intolerant compared to bigeye tuna (Bushnell et al., 1990; Graham et al., 1989). Similarly, although there are extensive records of the vertical movements of both Atlantic and Pacific bluefin tunas, these data do not allow inferences with respect to the hypoxia tolerance of these species. Both species do, however, make forays to depth where water temperature is ~10 °C and lower (Bauer et al., 2017; Block et al., 2005; Boustany et al., 2010; Kitagawa et al., 2004, 2007a, b; Patterson et al., 2008). Atlantic bluefin tuna reportedly reach depths of ~1000 m and water temperatures of ~5 °C (Block et al., 2001), but the accompanying oxygen levels at the depths and areas routinely occupied by Atlantic bluefin

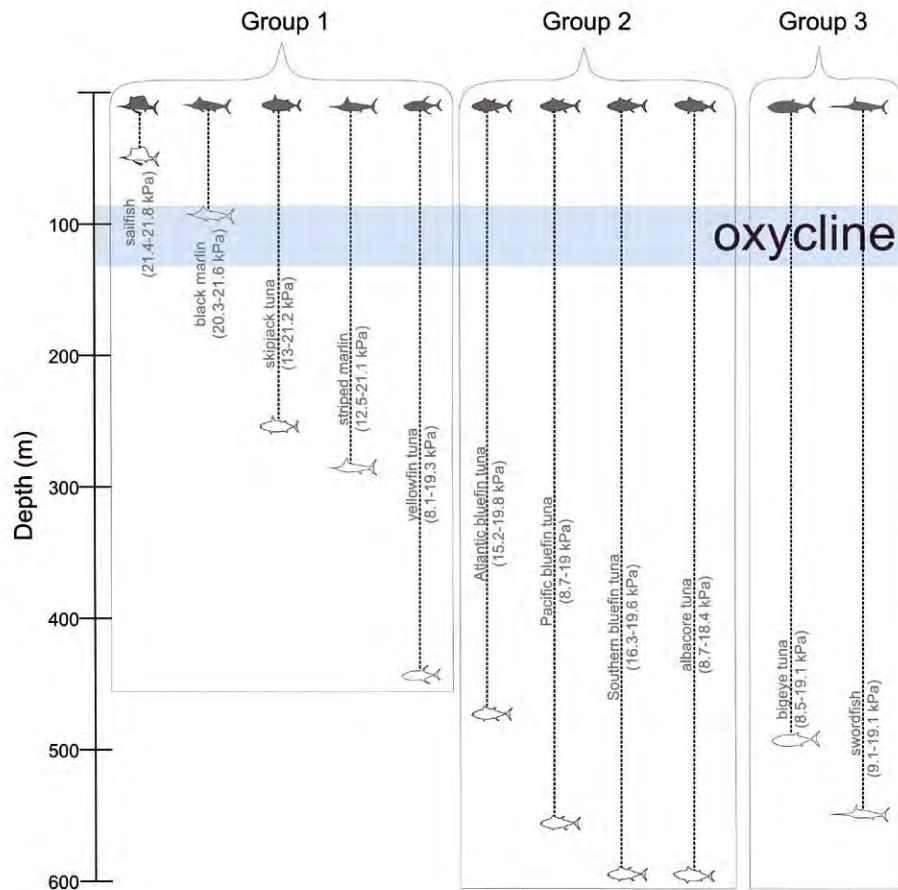


Figure 8.2.7 Schematic diagram of approximate depth ranges frequented by various tuna and billfish species. Depth ranges were taken and sometimes modified (see Table 8.2.3 caption) from the IUCN Red List (IUCN, 2011, 2014). Species are grouped by relative hypoxia tolerance, with Group 1 being least hypoxia-tolerant and Group 3 being most hypoxia-tolerant. The range (25th through 75th percentile) of oxygen partial pressure (PO_2) values encountered by each species within their assumed present-day habitats (delineated by the constant depth ranges listed in Table 8.2.3 and IUCN Red List horizontal distributions) is shown. Note that the amounts of time spent at depth by each species, as well as the environmental conditions within each species' range, differ. Drawing adapted from Figure 1 in Bernal et al. (2009).

tuna are unlikely to be limiting (Gilly et al., 2013; Teo & Boustany, 2016). Southern bluefin tuna can also spend periods of over 10 hours below ~400 m at temperatures <10 °C (Patterson et al., 2008), but oxygen levels in these same areas are relatively high (Mislán et al., 2017).

Tracking studies employing sonic telemetry and electronic data recording tags have shown that billfishes likewise display species-specific vertical movement patterns. Marlins and sailfishes (*Istiophorus platypterus*) (Figure 8.2.9) largely remain in the uniform temperature surface layer, although like skipjack and yellowfin tunas, they do make brief descents below the thermocline (Block et al., 1993; Brill et al., 1993; Holland et al., 1990; Hoolihan et al., 2005; Horodysky et al., 2007; Pepperell & Davis, 1999; Pohlot & Ehrhardt, 2017; Prince & Goodyear, 2006, 2007; Prince et al., 2010). Their vertical movements do, however, appear

to be strongly constrained to water with oxygen concentrations >3.5 ml L⁻¹ (Braun et al., 2015). In contrast, swordfish tracked in the Pacific and Atlantic Oceans and Mediterranean Sea have been shown to regularly descend and stay for up to eight hours below 550-600 m, where temperatures are ~5 °C and oxygen levels are below ~1.4 mg L⁻¹ (~1 ml L⁻¹, assuming 5 °C) (Figure 8.2.7) (Abascal et al., 2010; Canese et al., 2008; Carey, 1990; Carey & Robison, 1981; Dewar et al., 2011; Evans et al., 2014; Sepulveda et al., 2010; Takahashi et al., 2003). This result is congruent with the vertical movement patterns of bigeye tuna described above. The maximum depths reached by bigeye tuna and swordfish, and the concomitant reductions in temperature and low ambient oxygen, obviously imply similarly extraordinary physiological tolerances of both species; some convergent evolution in cardiac function between the two species has indeed been confirmed (Galli et al., 2009).

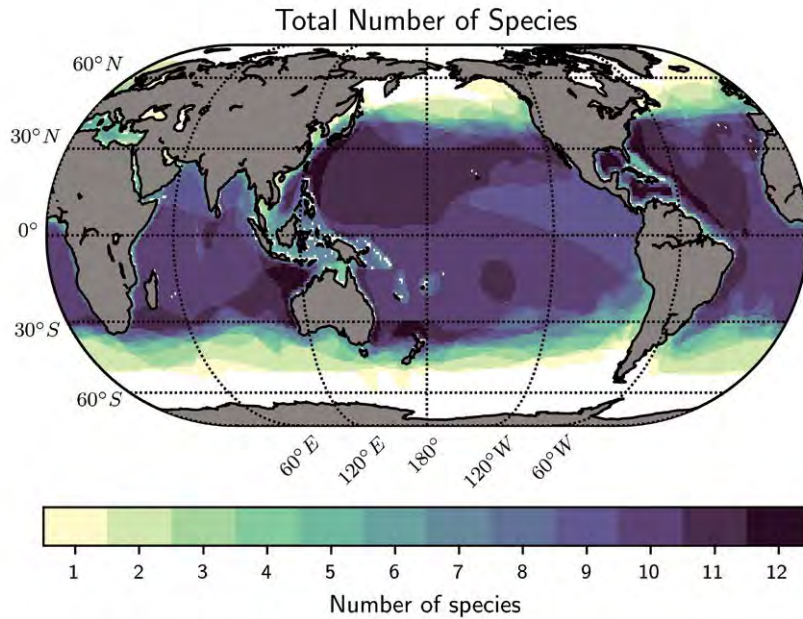


Figure 8.2.8 Global distribution of the number of species of tuna and billfish based on horizontal range data from the IUCN Red List (IUCN, 2011, 2014).

8.2.3 Trends and impacts

Climate change is projected to alter oxygen concentrations throughout the ocean, with most regions undergoing projected decreases owing to a slowdown in ocean ventilation and a decline in surface oxygen solubility (e.g. Bopp et al., 2013; Cabré et al., 2015; Cocco et al., 2013; Frölicher et al., 2009; Keeling et al., 2010). Agreement among models over how oxygen concentrations will change is greatest in the North Pacific and much of the Southern Ocean, and lowest in the tropical Pacific (Bopp et al., 2013; Cabré et al., 2015), though observations in the latter region indicate that oxygen concentrations have been decreasing there over the last several decades (Czeschel et al., 2012; Helm et al., 2011; Ito et al., 2017; Schmidtko et al., 2017; Stramma et al., 2008, 2010a, b).



Figure 8.2.9 Sailfin (*Istiophorus platypterus*) feeding on shoal of sardines © Nature Picture Library / Alamy stock photo.

8.2.3.1 Projecting oxygen changes in present-day tuna and billfish habitats

Output from Earth System Models included in the Coupled Model Intercomparison Project 5 (CMIP5) (Taylor et al., 2012) was used to project changes in global oceanic oxygen content set to occur by the end of the 21st century. These models, which simulate physical, chemical and biological processes, are run into the future under various plausible greenhouse gas emissions scenarios. Model output from years 2071–2100 within the RCP8.5 scenario, which represents a “business-as-usual” situation in which climate change goes unmitigated were utilized. To simulate present-day conditions, output from years 1971–2000 within the historical scenario was used, which is forced with historically observed atmospheric CO₂ emissions and concentrations. To calculate projected future changes, multi-model mean simulated differences between the RCP8.5 and historical scenarios were computed. The six models included here were CESM1-BGC (Gent et al., 2011; Lindsay et al., 2014), GFDL-ESM2G, GFDL-ESM2M (Dunne et al., 2012, 2013), HadGEM2-ES (Collins et al., 2011; Jones et al., 2011; Palmer & Totterdell, 2001), IPSL-CM5A-LR (Dufresne et al., 2013), and MPI-ESM-LR (Giorgetta et al., 2013; Ilyina et al., 2013).

Average oxygen concentrations between 200 and 700 m depth, where many tuna and billfish species forage, are projected to decrease throughout the mid- and

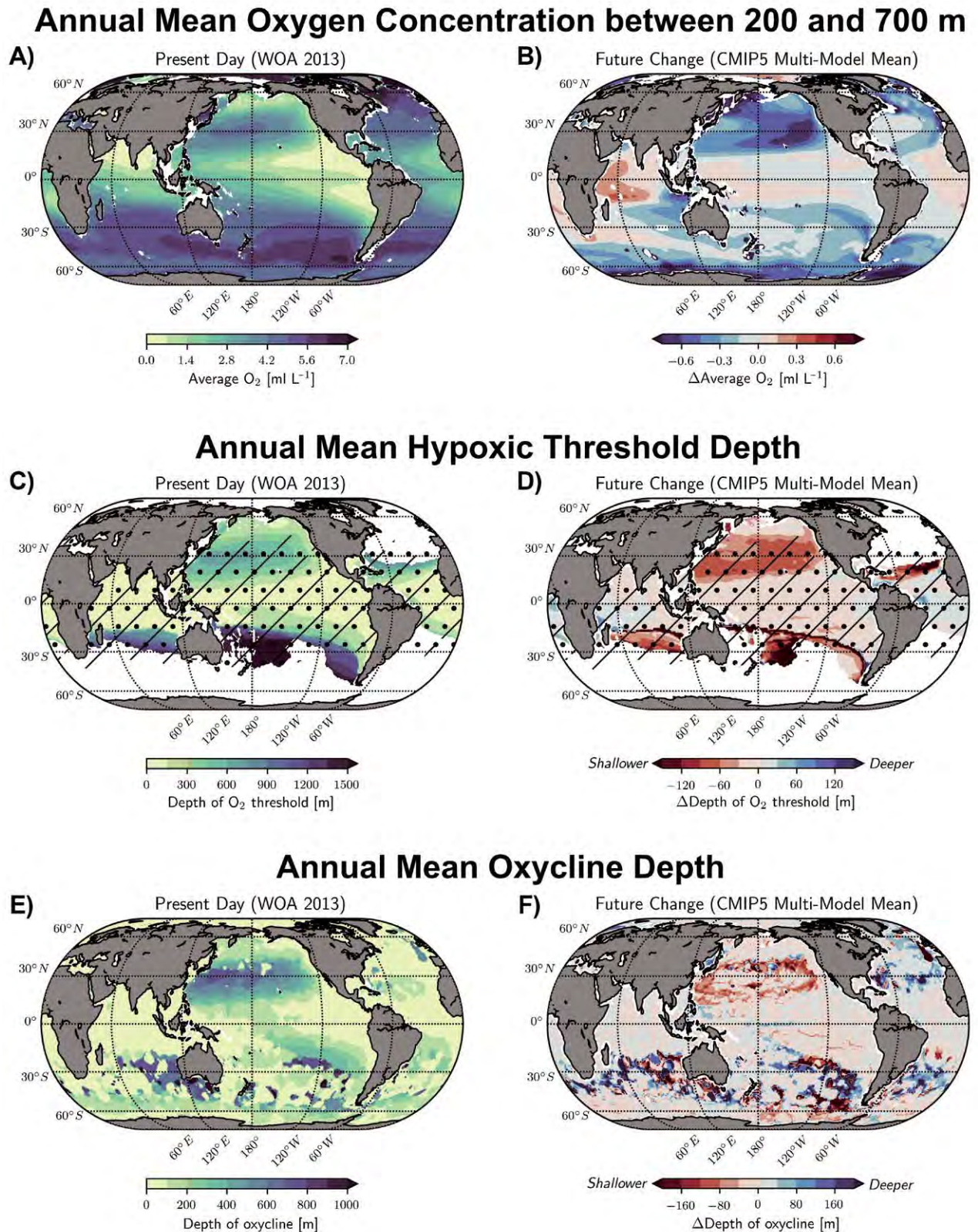


Figure 8.2.10 Historical and projected changes in annual mean (A-B) average oxygen concentrations between 200 and 700 m, (C-D) threshold hypoxic depths (where oxygen concentrations decrease below 3.5 ml L⁻¹), and (E-F) upper oxyclyne depths (lower row). Historical oxygen data are from WOA 2013. Projected changes (RCP8.5 scenario, 2071–2100 minus 1971–2000) are from six Earth System Models included in the Coupled Model Intercomparison Project Phase 5 (CMIP5), interpolated onto the same grid as WOA 2013 (1° × 1° horizontal grid with 25-m depth intervals). Hatching and stippling denote skipjack and yellowfin tuna habitat, respectively (IUCN, 2011, 2014). Threshold hypoxic and upper oxyclyne depths are shallowest in tropical regions and deepest in temperate regions. They are projected to be shallower in the North and South Pacific and the Southern Indian Ocean by 2100.

high-latitudes (Figure 8.2.10A-B). The greatest and most coherent decreases are projected to occur in the eastern North Pacific Ocean (Figure 8.2.10A-B), which already has lower mean oxygen concentrations compared to the western half of the basin (Figure 8.2.10A). Within the eastern North Pacific between 20–40°N, average oxygen concentrations between 200–700 m depth are projected to decrease by as much as 0.6 ml L⁻¹ from 1971–2000 to 2071–2100 (Figure 8.2.10B). The depth at which oxygen concentrations drop to 3.5 ml L⁻¹ (a threshold hypoxic concentration for several species of tuna and billfish including yellowfin and skipjack tunas, marlins, and sailfish) is also projected to shoal throughout most of the global ocean, reducing available oxygenated vertical habitat space for many species (Figure 8.2.10C-D). By 2071–2100, projected shoaling of the 3.5 ml L⁻¹ oxygen level is greatest in the North Pacific and parts of the Southern Ocean, moving upward by 60–100 m from a historical average of about 450–600 m depth in the former and by over 150 m from a historical average of >1,000 m depth in the latter. Projected changes in oxycline depth are spatially similar to those of the 3.5 ml L⁻¹ hypoxic depth, with a predicted shoaling of

over 150 m in some places within the North Pacific and Southern Oceans (Figure 8.2.10E-F). Along 160°W in the North Pacific, the largest projected decreases in oxygen concentration (between 0.8–1 ml L⁻¹) are centred around ~450 m depth, with the greatest potential impacts on swordfish and yellowfin, bigeye, Pacific bluefin, and albacore tunas residing in the area (Figure 8.2.11). Oxygen concentrations are projected to decrease greatly throughout most of the present-day range of Pacific bluefin tuna in particular. Comparisons between current and future oxygen conditions experienced by Pacific bluefin tuna within their present-day habitats (based on depth limits listed in Table 8.2.3) further support the notion that this species will likely experience some of the largest decreases in oxygen content, assuming that they maintain their present-day range (Figure 8.2.12).

It is important to note here (specifically, in the discussion of subsection 8.2.3.1 and in generating Table 8.2.3, Figure 8.2.7, Figure 8.2.11 and Figure 8.2.12) that all species-specific, present-day habitats are assumed to be rectangular boxes. In other words, we apply a single static, oft-frequented depth range (listed in Table 8.2.3)

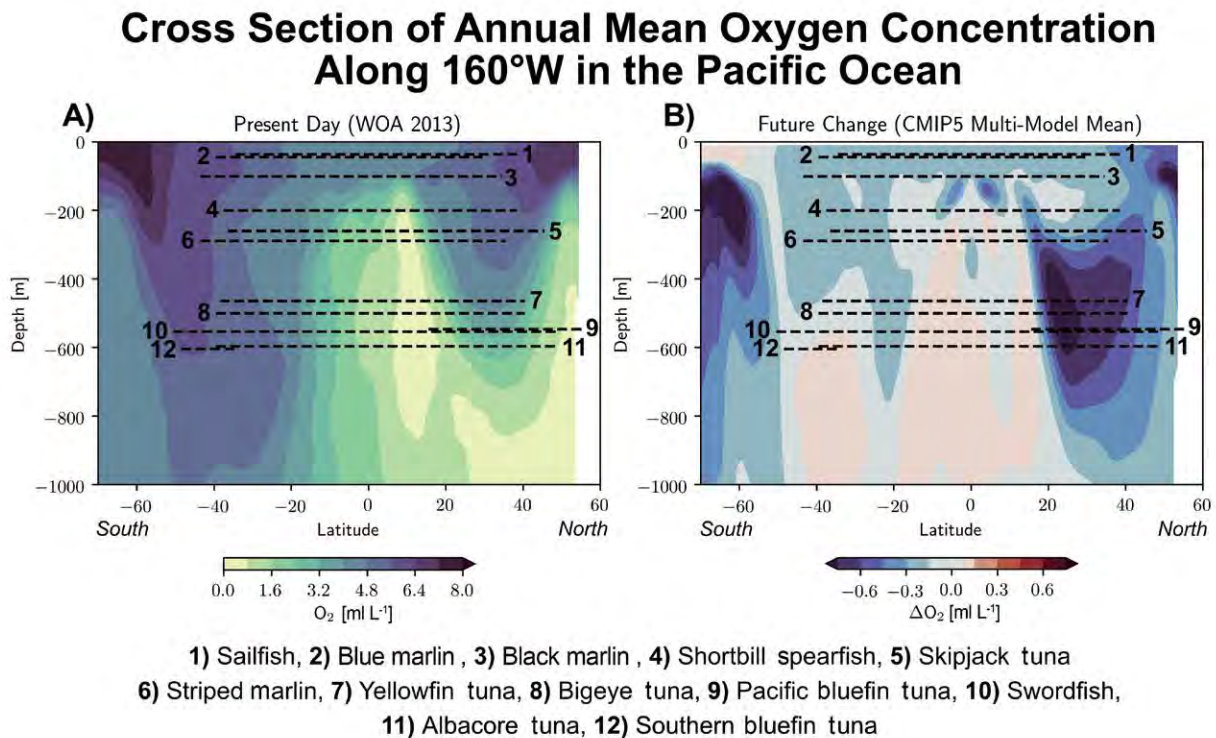


Figure 8.2.11 (A) Historical and (B) projected changes in annual mean oxygen concentrations along 160°W in the Pacific. Each species' present-day, frequently-visited lower depth range (as described in the caption of Table 8.2.3) is plotted across its latitudinal extent at this longitude. Historical oxygen data are from WOA 2013. Projected changes (RCP8.5 scenario, 2071–2100 minus 1971–2000) are from six Earth System Models included in CMIP5, interpolated onto the same grid as WOA 2013. Oxygen concentrations are the lowest in the tropics. The greatest decreases in oxygen concentrations by 2100 are projected to occur at temperate latitudes within the depth ranges of various tuna and billfish species.

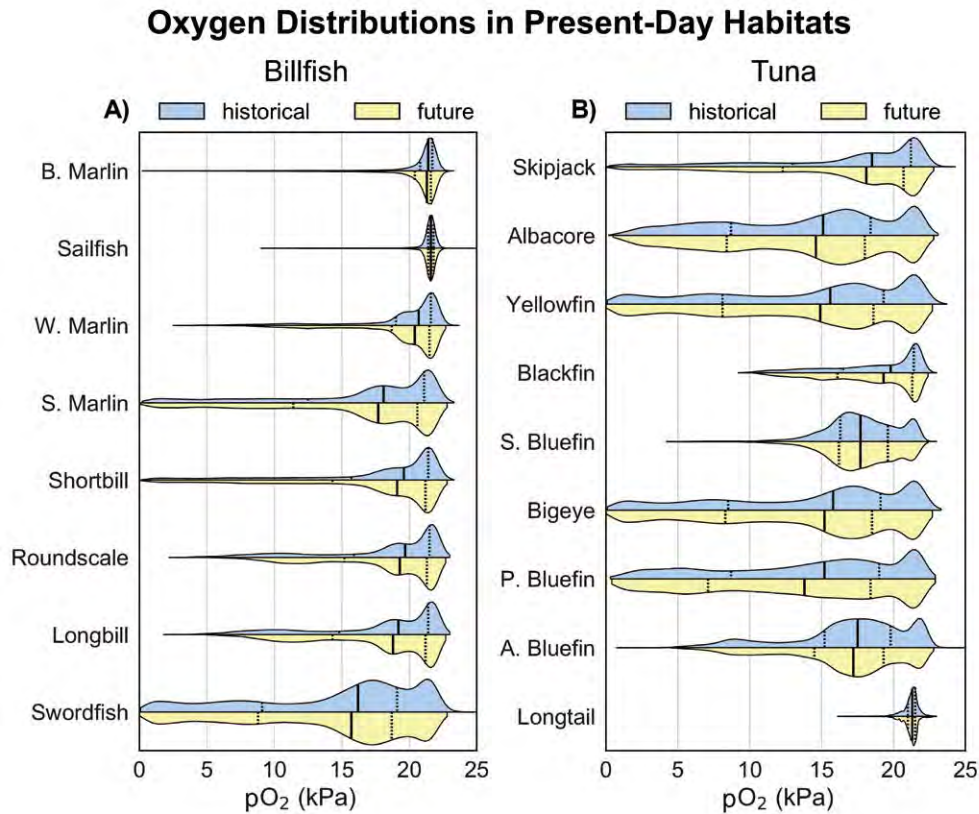


Figure 8.2.12 Historical and projected oxygen distributions encountered in present-day, species-specific (A) billfish and (B) tuna habitats. For simplicity, we assumed a constant, frequently-visited vertical range throughout each species' horizontal extent to delineate present-day, three-dimensional habitat. Species-specific horizontal ranges were taken directly from the IUCN Red List (IUCN, 2011, 2014), while depth ranges were taken from the IUCN Red List (IUCN, 2011, 2014) with six modifications, as detailed in the caption of Table 8.2.3. Historical oxygen partial pressure (PO_2) data are from WOA 2013. Future PO_2 projections were generated by adding CMIP5-modelled changes (RCP8.5 scenario, 2071–2100 minus 1971–2000) to WOA 2013 historical values. The two vertical dashed black lines within each distribution curve indicate the 25th and 75th percentiles of PO_2 encountered (as listed for each species in Figure 8.2.7), while the vertical solid black line indicates the 50th percentile. Oxygen partial pressures encountered vary greatly among the different species. Oxygen pressures are projected to decrease in the habitats of most tuna and billfish species by 2100.

over each species' horizontal habitat to represent its three-dimensional distribution (using data from IUCN, 2011, 2014 with minor modifications). In reality, each species-specific depth range (as well as the amount of time spent at each depth) varies greatly over space and time (e.g. Barkley et al., 1978; Block et al., 2001; Schaefer & Fuller, 2002, 2007, 2010; Schaefer et al., 2009a, b, 2014; Wilson et al., 2005, 2015). This is because temperature and oxygen levels also exhibit large spatio-temporal variabilities, and vertical movements are constrained by temperature and oxygen levels themselves rather than depth *per se* (Bernal et al., 2017; Prince et al., 2010). There are, however, currently not enough data to properly resolve the spatial and temporal variations of each species' vertical movements over its entire horizontal range. For simplicity, we therefore choose a spatio-temporally constant, oft-frequented depth range throughout each species' horizontal distribution to define its present-day three-dimensional habitat. Without more and better standardized data,

it is also difficult to distinguish between the absolute maximum depth to which each species can descend, the deepest average descent, and the depth above which they spend the majority of their time. Within these constraints, we attempt to define a reasonable depth range that each species frequently occupies, based on IUCN data and results from tagging studies (Table 8.2.3). We acknowledge, however, that there may be minor inconsistencies among species in how the depth range most frequently occupied is defined.

8.2.3.2 Projecting oxygen-induced habitat suitability changes with statistical models

One of the most straightforward and common approaches for projecting future habitat changes is to use statistical methods to relate present-day species distributions to observed environmental conditions, and to then apply these relationships to projections of future environmental conditions (Coro et al., 2016; Hartog et



Figure 8.2.13 Bigeye tuna (*Thunnus obesus*) © WaterFrame / Alamy stock photo.

al., 2011; Hazen et al., 2013; Muhling et al., 2015; Peck et al., 2016; Stock et al., 2011). The main advantages of these models are that they allow for multivariate, non-linear relationships among variables; require relatively few input variables; and are conceptually simple as they require no explicit parametrizations of physiology, behaviour, or ecosystem dynamics (Dormann et al., 2012; Peck et al., 2016). Because key mechanistic processes are not included in the models, however, present-day empirical relationships are assumed to hold into the future, which may not be a valid assumption in all cases (Dormann et al., 2012; Horodysky et al., 2015, 2016; Peck et al., 2016). Most statistical models also rely more on temperature than oxygen, due to the greater availability of temperature data (both environmental and from electronic tracks), and the abundance of studies showing the importance of thermal limits in determining the distributions of tuna and billfish species. Muhling et al. (2017a) were, however, able to use temperature and chlorophyll measurements at the surface, temperature and oxygen concentrations at 100 m depth, and concurrent data on the presence or absence of adult Atlantic bluefin tuna to create a statistical model capable of predicting this species' distributions in the North Atlantic Ocean. They found that oxygen concentration at 100 m depth was the most important predictor of habitat suitability out of the four variables considered. Application of the model to future projections from GFDL-ESM2M (one of the CMIP5 Earth System Models, using the RCP8.5 scenario and comparing 1971–2000 to 2071–2100) showed a general loss of habitat with climate change, especially south of $\sim 40^{\circ}\text{N}$ as well as in the region south of Greenland, which was in agreement with projections from an oxygen balance model (as discussed in subsection 8.2.3.4) applied to the same GFDL-ESM2M projections.

8.2.3.3 projecting oxygen-induced habitat suitability changes with a P_{50} depth-based trait analysis model

Blood oxygen affinity (quantified by the partial pressure of oxygen required to bring blood oxygen content to 50% of the maximum oxygen carrying capacity, and commonly referred to as the ' P_{50} ') can predict hypoxia tolerance in a range of fish species (Farrell & Richards, 2009; Mandic et al., 2009; Wells, 2009). Hypoxia-tolerant species (including bigeye tuna) have blood with high oxygen affinity (i.e. low P_{50}) (Lowe et al., 2000). While this high blood oxygen affinity allows species like bigeye (Figure 8.2.13) to be more tolerant of low ambient oxygen conditions, it may also lead to slower rates of oxygen delivery if blood oxygen affinity remains too high at the tissues (Yang et al., 1992). Blood oxygen affinity at tissues also depends, however, on whether arterial blood undergoes temperature changes as it passes through gills (i.e. 'open system' temperature changes where the blood is free to exchange oxygen and CO_2 with the respiratory medium) or as it passes through the vascular countercurrent heat exchangers possessed by tunas (i.e. 'closed system' temperature changes where blood is not free to exchange oxygen and CO_2 with the respiratory medium) (Brill & Bushnell, 1991, 2006; Carey & Gibson, 1977, 1983; Clark et al., 2008; Jones et al., 1986; Lowe et al., 2000; Rossi-Fanellai & Antonie, 1960; Stevens, 1982; Stevens & Carey, 1981). These countercurrent heat exchangers allow tunas to maintain muscle temperatures significantly above ambient water temperatures and can therefore help lower blood oxygen affinity at muscles, where oxygen off-loading and delivery is required. Bigeye tuna are particularly adept at maintaining elevated muscle temperatures during deep descents (into water as cold as $\sim 5^{\circ}\text{C}$) by controlling the efficacy of their vascular countercurrent heat exchangers before making rapid ascents back to the warm uniform temperature surface layer to get a 'gulp' of heat in a way analogous to a marine mammal returning to the surface to get a breath (Boye et al., 2009; Holland & Sibert, 1994). At depth where muscle temperatures are significantly above ambient temperature, arterial blood in bigeye tuna is thus subjected to 'closed system' temperature changes. The net result is large decreases in blood oxygen affinity from high (low P_{50}) to low (high P_{50}) values that are more characteristic of less hypoxia-tolerant species such as skipjack, yellowfin, and bluefin tunas (Brill & Bushnell, 1991, 2006; Clark et al., 2008). These large decreases in blood oxygen affinity (increases in P_{50}) as the blood

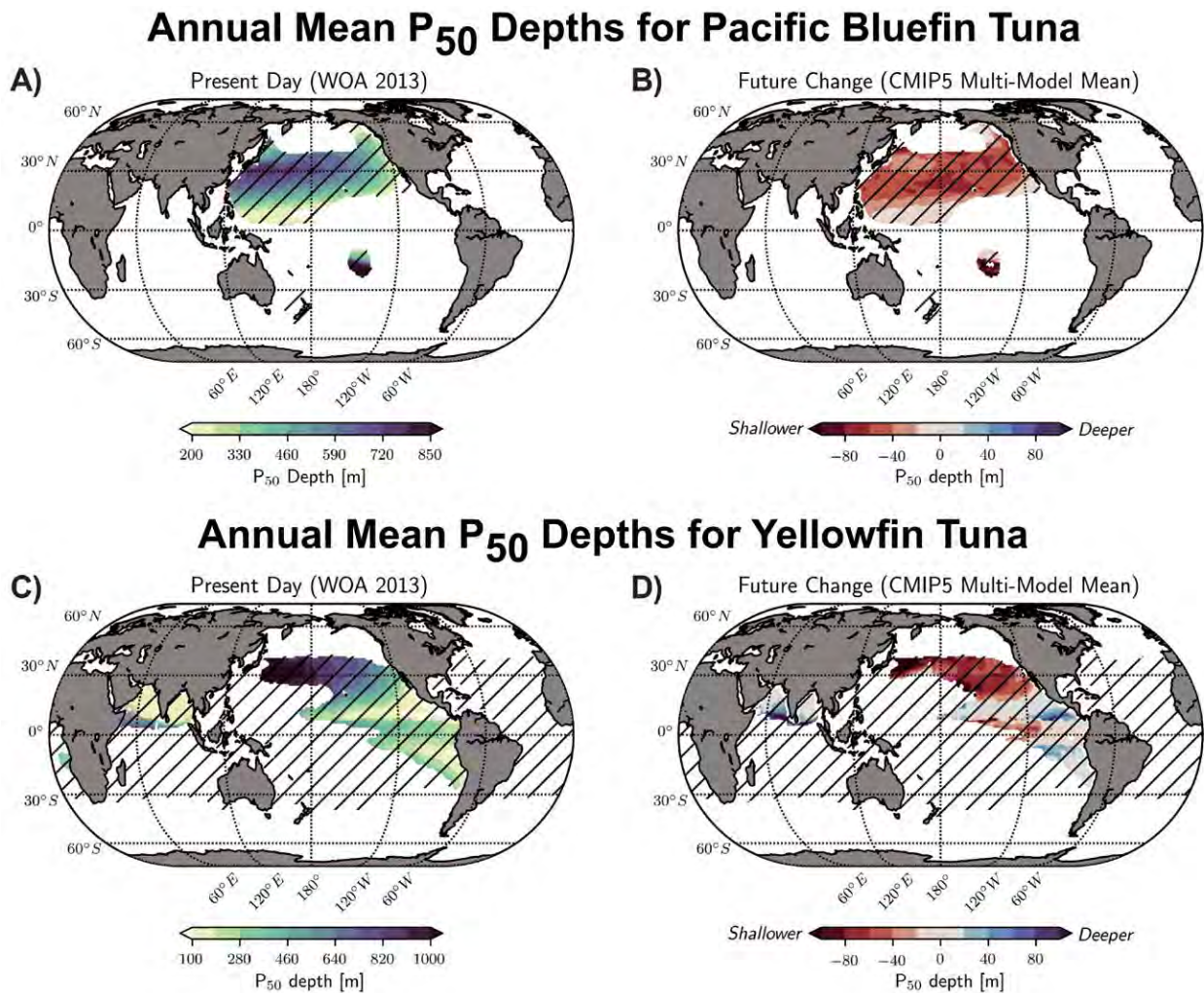


Figure 8.2.14 Historical and projected changes in P_{50} depths within the present-day habitats of Pacific bluefin tuna (A-B) and yellowfin tuna (C-D). P_{50} depth is the shallowest depth at which blood is <50% oxygenated. Historical data are from WOA 2013. Projected changes (RCP8.5 scenario, 2071–2100 minus 1971–2000) are from six Earth System Models included in CMIP5, interpolated onto the same grid as WOA 2013. White regions of the ocean do not contain P_{50} depths for the given species. Hatching denotes the given species' habitat, based on IUCN geographic ranges (IUCN, 2011, 2014). P_{50} depths in Pacific bluefin tuna habitats are projected to be universally shallower in 100 years. Changes in P_{50} depths within yellowfin tuna habitats are projected to vary spatially.

travels from gills to warm tissues ensures adequate rates of oxygen delivery in the swimming muscles of bigeye tuna. Studies quantifying the oxygen affinity of isolated haemoglobin (Sharp, 1975, 1983) and whole blood (Cech et al., 1984) from albacore all suggest that this species is relatively hypoxia-intolerant (although more hypoxia-tolerant than yellowfin or skipjack tunas).

P_{50} depth is the shallowest depth in the water column where the partial pressure of oxygen (PO_2) drops below the minimum value required for blood to reach its P_{50} value. It thus denotes the depth below which oxygen becomes limiting and serves as a mechanistic way of estimating species-specific vertical habitat range in regions where hypoxic conditions exist at depths reachable by tunas (Mislán et al., 2016). The spatial

distribution and extent of P_{50} depths vary greatly among tuna species. For example, the vertical movements of more hypoxia-tolerant species (e.g. bigeye tuna) are constrained by P_{50} depth over smaller geographic areas than less hypoxia-tolerant species (e.g. yellowfin or Pacific bluefin tunas) (Mislán et al., 2017) (Figure 8.2.14). The shallowest P_{50} depths are in the tropics, occurring above 100 m in some areas for the least hypoxia-tolerant tuna species, including yellowfin tuna (Figure 8.2.14) (Mislán et al., 2017).

By the end of the 21st century, P_{50} depths of multiple tuna species are projected (under the RCP8.5 scenario, using the six CMIP5 models listed in subsection 8.2.3.1) to shoal in temperate regions, and to either shoal or deepen within the tropics depending on the specific

location. Multi-species P_{50} depths are projected to become shallower in the subtropical and mid-latitude North Pacific Ocean in particular (Figure 8.2.14), where the greatest decreases in oxygen content are projected to occur (Bopp et al., 2013; Mislán et al., 2017). For Pacific bluefin tuna, whose geographic range is almost entirely in the North Pacific, P_{50} depths are projected to be shallower throughout its range (Figure 8.2.14). Yellowfin tuna, on the other hand, have a broader geographic range than Pacific bluefin tuna, with populations in the temperate and tropical Pacific as well as the Arabian Sea and the Bay of Bengal. The P_{50} depths of yellowfin tuna are very shallow in the tropics but are projected to become deeper by 2100 in the areas where they are currently shallowest (i.e. between 5°N-20°N and 5°S-20°S in the eastern Pacific) (Figure 8.2.14). In other regions within the eastern Pacific (poleward of 20°N and within 5° of the equator), P_{50} depths of yellowfin tuna are projected to be shallower by 2100. These bidirectional changes could potentially alter the vertical range of yellowfin tuna over large geographic areas. Projections of oxygen levels in the eastern Pacific within 20° of the equator are not considered to be robust (Bopp et al., 2013; Cabre et al., 2015), however, and may change as models are improved. Changes in spawning regions are another factor that needs to be considered. P_{50} depths of southern bluefin tuna are projected to be 80 to 600 m shallower by 2100 in their main spawning region off the west coast of Australia (Mislán et al., 2017). P_{50} depths are likely key in determining billfish habitat use as well, but physiological parameters needed to calculate species-specific P_{50} depths for billfish are not available. Based on their similar vertical ranges and hypoxic tolerances (Figure 8.2.7), however, we hypothesize that future changes in P_{50} depths of marlin will be closer to those of yellowfin tuna and those of swordfish will be closer to those of bigeye tuna. In summary, P_{50} depth analysis is important for understanding how climate change-driven alterations in oxygen levels within the pelagic environment will impact individual species with different hypoxic tolerances.

8.2.3.4 Projecting oxygen-induced habitat suitability changes with metabolic oxygen balance models

The oxygen balance model used to evaluate future changes in Atlantic bluefin tuna habitat by Muhling et al. (2017a) includes three sub-components: an oxygen demand model, an oxygen supply model, and a cardiac transport model. Overall 'oxygen balance' is calculated

by subtracting metabolic oxygen demand from estimates of oxygen supply, both of which are influenced by water temperature, the amount of dissolved oxygen in the water, and fish swimming speed. All three sub-models were parameterized using published studies on captive tunas (yellowfin, skipjack and bluefin tunas). Muhling et al. (2017a) show a case study for Atlantic bluefin tuna, but the oxygen balance model has also been modified for yellowfin tuna. Projections for both species groups (i.e. combined bluefin tunas, yellowfin tuna) are thus shown here. As experimental data are from juvenile fish (due to difficulties keeping adults in captivity), the oxygen balance models may be overly conservative at cooler temperatures (Graham & Dickson, 2001).

Metabolic oxygen demand (MO_2) with water temperature and swimming speed is estimated from Generalized Additive Models (GAMs) trained on experimental data (Blank et al., 2007; Brill, 1987; Clark et al., 2010; Dewar & Graham, 1994). Yellowfin tuna MO_2 is assumed to be constant when temperature is <15 °C, as no measurements are available from lower temperatures. Bluefin tuna MO_2 increases when temperatures fall below ~15 °C, but there is no evidence that tuna species predominately caught in tropical and subtropical areas (e.g. skipjack and yellowfin tunas) respond similarly. The oxygen supply model is adapted from equations reported by Bushnell and Brill (1991). The volume of water passing through the gills (ventilation volume) depends on swimming speed and mouth gape, with the latter increasing under hypoxic conditions. Oxygen delivery is then dependent on ambient dissolved oxygen concentration, ventilation volume, and percentage utilization (i.e. the percentage of the oxygen content in the inhaled water stream removed by the cardio-respiratory system). Delivery of oxygen to tissues is dependent on cardiac output, and the difference in oxygen content of arterial and venous blood (Brill & Bushnell, 2001). These equations are parameterized by combining results from Blank et al. (2002, 2004), Korsmeyer et al. (1997 a, b) and Clark et al. (2008, 2013) into a multivariate exponential relationship, where both temperature and swimming speed determine heart rate, and thus cardiac output (assuming the volume of blood pumped per heartbeat remains constant, which is true in tunas; Brill & Bushnell, 2001). Oxygen balance (i.e. surplus or deficit) is determined by subtracting metabolic demand from the lesser of oxygen delivery through the gills, and oxygen delivery via the circulatory system.

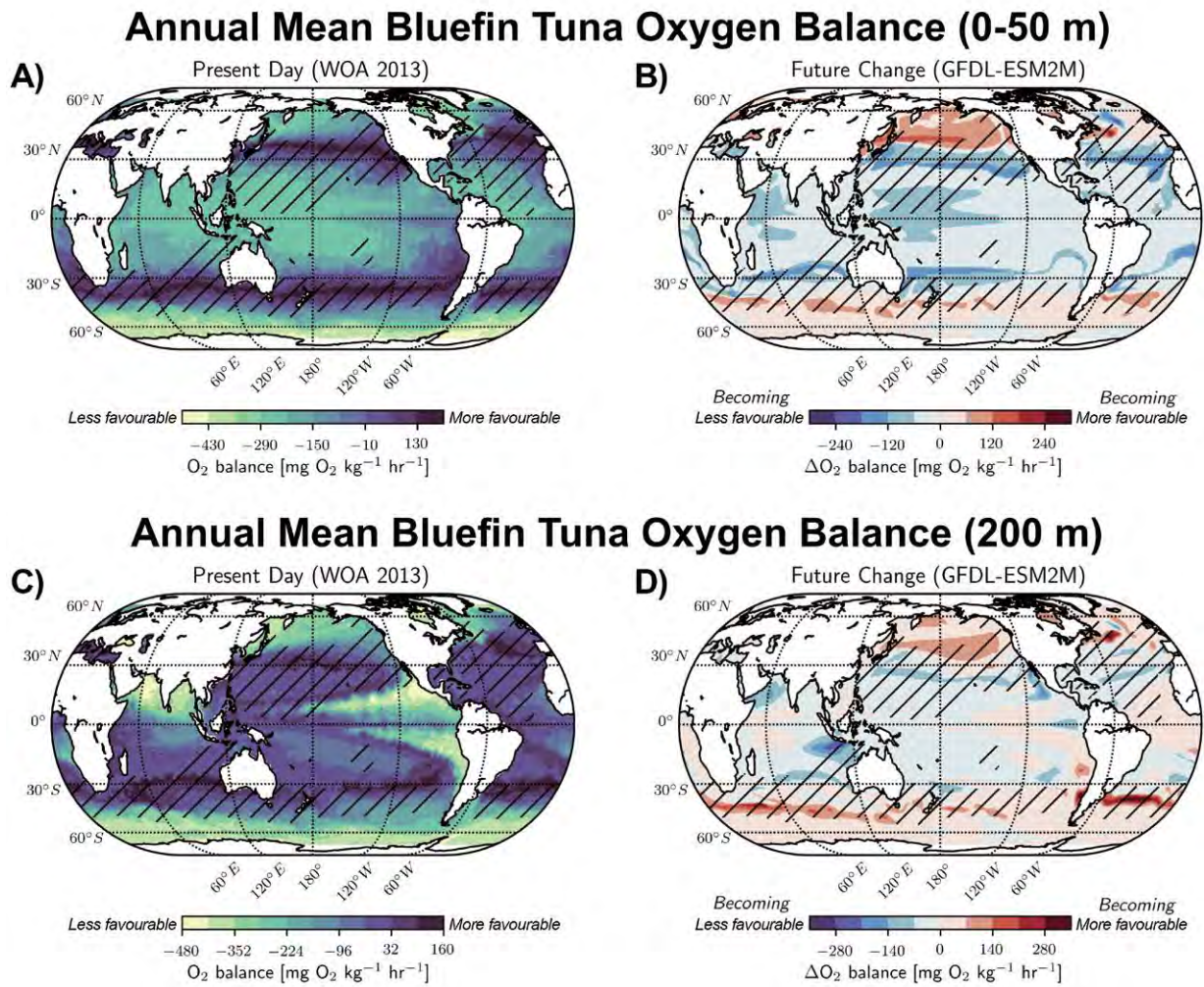


Figure 8.2.15 Annual mean bluefin tuna (all three species combined) oxygen balance. Hatching represents current bluefin (all three species) tuna habitat (IUCN, 2011, 2014). (A) 0–50 m depth oxygen balance in recent historical past (from World Ocean Atlas, temperature climatology 1995–2012, oxygen climatology 1900–2012). (B) Future change in 0–50 m depth oxygen balance from GFDL-ESM2M (RCP8.5 scenario, 2071–2100 minus 1971–2000). (C) Same as (A), but at 200 m depth. (D) Same as (B), but at 200 m depth.

Application of the oxygen balance model (Muhling et al., 2017a) to annual temperature and dissolved oxygen climatologies from the World Ocean Atlas (Garcia et al., 2014; Locarnini et al., 2013) shows that regions of highest oxygen balance in the upper 50 m of the water column correspond closely to regions of highest catch for both yellowfin and bluefin tunas (FAO, 2017). In particular, favourable conditions are present on Atlantic bluefin tuna fishing grounds in the north-east Atlantic Ocean and Mediterranean Sea (Teo & Boustany, 2016), on southern bluefin tuna fishing grounds along 40°S between South Africa and New Zealand (Hobday et al., 2016), and along migratory pathways used by Pacific bluefin tuna to cross between Japan and the California Current region (Fujioka et al., 2016) (Figure 8.2.15A, C). Metabolic stress in the upper ocean is thought to be higher on Atlantic and Pacific bluefin tunas' spawning

grounds in the Gulf of Mexico, south of Indonesia, and between Taiwan and Japan, due to warm upper ocean conditions in these areas. Conditions at 200 m are, however, more favourable and it has been proposed that adult Atlantic bluefin tuna may thermoregulate by descending to cooler depths in these areas (Teo et al., 2007).

Projections from GFDL-ESM2M (one of the CMIP5 Earth System Models, using the RCP8.5 scenario and comparing 1971–2000 to 2071–2100) show poleward shifts in annual mean favourable metabolic habitat for all three species of bluefin tunas in the upper 50 m of the water column as a result of warming and deoxygenation (Figure 8.2.15B). There is also a projected reduction in suitability at 200 m depth on southern bluefin tuna spawning grounds south of Indonesia and in Pacific

bluefin tuna habitat in the southern California Current, primarily due to stronger deoxygenation at depth in these areas (Figure 8.2.15D). Conversely, some parts of the Southern Ocean may become more favourable, both in the upper 50 m of the water column and at 200 m depth. The P_{50} depth-based trait analysis model discussed in subsection 8.2.3.3 projected a shoaling of Pacific bluefin tuna P_{50} depth throughout the North Pacific, while the oxygen balance model discussed here suggests that habitat suitability in the upper water column may decline as a result of warming and deoxygenation. In some parts of the North Pacific, it is therefore possible that certain species, such as Pacific bluefin tuna, may experience habitat loss at both the upper and lower bounds of their vertical habitat within their current range.

In contrast to the three species of bluefin tunas, present-day favourable metabolic habitat for yellowfin tuna covers most of the tropics and subtropics between 40°N and 40°S, with some lower suitability near the equator (Figure 8.2.16A). This corresponds well with the observed distribution of yellowfin tuna, which are caught on various fishing gears between these latitudes in all oceans, except for some parts of the eastern Pacific Ocean (FAO, 2017). Conditions at 200 m depth also appear to be favourable for yellowfin tuna throughout much of the subtropics, with the exception of the oxygen minimum zones in the eastern equatorial Atlantic and Pacific Oceans as well as the northern Indian Ocean (Figure 8.2.16C). Projections of future conditions suggest a loss of yellowfin tuna habitat in near-surface waters within the tropics, due to warming and deoxygenation, though this may be partially offset by poleward habitat expansion (Figure 8.2.16B). Habitat suitability at 200 m depth of some subtropical regions may improve, with warming temperatures and weaker deoxygenation. The area south of Indonesia may, however, become less habitable in association with stronger deoxygenation (Figure 8.3.16D).

8.2.3.5 Projecting oxygen-induced habitat suitability changes with process-based models (SEAPODYM and APECOSM-E)

Based on advection-diffusion-reaction equations, the spatial ecosystem and population dynamics model (SEAPODYM) was developed to investigate spatial tuna population dynamics under the influence of both environmental conditions and fishing (Lehodey et al., 2003). It has undergone various refinements since its

initial development and includes all of the following features: (1) forcing by temperature, currents, primary production, and oxygen concentration; (2) predictions of spatio-temporal distributions of mid-trophic level micronekton; (3) predictions of spatio-temporal distributions of tuna populations by age; (4) predictions of total catch size by fleet; and (5) parameter estimation (Lehodey et al., 2010, 2013, 2015). Tunas' spatial and population dynamics are determined using modelled habitat indices, growth rates, and mortality rates. Feeding habitat is determined by the accessibility of prey, while spawning habitat is determined by temperature preferences, availability of food suitable for larvae, and predator pressure. Larval recruitment is assumed to be a function of spawning stock biomass, the extent of spawning habitat, larval food availability, and larval mortality during advection by currents.

Using SEAPODYM and future biogeochemical changes from IPSL-CM4 (an older CMIP3, rather than CMIP5, Earth System Model) under scenario A2 (similar to scenario RCP8.5, but reaching ~850 ppm CO₂ rather than ~950 ppm by 2100), Lehodey et al. (2013) projected that skipjack tuna habitat will expand within the central and eastern Pacific as well as towards higher latitudes, but will shrink within the increasingly warm and decreasingly productive west-central tropical Pacific by the end of the 21st century. A simulation replacing projected oxygen concentrations with present-day climatologies did not change these results, indicating that the projected changes in skipjack tuna habitat are principally driven by changes in temperature, primary productivity, and currents (Lehodey et al., 2013). Similar projections of future albacore habitat, on the other hand, indicate that oxygen concentration decreases in the South Pacific projected by IPSL-CM4 in the next half-century will lead to weaker recruitment here, with a strong negative impact on the abundance of young South Pacific albacore (Lehodey et al., 2015). Projected changes in bigeye tuna habitats and populations are also likely to be heavily influenced by spatially variable changes in oxygen concentrations by 2100 (Lehodey et al., 2010). For example, the feeding habitat of adult bigeye tuna is projected to improve in the eastern tropical Pacific because subsurface increases in dissolved oxygen concentrations will allow for access to deeper prey. At the same time, natural mortality rates of older bigeye tuna are projected to increase within the western-central Pacific due to decreasing oxygen concentrations (along with overly warm temperatures and decreases in food supply) (Lehodey et al., 2010).

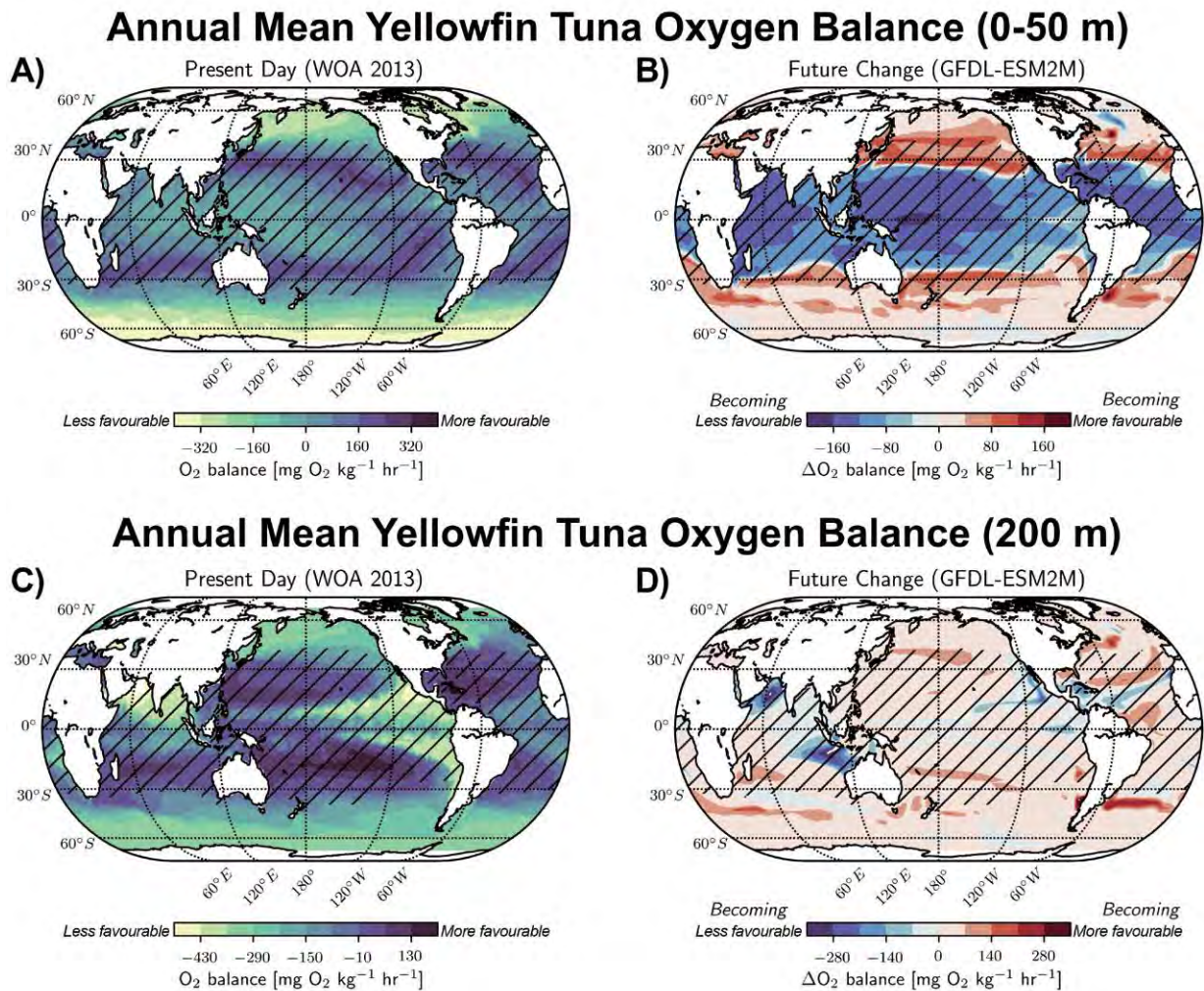


Figure 8.2.16 Annual mean yellowfin tuna oxygen balance. Hatching represents current yellowfin tuna habitat (IUCN, 2011, 2014). (A) 0-50 m depth oxygen balance in recent historical past (from World Ocean Atlas, temperature climatology 1995–2012, oxygen climatology 1900–2012). (B) Future change in 0-50 m depth oxygen balance from GFDL-ESM2M (RCP8.5 scenario, 2071–2100 minus 1971–2000). (C) Same as (A), but at 200 m depth. (D) Same as (C), but at 200 m depth.

This increase in mortality, coupled with the migration of surviving fish to more favourable habitat in the east, may lead to declining adult biomass in the western Pacific by the end of the 21st century.

Like SEAPODYM, the Apex Predator ECOSystem Model - Estimation (APECOSM-E) simulates both spatial and temporal dynamics of skipjack tuna biomass and abundance. Unlike SEAPODYM, however, APECOSM-E mechanistically (rather than empirically) links environmental factors, metabolic rates, and behavioural responses via dynamic energy budget theory. This technique involves tracking the energy budget of an individual organism throughout its life stages (Dueri et al., 2014). Despite their different methods of representing biological processes and the slightly different Earth System Models driving their ocean

biogeochemistry (APECOSM-E uses CMIP5 model IPSL-CM5A-MR and scenario RCP8.5), both models exhibit similar changes in skipjack tuna distribution within the Pacific Ocean by 2100, projecting shifts away from the western Pacific and expansions into the eastern Pacific and towards higher latitudes. In both models, changes in temperature and access to food were the dominant factors driving these distribution shifts, while changes in oxygen content played a relatively minor or insignificant role.

8.2.4 Ecosystem consequences

A thorough understanding of the ecological relationships that exist within the modern-day ocean is needed to better predict how species-specific responses to three-dimensional changes in temperature and oxygen will

affect ecosystem structure and dynamics. Currently available data suggest that species-specific vertical movements result in niche partitioning in areas where different species are sympatric (e.g. Bernal et al., 2009, 2017). For example, the vertical movement patterns of swordfish and bigeye tuna appear to directly follow the diurnal vertical movements of the squid, euphausiids, and mesopelagic fish that are associated with the deep sound scattering layer (SSL) (Bertrand et al., 1999, 2002a, b; Carey, 1990; Carey & Robison, 1981; Dagorn et al., 2000a, b, c; Grudinin, 1989; Josse et al., 1998; Longhurst, 1976; Marchal et al., 1993; Marchal & Lebourges, 1996; Nakamura, 1993; Roger & Grandperrin, 1976; Yatsu et al., 1999). This is in contrast to the shallower habitat use of yellowfin and skipjack tunas, although both of these species do appear to make descents, albeit brief, to depths occupied by SSL organisms during the daytime (Schaefer & Fuller, 2007; Schaefer et al., 2007, 2009a, b). This apparent resource partitioning is supported by stomach content analyses, which show that bigeye tuna generally select mesopelagic prey from the SSL, while yellowfin tuna feed primarily on epipelagic prey from the mixed layer when the two tuna species are caught in the same areas (Holland & Grubbs, 2007; King & Ikehara, 1956; Kornilova, 1981; Pelczarski, 1988; Portier et al., 2004, 2007). The fishes and crustaceans of the SSL migrate downward during the day into cold, dark, low-oxygen waters as a refuge against predation, and can do so due to a suite of morphological, physiological, and biochemical adaptations (e.g. Belman & Childress, 1975; Childress, 1971; Childress & Nygaard, 1974; Sanders & Childress, 1990). Bigeye tuna and swordfish have, however, also obviously evolved physiological abilities to sustain extended forays into the SSL organisms' predator refuge.

Tunas and billfishes are likely to display species-specific three-dimensional habitat changes due to future climate change, just as they currently display species-specific movement patterns and ecological niches. Differential changes in hypoxia-induced vertical habitat extents, in particular, can either decouple or enhance competition among different species. For example, in the North Pacific Ocean, projected decreases in vertical separation among several pairs of tuna species due to species-specific changes in P_{50} depths suggest future increases in the frequency of competitive interactions between tuna here (Mislán et al., 2017). Species-specific responses to climate-driven changes in oxygen and other environmental conditions may also impact

bycatches (i.e. unintended catches) of tunas, billfishes, and other species (Hobday et al., 2015; Komoroske & Lewison, 2015). To our knowledge, there are currently no studies exploring the effects of climate-driven oxygen changes on bycatches of tuna and billfish in fisheries targeting other species, nor on bycatches of other non-targeted species in tuna and billfish fisheries. Hartog et al. (2011), however, suggest that a temperature-driven increase in overlapping habitats of yellowfin and southern bluefin tunas in the yellowfin-targeting, eastern Australian longline fishery may lead to increased bycatches of southern bluefin tuna if current management policies do not adapt.

Future oxygen-driven changes in vertical movements and spatial distributions of prey species exploited by tunas and billfish will also play an important role in determining the overall ecosystem effects induced by oxygen changes. As is the case for tunas and billfishes, changing oxygen concentrations may impact prey in species-specific ways, potentially altering established ecosystem structures and food web dynamics (e.g. Gallo & Levin, 2016; Koslow et al., 2011). Koslow et al. (2011) showed that the abundance of mesopelagic prey species decreased by 63% during periods of reduced oxygen concentration within the oxygen minimum zone of the southern California Current. This likely occurred because the prey species were forced to occupy better-oxygenated shallow (and subsequently more well-lit) waters, rendering them more vulnerable to visually orienting predators such as tunas and billfishes. Changes in populations of these mid-trophic level mesopelagic prey species (which are both major consumers of zooplankton and major food sources for tunas, billfishes, and a wide range of other fish, squids, seabirds, and marine mammals) could have far-reaching impacts on the abundance of tunas and billfishes in particular, and the structure of pelagic food webs in general, which may be either positive or negative. Future changes in vertical habitat usage driven by changes in oxygen content may also alter population structures via changes in species size and productivity. For example, Prince and Goodyear (2006) showed that enhanced coupling between predator and prey likely leads to increased foraging opportunities and therefore larger mean body sizes of sailfish in the hypoxia-compressed habitats of the eastern tropical Pacific and Atlantic Oceans, as compared to the well-oxygenated western North Atlantic Ocean. Whether climate change will lead to enhanced or decreased coupling between predator and prey will depend on region-specific changes

Summary of Projected Oxygen-Driven Tuna Habitat Changes

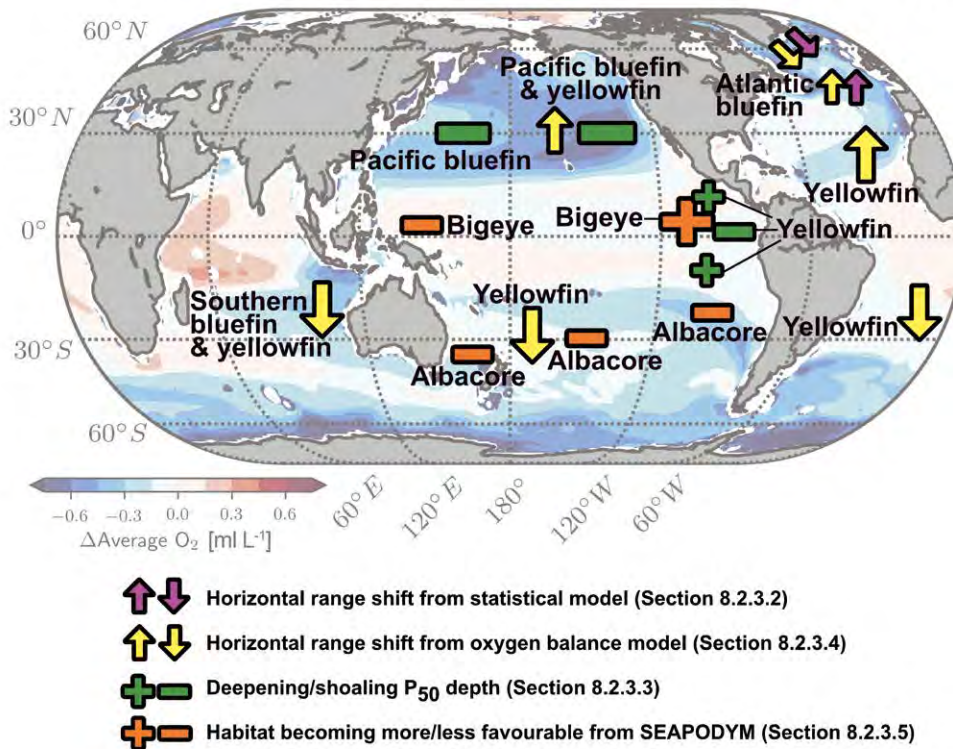


Figure 8.2.17 Summary of projected changes in species-specific tuna habitats by the end of the 21st century, driven (at least partially) by projected changes in oxygen content. The background map of projected changes in average oxygen concentrations between 200 and 700 m depth is taken from Figure 8.2.10B. Changes in habitat driven by factors unrelated to or not including oxygen are not shown here. For example, changes in skipjack tuna distributions within the Pacific Ocean are expected to be driven primarily by temperature and access to food; because oxygen plays an insignificant role in this case, these projected distributional shifts are not depicted here. It is important to note that there are substantial uncertainties associated with each habitat projection. Uncertainties are especially large in the eastern tropical Pacific, due mainly to lack of model agreement on how oxygen concentrations will change within this region. For more information on uncertainties, see the subsections cited in the figure.

in oxygen and temperature distributions, as well as species-specific differences in hypoxic and thermal tolerances.

8.2.5 Societal consequences

Different tuna and billfish species are fished by different gears, depending on targeted species size and depth range, vessel capacity, and applicable regulations, among other factors (ICCAT, 2016; Ward & Hindmarsh, 2007; Williams & Terawasi, 2011). Skipjack and yellowfin tunas (the two tuna species dominating worldwide landings, Table 8.2.1) are primarily taken by purse seine fisheries (Figure 8.2.2), which are concentrated in the tropical waters of the Pacific, Atlantic, and Indian Oceans (FAO Fisheries & Aquaculture “Global Capture Production” and “Global Catches by Stock” databases consulted on 20/12/2017). Purse seines largely target the upper water column and may fish down to ~200 – 300 m depth depending on the target species (ICCAT, 2016; Lennert-Cody et al., 2008). Purse seining thus

depends on oxycline and/or thermocline depths (below which skipjack and yellowfin tunas do not frequently dive) being shallower than ~200 – 300 m. Pelagic longline gear primarily catches larger fish (ICCAT, 2016) and can be placed in different configurations in order to set the majority of hooks at the desired depths. For example, hooks are set to occupy 50 – 100 m depth to target swordfish (at night, when this species occupies the upper water column) and 200 – 300 m depth to target tunas (Bigelow et al., 2006; Nakano et al., 1997; Ward & Myers, 2005). In general, skipjack tuna and billfishes are caught on shallower set hooks, while albacore and bigeye tunas are more likely to be caught on deep-set gear, due to their species-specific vertical movement patterns (described in subsection 8.2.2). Yellowfin tuna longline catchability is less correlated with depth within their vertical range (above about 300 – 500 m) (Nikolic et al., 2017; Prince et al., 2010; Ward & Myers, 2005). Surface gears including trolling and hook-and-line are used to catch smaller or juvenile tunas in some areas, such as the juvenile albacore fishery off of the western

United States and the juvenile Atlantic bluefin tuna fishery in the north-eastern Atlantic Ocean (Fromentin, 2009; Nikolic et al., 2017; Xu et al., 2015). Other gears, such as fixed traps, drift gillnets, and harpoons, are also used to target tunas and billfishes, but fishing effort and landings are generally small compared to purse seine and longline fisheries (Miyake et al., 2010).

Ocean warming and deoxygenation have the potential to change the distribution and catchability of tunas and billfishes in three dimensions. Because tunas and billfishes are highly mobile and patchily aggregated, they are likely to exhibit complex shifts in their distributions in response to changing environmental conditions. Where surface layer temperatures become too warm, they may spend more time at depth (assuming oxygen concentrations are sufficient), potentially decreasing their vulnerability to surface-oriented fishing gears. In contrast, if oxygen minimum layers expand and shoal, relatively hypoxia-intolerant species (e.g. skipjack and yellowfin tunas) may be pushed towards the surface (assuming temperatures are not too warm), potentially increasing their vulnerability to surface-oriented fishing gears (e.g. Stramma et al., 2012). If no vertical refuge from unsuitable conditions is available, the fish may shift their distributions horizontally, moving towards areas with temperatures or oxygen levels that are more tolerable. To maintain their livelihoods, fishers will need to adapt to potential changes in species distributions, vulnerabilities to different gear types or fishing fleets, and efficiencies of supply chains, which can be further exacerbated by factors such as rising fuel prices and decreasing government subsidies (Jones et al., 2015). Where populations of target species decrease or move away from traditional fishing grounds, fishers will have to spend more resources to catch the same species or adapt their gear and vessel configurations to target new ones. Economic and regulatory constraints can, however, hamper the ability of fishers to effectively adapt to changing species availability, particularly if species movements cross management boundaries (Pinsky & Fogarty, 2012). Smaller-scale fisheries in developing nations and fisheries relying on vessels with limited range and low technological capabilities are likely to be most vulnerable, particularly if their exposures to the effects of climate change are also high (Guillotreau et al., 2012; Ommer et al., 2009). Communities that are strongly economically dependent on these types of small-scale fisheries for livelihoods and incomes are therefore likely to be hardest hit by climate-driven changes to fish distributions.

Climate-driven changes in habitat suitability and population structures are also likely to complicate stock assessment and management. Most current stock assessment models use standardized indices of abundance derived from fishery-dependent catch per unit effort (CPUE) data to infer changes in stock size. Environmentally-driven changes in species distribution, range, or population structure can, however, lead to trends in catchability and subsequently CPUE data that are unrelated to abundance (Bigelow & Maunder, 2006; Link et al., 2011). If not accounted for, these types of changes in CPUE data can bias estimates of abundance used in population assessment models (Wilberg et al., 2010). Some newer stock assessment methods can incorporate effects of time-varying selectivity (Methot & Wetzel, 2013), however, and spatio-temporal models are becoming more feasible (Berger et al., 2017). In addition, indices derived from survey or fisheries data can be standardized to account for environmental effects (e.g. Cao et al., 2017; Lynch et al., 2012). Misspecification of these processes can, however, lead to biases (Hulson et al., 2013). Increasing model complexity to deal with changing environmental factors thus requires caution. Managers will have to carefully adapt their stock assessment strategies in the face of climate change in order to remain effective and ensure resource sustainability.

8.2.7 Conclusions / Recommendations

We conclude (as have numerous other authors cited here) that climate change occurring over the next 100 years will drive species-specific changes in the population structures and (more importantly) the horizontal and vertical movement patterns of tunas and billfishes in the open ocean through changes in habitat suitability. We contend that a major factor contributing to these changes will be altered oxygen distributions throughout the global ocean. The temperate North Pacific Ocean is projected to undergo some of the largest overall decreases in oxygen content within the upper water column across ocean basins, as well as some of the most pronounced shoaling of hypoxic layers (subsection 8.2.3.1). Species which currently reside in this region (e.g. swordfish and yellowfin, bigeye, Pacific bluefin, and albacore tunas) are thus expected to experience the most dramatic decreases in oxygen content and shoaling of P_{50} depths in their present-day habitat (subsection 8.2.3.3). In response to these changes in oxygen (and temperature), Pacific bluefin tuna are expected to shift northward toward

more favourable oxygen conditions and to adjust their vertical habitat usage to avoid oxygen limitation from shoaling P_{50} depths (subsections 8.2.3.3 and 8.2.3.4). Atlantic bluefin tuna are projected to shift northward as well, propelled by warming, unfavourable oxygen balances (subsection 8.2.3.4), and a loss of habitat south of $\sim 40^{\circ}\text{N}$ (subsection 8.2.3.2). Yellowfin tuna are likewise expected to shift poleward toward habitats with more favourable temperature and oxygen balances (subsection 8.2.3.4), as well as to potentially move upward in the water column within the temperate North Pacific due to shoaling P_{50} depths (subsection 8.2.3.3). Skipjack tuna, on the other hand, are less likely to be affected by future changes in oxygen concentrations at depth because they generally remain within the well-oxygenated surface layer (subsection 8.2.3.5). The combined effects of warming and slight deoxygenation of the upper mixed layer in tropical regions on species such as skipjack tuna remain uncertain, however. The effects of future oxygen changes on bigeye tuna population dynamics are more mixed, in that projected changes in subsurface oxygen concentrations in the eastern and western tropical Pacific drive both increases and decreases, respectively, in SEAPODYM-predicted adult biomass (subsection 8.2.3.5). In the South Pacific, SEAPODYM projects that younger cohorts of South Pacific albacore will be negatively affected by decreases in oxygen concentrations within their spawning grounds (subsection 8.2.3.5). These projected changes are summarized in Figure 8.2.17.

Each type of model used to predict the effects of future oxygen changes on tunas and billfishes has its own advantages and disadvantages. The trait-based, oxygen balance, and statistical models we describe here account for only the direct effects of oxygen (and temperature) changes on tuna and billfish physiology and therefore movements. The more complex process-based models (SEAPODYM and APECOSM-E), on the other hand, account for these direct effects as well as the indirect effects of potential oxygen-driven food-web and population structure changes. Additionally, the trait analysis, oxygen balance, and statistical models are distribution models that only consider climate change impacts in terms of potential horizontal and vertical range shifts, while SEAPODYM and APECOSM-E takes into account life histories and phenologies to produce more detailed projections of population and age structures. More complex models can be more difficult to parameterize, however, which can lead to greater uncertainty in projections. Continued work on all types

of species-specific models will therefore be necessary for generating more accurate projections and reducing uncertainties.

Improvements in Earth System Models used to project future environmental conditions will also help increase the accuracy of projections related to tuna and billfish distributions in response to climate change. Current Earth System Models, including the ones used in this report, typically have horizontal resolutions of 1° or coarser. This coarse resolution cannot distinguish many important meso- and sub-mesoscale processes that can oftentimes drive observed species distributions. Furthermore, projections of biogeochemical variables (such as oxygen concentration) can be highly uncertain within these models compared to projections of purely physical variables (such as temperature). Projections of changes in oxygen concentrations in the tropical Pacific Ocean, where the interactions between biology and the physics of ocean circulation are complicated, are especially uncertain. Part of the reason for these uncertainties is the relative lack of actual biogeochemical measurements that can be used for calibration and improvements in mechanistic understanding. Increased *in situ* monitoring of oxygen concentrations throughout the global oceans is therefore crucial for improving Earth System Model predictions of biogeochemistry.

To further improve projections of future habitat and population changes, greater numbers of *in situ* observations of tuna and billfish habitat use are also needed. More *in situ* habitat observations, along with more laboratory studies of physiological traits, will lead to a better understanding of the environmental conditions that can predict species-specific movement patterns and therefore species-specific responses to climate change. Data products that synthesize and standardize multiple sources of information would be particularly useful. For example, contradictory records for the depth ranges frequented by various tunas and billfishes sometimes occur because a standard method for calculating these ranges does not exist. In addition, the development of a four-dimensional (three spatial dimensions and time) gridded atlas documenting the spatio-temporally variable habitats of tunas and billfishes, derived from tagging data and species-specific physiological abilities and tolerances, would be invaluable for analysing how regional and seasonal variations in habitat usage will be impacted by deoxygenation. More detailed *in situ* observations of prey abundances and behaviours would also help improve projections of future habitat suitability

changes by improving our understanding of the effects of oxygen and other environmental conditions on prey distributions and predator-prey interactions.

The most obvious way to slow or prevent projected changes in global oxygen content and resultant changes in the populations and distributions of tunas and billfishes is to reduce greenhouse gas emissions. Besides preventing climate change, however, we can also adapt to and prepare for potential future effects. A sound mechanistic understanding of how tunas and billfishes respond to their ocean environment is key to successful adaptation. We thus argue (as have others, e.g. Brill & Hobday, 2017; Hobday et al., 2013; Lehodey et al., 2011; Mislan et al., 2016; Watters et al., 2003) that illuminating the interactions between fishes, fisheries, and climate change is, and will continue to be, critical for ensuring the sustainability of tunas and billfishes into the 21st century.

8.2.8 References

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8.3 The significance of ocean deoxygenation for kelp and other macroalgae

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Summary

- Because kelps and other macroalgae are primary producers and absorb carbon dioxide and produce oxygen, one might expect the effects of hypoxia to be modest. However, kelps and macroalgae also respire, which requires oxygen. Therefore, hypoxia may have detrimental effects on processes like net primary production (NPP), which supplies organic matter to support kelp food webs and ecosystems. However, the effects of hypoxia are expected to vary widely depending on the species of macroalgae and their habitat, since this group of organisms is diverse in their morphology and distribution. Here we describe predicted impacts of deoxygenation on kelps and other macroalgae and discuss consequences for kelp ecosystems.
- Kelps and other macroalgae occur in nearshore systems across the world, which are dynamic and experience large fluctuations in oxygen, pH, and temperature. In dynamic coastal upwelling zones, low-oxygen events are often more episodic. Unlike respiration-driven hypoxia in bays and estuaries, these upwelling-driven exposures to hypoxia tend to be acute, with rapid onsets and recoveries, and typically lasting less than 24 hours each. It remains to be seen whether it is less likely for organisms in these systems to experience direct mortality due to adaptations to high degrees of natural variability in dissolved oxygen (DO) or whether they are close to their physiological limits.
- Very little is known about the direct impacts of deoxygenation on macroalgae. On one hand, hypoxia may detrimentally affect metabolic processes, leading to lower net primary production. These processes are also expected to be affected during various stages in the macroalgal life cycle. However, many marine algae photorespire (using oxygen instead of carbon dioxide), reducing their photosynthetic efficiency, so decreasing oxygen concentrations may actually increase photosynthetic rates in some marine macroalgae. These predictions become complicated when considering the effects of oxygen in combination with co-occurring stressors like ocean acidification and warming. Depending on factors like calcification, proximity to the benthos, growth rate, and carbon concentration mechanisms, these three stressors are predicted to differentially affect groups of macroalgae.
- In addition to direct impacts on macroalgae, low oxygen (and upwelling-associated fluctuations in pH and temperature) could have profound effects on the grazers, decomposers, and predators that drive the structure and function of kelp ecosystems. There is a dearth of published studies on the responses of kelp forest organisms to low oxygen, but those that do exist suggest changes in foraging, feeding, and movement. Sedentary benthic invertebrates such as abalone may be detrimentally affected because depressions in the rocky bottom may retain pools of cold, acidic, low-oxygen water for hours after internal waves pass, much like a tide pool retains water from a retreating tide. Additionally, deoxygenation effects on organisms will likely alter trophic interactions and energy flow. Differences in vulnerability between grazers and predators may strengthen or weaken trophic cascades and top-down control on kelp populations.

Hypoxia effect	Potential consequences
Hypoxia may affect oxygen available for metabolic demands.	<ul style="list-style-type: none"> Positive effects on photosynthesis (but this is species dependent) and negative impacts on respiration might alter NPP, which would have cascading effects on food webs.
Hypoxia may interact with other climate related stressors like ocean acidification, especially in upwelling regions where low pH and oxygen co-occur.	<ul style="list-style-type: none"> Growth might be most negatively impacted, especially in calcified macroalgae. Sub-canopy species under lower irradiances or rocky reef depressions might be disproportionately affected due to lower photosynthetic rates and exposure to more prolonged and more severe hypoxic conditions.
Hypoxia may differentially impact algae with different photosynthetic physiologies.	<ul style="list-style-type: none"> Algae with high O₂ sensitivity might fare better (in terms of photosynthetic rate) under lower oxygen concentrations, since Rubisco can uptake CO₂ more efficiently. Altered competitive interactions between different species, leading to changes in macroalgal assemblages (i.e. simplification).
Hypoxia may impact macroalgae throughout their life cycle.	<ul style="list-style-type: none"> Increased bottlenecks at early life stages will impact macroalgal populations. Buffering capacity of algae to low pH and oxygen, especially at boundary layers, could benefit algae at local scales.
Direct effects of hypoxia on macroalgae may impact food webs due to altered species interactions.	<ul style="list-style-type: none"> Reduced transfer of primary productivity if macroalgal communities are altered (i.e. simplification or degradation). Simplified food webs more susceptible to invasion by non-natives or closer to reaching “tipping points”.

8.3.1 Introduction

Marine macroalgae and kelps provide a tremendous amount of primary production globally, capable of producing 1 Pg carbon year⁻¹ (i.e. 1 Gigatonne) (Raven & Hurd, 2012; Smith, 1981). Macroalgae generally comprise a holdfast, stipe, and blade, but they are highly diverse in their morphology with many lacking one or more of these structures (Abbott & Hollenberg, 1976). This group which can have a range of body types from single-celled, multinucleate algae to large, structurally complex algae comprise various tissue layers (Graham et al., 2009). They provide important habitat, food, and refuge for other organisms in addition to providing extracts used in the food, pharmaceutical, and cosmetic industries, making them ecologically and economically important (McLachlan, 1985; Raven & Hurd, 2012).

Kelp forests are distributed in temperate seas worldwide (Steneck & Johnson, 2014) (Figure 8.3.1). Often

considered ecosystem engineers (Holdolero & Edwards, 2017; Jones et al., 1994), kelp and other macroalgae provide habitat and mediate energy flow across the diverse and highly productive marine ecosystems in which they are found (Steneck et al., 2002). The natural history of kelp forests and the processes that shape their associated animal and algal communities are relatively well understood (Schiel & Foster, 2015). But major gaps in knowledge remain concerning how these systems respond to the stressors and variability associated with climate change (Krumhansl et al., 2016). High temperature—and associated low nutrient conditions—and extreme storms can lead to full deforestation, though recovery is typically fast (1-5 years; Dayton et al., 1992; Edwards, 2004). Much less is known about the impacts of deoxygenation and acidification. Because kelps and other macroalgae are primary producers and absorb CO₂ and produce O₂, one might expect the effects of hypoxia to be modest. But diel swings in production lead to significant fluctuations in pH and O₂ levels.

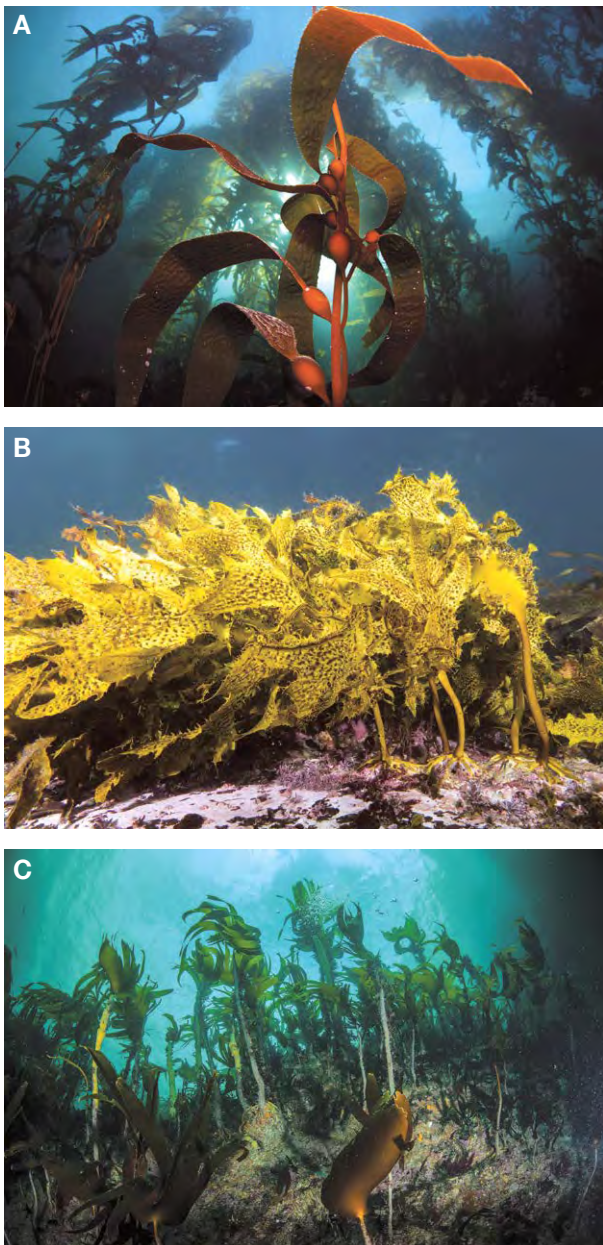


Figure 8.3.1 A) Giant kelp (*Macrocystis pyrifera*) © Shutterstock; B) *Ecklonia radiata* © John Turnbull; C) Cuvie (*Laminaria hyperborea*) © SNH/George Stoyle.

These ecosystems are also impacted by both offshore and inshore processes that can drive deoxygenation (Walter et al., 2014; Woodson et al., 2018) In addition to direct impacts on kelps and other macroalgae, low oxygen (and upwelling associated fluctuations in pH and temperature) could have profound effects on the grazers, decomposers, and predators that drive the structure and function of kelp ecosystems. Given the significant overlap between the distribution of kelp forests and the deoxygenation of coastal, near-coastal, and open ocean waters worldwide (Figure 8.3.2), the need for further research is critical. Though the impacts

of deoxygenation on kelps, macroalgae and associated animals are likely to be biogeographically explicit, here we rely upon existing empirical evidence and primarily focus on relevant communities and populations across the Northeast Pacific.

In the California Current, waters are increasingly experiencing oxygen depletion (Chan et al., 2008), concomitant with an expanding Eastern Pacific oxygen minimum zone (OMZ) (Stramma et al., 2010). Some of these changes are in response to natural climate variability, such as the Pacific Decadal Oscillation (PDO) and El Niño Southern Oscillation (ENSO) (Nam et al., 2011). But there also appear to be non-cyclical changes associated with climate variability affecting dissolved oxygen (DO) concentration of ocean waters across the Eastern Pacific (Brewer & Peltzer, 2009). Shoaling of deep, low-DO waters is particularly pertinent in the California Current because the Eastern Pacific Ocean contains the world's largest midwater OMZ (250-400 m deep) (Keeling et al., 2009), and the coastal region has a narrow continental shelf (Pennington et al., 2006) making the coastline susceptible to OMZ intrusion. Bograd et al. (2008) documented mean declines in DO concentration of 20% below the mixed layer from 1984–2006, and an 80 m shoaling of the hypoxic zone, with more intense shoaling at inshore locations of the Southern California Bight. Observed DO declines are not limited to OMZ depths, as oxygen-depleted offshore waters episodically intrude on the coast through seasonal upwelling, tides, and coastally trapped waves (Bakun, 1990; Booth et al., 2012).

Based on 50+ year data set from the Southern California Bight, Booth et al. (2014) documented changes in DO concentration similar to those reported offshore. But DO in sub-mixed layer nearshore waters (10 km from shore) declined up to four times faster than reported for offshore waters over the last 15 years. These rapid declines have no precedent over the past 50 years and are not attributable to large-scale climate variability in ocean DO. Coastal biophysical processes, including increased phytoplankton biomass in surface waters, are likely contributing to the recent elevated rate of DO decline in nearshore waters, as evidenced by higher rates of apparent oxygen utilization. The combined impact of shoaling of the oxygen minimum layer and possible coastal eutrophication can produce low DO dynamics that have detrimental impacts on kelp forest ecosystems, particularly on sedentary benthic invertebrates such as abalone (Micheli et al., 2012).

World Kelp Forests, Low Oxygen Zones, and Hypoxic and Eutrophic Coastal Areas

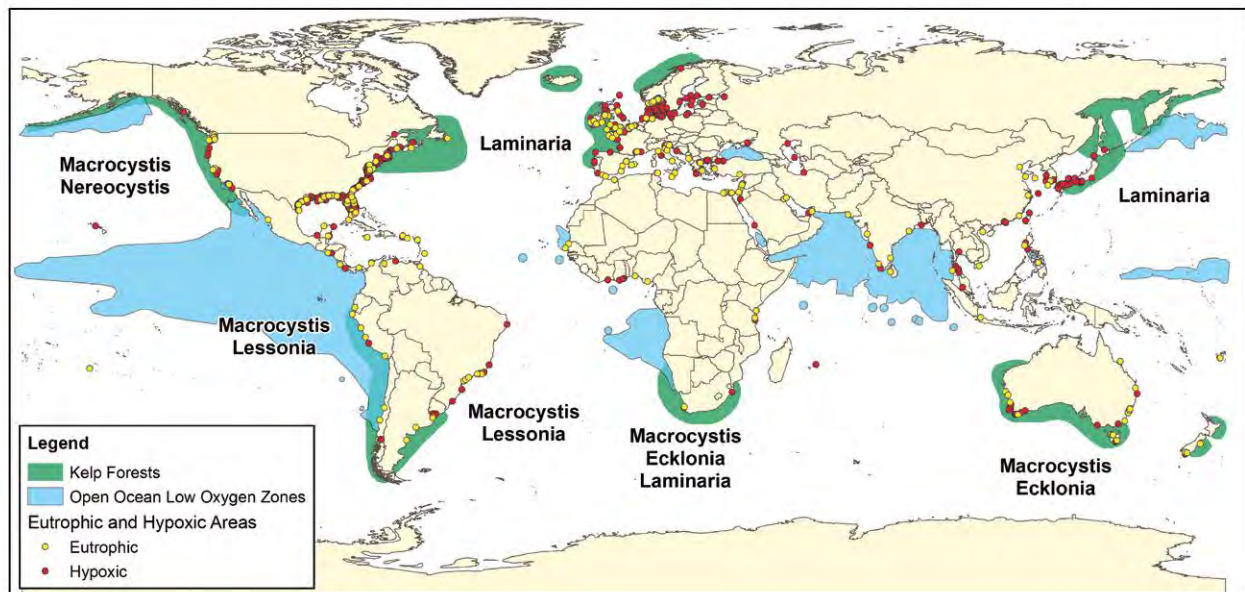


Figure 8.3.2 Global distribution of forest forming kelps (Steneck et al., 2002), open ocean low oxygen zones (2 mg L⁻¹ of O or less) (Garcia et al., 2014), and eutrophic and hypoxic coastal areas (Diaz et al., 2011). Map produced by Hannah Blondin.

Laboratory studies indicate that biological impacts of hypoxia on marine invertebrates are compounded by co-occurring fluctuations in pH and temperature (Boch et al., 2017; Kim et al., 2013), but the cumulative impacts on kelps are still largely unaddressed.

8.3.2 Spatio-temporal variability in oxygen conditions within kelp forests

DO concentrations in kelp forests are highly variable in both space and time, and the potential effects of deoxygenation in this ecosystem must be considered within the context of natural patterns of variability. The substantial horizontal, vertical, and temporal oxygen variability in kelp forests is influenced by multiple physical and biological processes. Seasonal upwelling along the west coast of North America primarily occurs during the spring and summer months, and brings cold, acidic, low-DO, and nutrient-rich water onto the continental shelf. This deep water is then further transported into nearshore kelp forest ecosystems by internal waves (Booth et al., 2012; Walter et al., 2014). In southern and central California kelp forests, these internal waves drive semidiurnal and diurnal patterns of oxygen and pH variability (Booth et al., 2012; Frieder et al., 2012; Koweek et al., 2017). As a result, some of these kelp forests already encounter sublethal levels of hypoxia for animals according to the 4.6 mg L⁻¹ threshold of Vaquer-Sunyer and Duarte (2008). Unlike respiration-driven hypoxia in bays and estuaries, these upwelling-driven

exposures to hypoxia tend to be acute, with rapid onsets and recoveries, and typically lasting less than 24 hours each. (Booth et al., 2012; Leary et al., 2017; Walter et al., 2014).

The intrusions of cold, acidic, low-DO deep water into the kelp forest lead to increased stratification of the water column, which creates strong gradients of oxygen and pH between the surface and the bottom (substrate) of the kelp forest (Frieder et al., 2012; Koweek et al., 2017). These vertical gradients in DO and pH can be amplified by vertical gradients in kelp photosynthesis. Kelp biomass is concentrated near the surface in the canopy region, so an increase in kelp photosynthesis can further elevate dissolved oxygen and pH in surface waters relative to deeper water (Frieder et al., 2012; Koweek et al., 2017).

Horizontal variability in dissolved oxygen at the kelp forest floor (substrate and benthos) is generated by the interactions of internal waves with upwelling conditions and bottom topography (Koweek et al., 2017; Leary et al., 2017; Walter et al., 2014; Woodson et al., 2018). For example, depressions in the rocky bottom may retain pools of cold, acidic, low-oxygen water for hours after an internal wave passes, much like a tide pool retains water from a retreating tide (Leary et al., 2017). These 'internal tide pools' of low-oxygen water can create a fine spatial mosaic of oxygen conditions within the kelp forest. At larger spatial scales, wave-exposed regions

of the kelp forest may experience different conditions than the wave-protected areas due to different levels of exposure to the internal waves which transport acidic, low-DO water into nearshore habitats (Koweek et al., 2017).

8.3.3 Impacts of deoxygenation on macroalgae and kelps

Due to their ability to photosynthesize, macroalgae are not thought to be vulnerable to deoxygenation directly. Despite many studies examining oxygen effects on macroalgae (e.g. Black et al., 1976; Downton et al., 1976; Dromgoole, 1978; Turner et al., 1956), virtually nothing has been published under the context of climate-driven hypoxia. While the literature focuses much more on the effects of temperature and ocean acidification (e.g. Shukla & Edwards, 2017), we argue that hypoxia should also be examined with a consideration of its effects on macroalgae throughout their life cycles. Because multiple climate change stressors are occurring concomitantly across the globe, it is also imperative to understand the impacts of hypoxia in relation to the impacts of other co-occurring stressors like ocean acidification and warming.

As well as photosynthesizing, kelps and macroalgae also respire, which requires oxygen. Thus, deoxygenation may impact net primary production (NPP), which supplies organic matter to support food webs and ecosystems. NPP considers both the production of oxygen through photosynthesis and the use of oxygen through respiration. Previous research has shown that photosynthetic capacity decreases with depth due to reduced light (Arnold & Manley, 1985; Gerard, 1986), so sub-canopy and smaller macroalgae may be impacted by an already lower photosynthetic capacity in addition to limitations on respiration by hypoxia. For large and canopy forming kelps that create habitat complexity and drive primary production within a system, understanding their fate under hypoxia is also important to consider, since canopy blades are closer to the air-sea interface and may not experience levels of hypoxia comparable to the benthos or in depressions in rocky reefs (Leary et al., 2017). With the large habitat-forming kelp *Macrocystis pyrifera*, canopy and apical blades have higher net photosynthetic rates even under high irradiance, raising the question whether these blades may be able to compensate for any negative effects that hypoxia may have on respiration for lower blades (Figure 8.3.3).

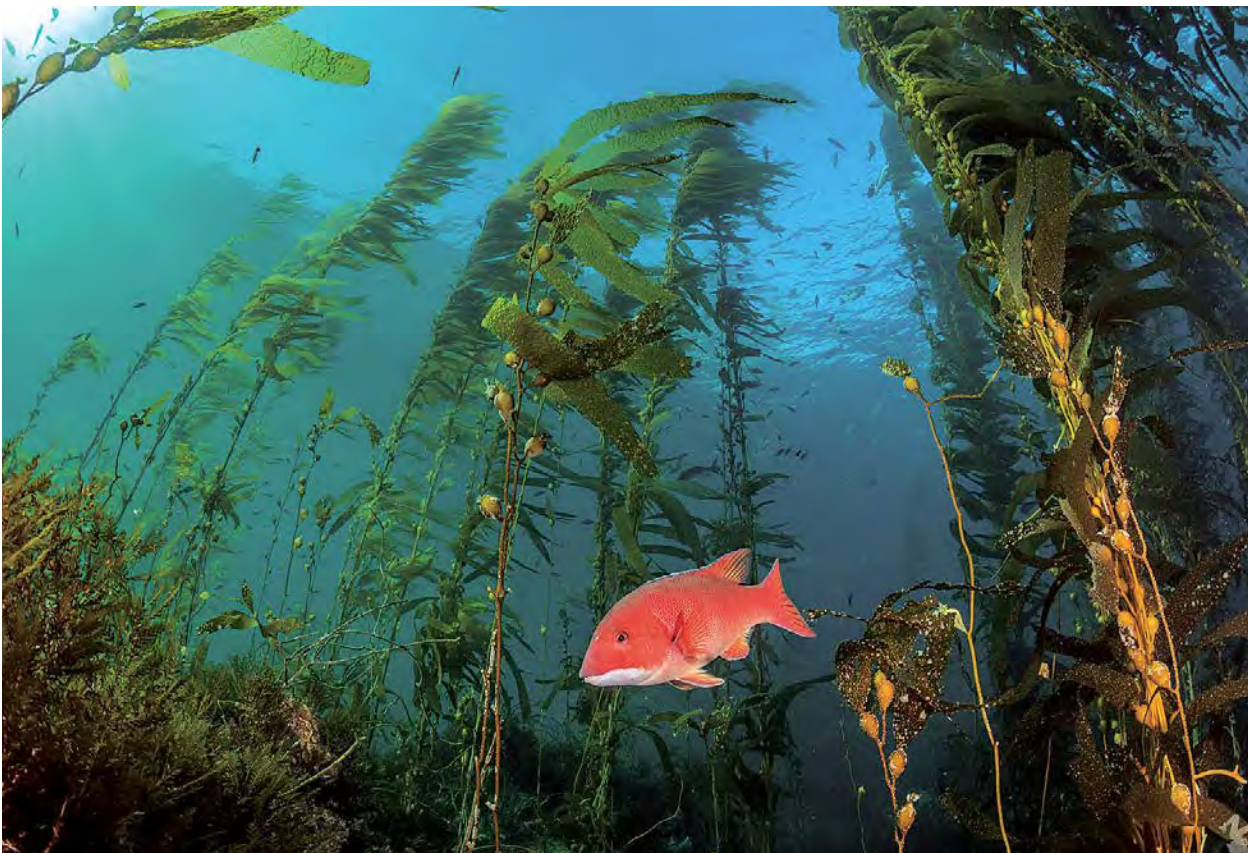


Figure 8.3.3 Giant kelp forest (*Macrocystis pyrifera*) with sheephead (*Semicossyphus pulcher*) in foreground. © Brent Durand.

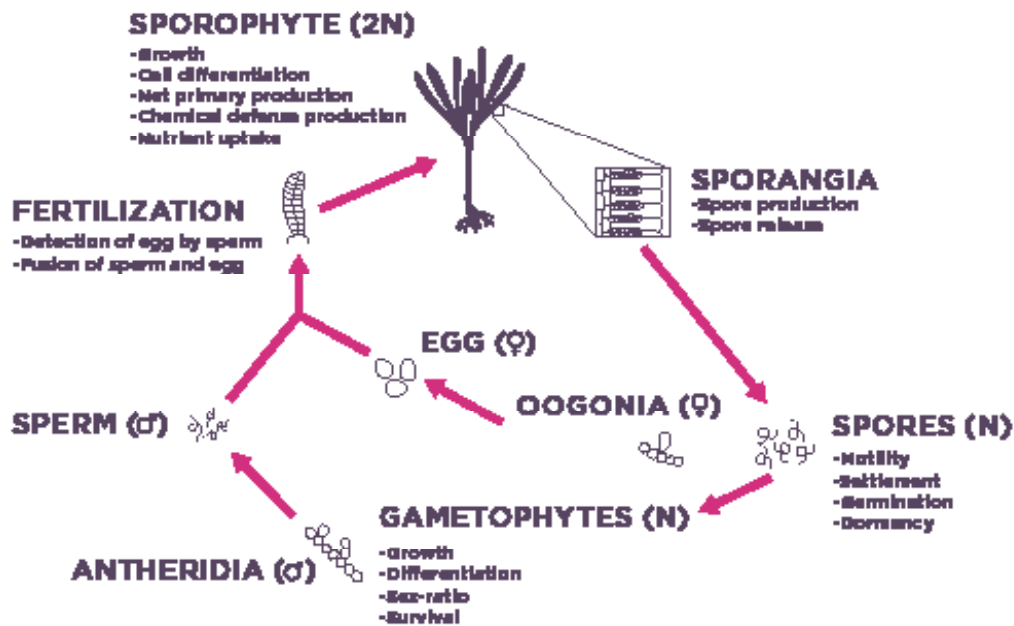


Figure 8.3.4 General life cycle of macroalgae. Under the different life stages are important processes to consider when examining the impacts of deoxygenation.

Previous work looking at the effects of oxygen on kelp and other macroalgae gives us some insight into how these processes may be altered, particularly oxygen effects on photosynthesis. Many marine algae photorespire, since Rubisco, the enzyme that catalyzes CO_2 for photosynthesis also catalyzes a reaction with oxygen, leading to the loss of fixed carbon (Bowes et al., 1971). Because of this, decreasing oxygen concentrations can actually increase photosynthetic rates in some marine macroalgae (Burris, 1980; Downton et al., 1976; Turner et al., 1956). Moving forward, it is important to consider the consequences of this for overall NPP, which would incorporate oxygen effects on both photosynthesis and respiration.

Largely missing from the literature on the effects of climate change on macroalgae is research on juvenile stages. Studies of the direct effects of hypoxia on the performance and success of macroalgae throughout their life cycles would provide insight into how these important organisms will develop under a changing climate. Despite the current research emphasis on the effects of ocean acidification on macroalgae, the understanding of its impacts on different life stages is very limited (Gaitán-Espitia et al., 2014; Harley et al., 2012; Roleda et al., 2012; Shukla & Edwards, 2017), whereas the effects of hypoxia are unexplored. Because macroalgae undergo significant morphological and physiological changes through their life cycle from spore to the adult stage, several processes could be impacted by low oxygen, including settlement, early

post-settlement survival, gametogenesis, and growth (Figure 8.3.4). A focus on multiple stressors on the adult stage means over-looking other crucial periods within the macroalgal life cycle. For example, spores and gametes lack an outer cell wall, potentially making them more susceptible to climate stressors like low pH and oxygen (Gaitán-Espitia et al., 2014; Reed & Lewis, 1994), while small, low lying sporophyte stages that are expending energy for growth may be negatively impacted by hypoxia. However, also important to consider is that algae can modify micro-environments within their boundary layer, potentially buffering the effects of acidification and hypoxia (Cornwall et al., 2013), and smaller stages live within the diffusive boundary layer (Gundersen & Jorgensen, 1990), which experience different oxygen levels than the bulk water above. Therefore, it is important to consider several factors that influence macroalgae and kelps throughout their life cycles, since they undergo large transitions in size and metabolic demands, all of which could be influenced by deoxygenation.

Due to the co-occurrence of multiple stressors, deoxygenation will never act in isolation. In upwelling systems where physical processes force low DO, low pH waters to nearshore habitats like rocky reefs and kelp forests, both hypoxia and ocean acidification should be considered when designing experiments. With continued ocean warming, it is also important to consider the possibility of these three stressors acting in concert to affect macroalgae (Pörtner et al., 2005).



Figure 8.3.5 *Ecklonia radiata* kelp forest © Daniel Poloha / Shutterstock.com.

Under warming, rates of respiration may increase faster than rates of photosynthesis (Hancke & Glud, 2004; Masini & Manning, 1997; Tait & Schiel, 2013), which has implications for multiple stressor impacts on macroalgae and kelps. In macroalgal assemblages in New Zealand and Australia, rising temperatures led to higher rates of respiration compared to rates of NPP. This suggests that warming can alter the balance between respiration and photosynthesis, leading to overall declines in NPP. Sub-canopy algae that experience lower light may be particularly susceptible to warmer temperatures due to increased respiration rates in combination with reduced light for photosynthesis (Tait & Schiel, 2013). This increased rate of oxygen use may be inhibited if warming co-occurs with hypoxia. On the other hand, in upwelling systems where low oxygen and low pH often occur with lower temperatures, there may be a mitigating effect of low temperature by decreasing metabolic demands (Vaquer-Sunyer & Duarte, 2011). Interactions with low pH may also lead to variable responses, since acidification itself can negatively impact the growth of calcifying macroalgae (Kuffner et al., 2008), but because acidification can benefit photosynthesis (Koch

et al., 2013), this may counterbalance the negative impacts of hypoxia. As research moves forward, it is imperative to consider the effects of multiple stressors, since deoxygenation is occurring alongside ocean acidification and warming, and the interaction between these stressors may lead to unexpected consequences for macroalgal communities.

Macroalgae differ in their photosynthetic and respiration rates, so understanding the impacts of climate change on whole communities will require detailed experiments using multiple species to elucidate ‘winners’ and ‘losers’. Few studies have examined how whole assemblages of macroalgae are affected under climate change but work in intertidal rock pools show that high temperatures and acidification impact biomass, productivity, and respiration (Olabarria et al., 2012). But the effects vary depending on species composition. For example, turf algae are thought to fare better under future scenarios, and work done in Australian *Ecklonia radiata* kelp forests (Figure 8.3.5) showed that warming and acidification act synergistically to promote the growth of turf algae over recruits of *E. radiata*, so climate change may directly benefit faster growing, more opportunistic algae (Connell & Russell, 2010; Russell et al., 2009). Some calcifying algae (Figure 8.3.6) have been shown to undergo necrosis and die under higher temperatures and lower pH (Martin & Gattuso, 2009), while others seem quite resilient to acidification (O’Leary et al., 2017). When thinking about hypoxia, different photosynthetic physiologies, including oxygen sensitivity (Beer & Israel, 1986; Kübler et al., 1999) and different strategies for carbon uptake (Cornwall et al., 2012; Hepburn et al., 2011; Koch et al., 2013), will play an important role in determining which species may fare better or worse under a changing climate.

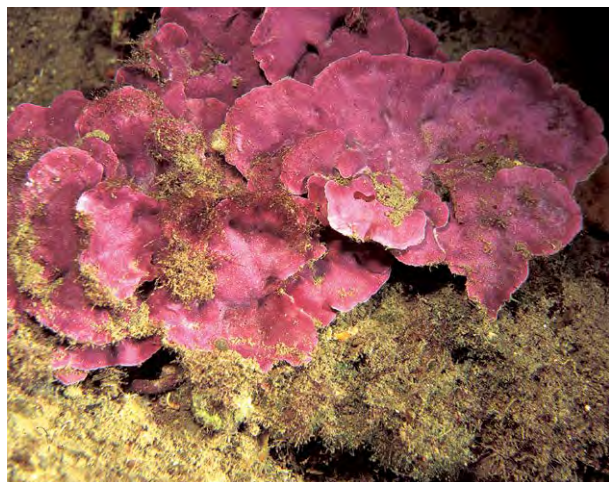


Figure 8.3.6 *Lithophyllum stictiforme* complex © David Luquet.

8.3.4 Deoxygenation impacts on kelp fauna

In estuaries and inner shelf systems, prolonged hypoxic events can lead to mass mortality of both fish and invertebrates, generating areas devoid of life often referred to as 'dead zones' (Chan et al., 2008; Diaz, 2001; Grantham et al., 2004). In dynamic coastal upwelling zones low-oxygen events are often more episodic; it is less likely for organisms in these systems to experience direct mortality as they may be adapted to a higher degree of natural variability in DO. But deoxygenation and associated environmental stressors may impact kelp and other macroalgae indirectly, through lethal and sublethal impacts on grazers and predators (e.g. Low &

Micheli, 2018). Research from other systems suggests that the cumulative effect of sub-lethal impacts may be comparable to those of direct mortality (Breitberg et al., 2009). There is a dearth of published studies on the responses of kelp forest organisms to low oxygen, as most studies have been conducted on estuarine and infaunal organisms (e.g. Vaquer-Sunyer & Duarte, 2008), therefore we discuss general expectations.

Kelp forest ecosystems include structure-producing kelps and associated biota including marine mammals, fishes, crabs, sea urchins, and algae (Mann, 1973). Though these ecosystems persist between ecological processes driving their development and deforestation,

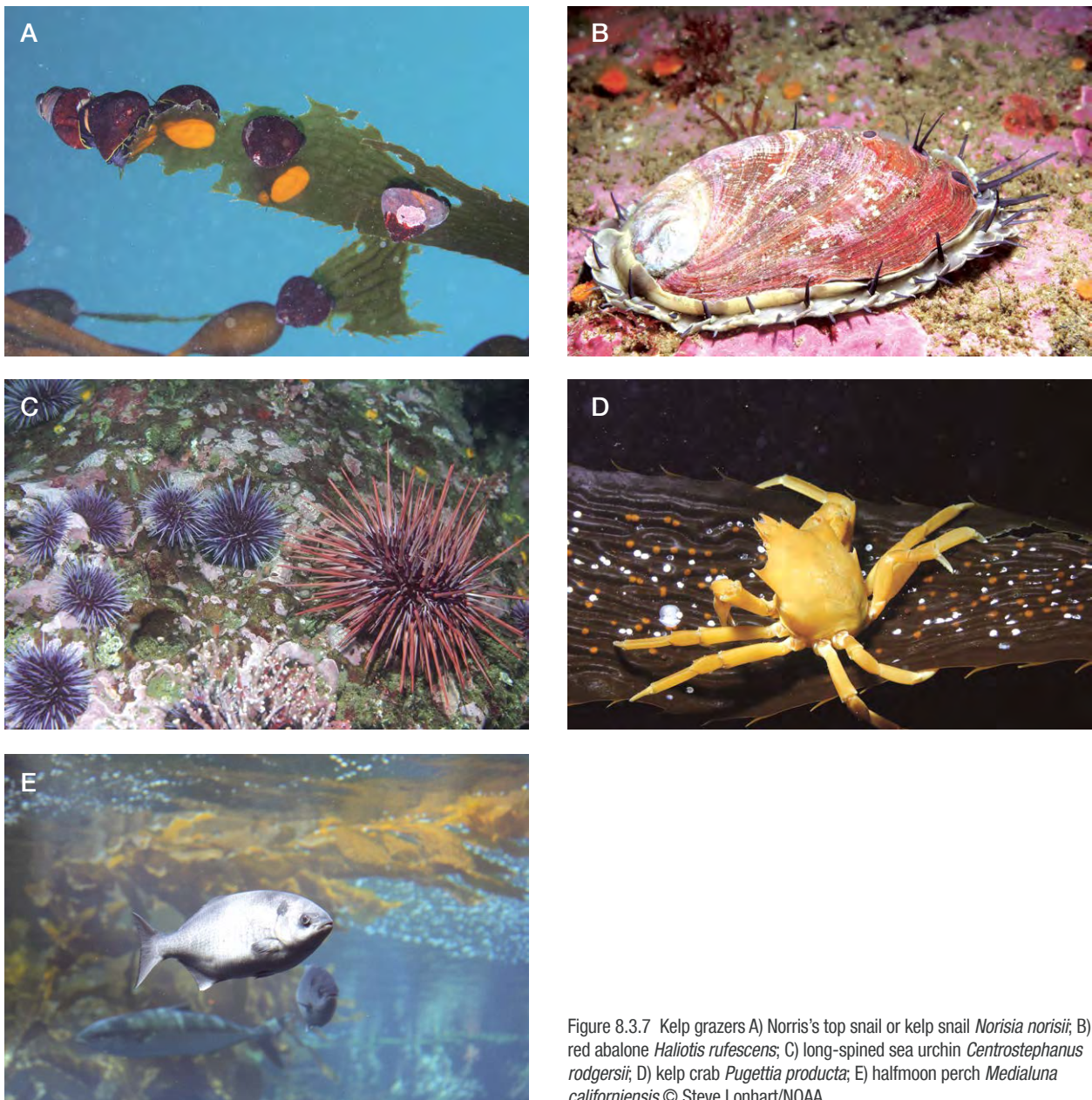


Figure 8.3.7 Kelp grazers A) Norris's top snail or kelp snail *Norisia norisii*; B) red abalone *Haliotis rufescens*; C) long-spined sea urchin *Centrostephanus rodgersii*; D) kelp crab *Pugettia producta*; E) halfmoon perch *Medialuna californiensis* © Steve Lonhart/NOAA.



Figure 8.3.8 Kelp grazer predators A) sun star © Ethan Daniels; B) sea otter *Enhydra lutris* © Chase Dekker.

empirical evidence suggests that their structure and function is dictated primarily by top-down forces rather than bottom-up control (Halpern et al., 2006). Consumers structure kelp forest interactions via two primary ‘drivers’: herbivory by grazers and carnivory by predators of grazers. Kelp grazers span multiple taxa, including echinoderms (sea urchins), gastropods (snails, abalone), crustaceans (kelp crabs, amphipods, isopods), and herbivorous fish (Graham et al., 2008) (Figure 8.3.7). Predators of these grazers are also taxonomically diverse, including carnivorous crustaceans such as crabs and lobsters, echinoderms like predatory sea stars, invertivorous fish, and air-breathing mammals like sea otters (Figure 8.3.8). Sea urchins are particularly known for their ability to overgraze kelp forests and bring about ecosystem state shifts that produce ‘urchin barrens’ (Ling et al., 2015). The loss of predator control on sea urchin populations has led to well-documented trophic cascades in kelp forests (Estes et al., 1998). Other grazers such as gastropods may also have strong impacts on kelp populations, especially at the juvenile stages (Dayton et al., 1984; Henriquez et al., 2011; Sala & Graham, 2002) and the potential indirect effects of their predators on juvenile kelp are unknown.

Few published studies have examined how kelp forest organisms respond to low DO. Those that do exist, together with evidence from other ecosystems, suggest that changes in foraging, feeding, and movement are likely sublethal responses for many organisms (e.g. Eby & Crowder, 2002; Low & Micheli, 2018). Thresholds for these sublethal responses vary across taxa, with cnidarians among the most tolerant and crustaceans and fish being the most sensitive (Vaquer-Sunyer & Duarte, 2008). Air-breathing predators like sea otters will not experience any direct impacts from hypoxia. Mobile organisms may be able to avoid hypoxic areas, leading to the concentration of animals in habitat

refuges (Craig, 2012; Eby & Crowder, 2002), and impacts on density-dependent processes (Vanderploeg et al., 2009). Avoidance strategies may be dictated by the trade-offs between oxygen stress and other factors like predation risk and food availability (Craig, 2012; Vaquer-Sunyer & Duarte, 2008). For example, benthic fishes have been reported to move towards near-surface waters to breathe when bottom waters become hypoxic (Wu, 2002) while other fishes and crustaceans move to shallow waters (Bell, 2003). Such behavioural responses, in conjunction with decreased sensory abilities (Domenici et al., 2013), may increase the vulnerability of mobile taxa to natural predators and fishing effort (Domenici et al., 2007; Prince et al., 2010). Furthermore, kelp fauna across a wide variety of taxa may exhibit reduced feeding, growth, and reproductive processes under hypoxia (e.g. Kim et al., 2013; Low & Micheli, 2018; McNatt & Rice, 2004; Siikavuopio et al., 2007; Wu, 2009). Finally, micro-organisms involved in kelp and macroalgae decomposition, including bacteria and fungi, are also likely to be differentially affected by hypoxic conditions, but to our knowledge no studies have examined how kelp decomposition rates and nutrient regeneration may be influenced by hypoxia.

Although upwelling-driven hypoxia in kelp forests generally occurs together with exposure to low pH, even fewer studies have addressed how kelp fauna respond to these multiple stressors. Existing studies suggest that the co-occurrence of low DO and low pH is most likely to have negative synergistic impacts (Kim et al., 2013; Steckbauer et al., 2015), and much more work in this area is needed.

8.3.5 Ecosystem impacts

Due to human-mediated impacts upon their physical or biological components, many kelp forests today look

and behave differently from their historical counterparts (Steneck et al., 2002). Trophic cascades resulting from the local extirpation of the large predators are well-documented (Estes et al., 1989; Steneck, 1998). Complex interactions and non-linear thresholds (Tegner et al., 1996) complicate efforts to predict how kelp forests will respond to ocean deoxygenation, but global case studies confirm the existence of “tipping points” beyond which these systems will reorganize (Ling et al., 2015; Selkoe et al., 2015; Steneck et al., 2002)

The responses of kelp forest organisms to hypoxia will likely alter trophic interactions and energy flow in kelp forest food webs. Differences in vulnerability between grazers and predators may strengthen or weaken trophic cascades and top-down control on kelp populations (Menge & Olson, 1990; Menge & Sutherland, 1987). Effects are likely to be most severe in ecosystems where air-breathing marine mammal predators such as sea otters are absent and coastal food webs have been fished down. In regions where predation on sea urchins is driven by crustaceans and large fish, hypoxia may increase grazing and deforestation if predator species are excluded by the persistence of low oxygen waters and/or a decline in the availability of alternative prey species.

Community-wide impacts of periodic hypoxic events in other ecosystems include reduced community biomass and species richness (Dauer, 1993; Nilsson & Rosenberg, 1994). In kelp forests, this relationship is particularly troubling as diversity may buffer against phase shifts and facilitate recovery from physical disturbance. Kelp forest systems with functional redundancy among predators and herbivores are thought to be comparatively resilient while decreased diversity may amplify the effects of species interactions and accelerate the transition to alternative stable states (Steneck et al., 2002). If environmental and anthropogenic drivers reduce biodiversity in kelp forests, these systems may be more susceptible to invasion from non-native species (Stachowicz et al., 1999). Where limited diversity has simplified trophic interactions and community structure (Steinberg et al., 1995), deforestation has been linked to the range expansion of tropical, herbivorous fish (Vergés et al., 2016) and the proliferation of non-native algae and encrusting bryozoans (Levin et al., 2002). The role of disease in structuring the interaction between grazers and kelp may also be impacted by increases in the frequency and duration of low oxygen events. Hypoxic conditions create physiological stress that can

increase an organism’s susceptibility to disease (Harvell et al., 1999) and the proliferation of species resilient to environmental stressors like hypoxia can set the stage for disease-related mass mortalities. Though disease outbreaks amongst grazer populations can facilitate the expansion of kelp forests (Lafferty, 2004; Pearse & Hines, 1979; Scheibling et al., 1999), when organisms associated with control and regulation of herbivore (i.e. sea star) populations are affected, destructive grazing and deforestation may increase (Schultz et al., 2016; Tegner & Dayton, 1987).

8.3.6 Conclusions

The substantial spatio-temporal variability in oxygen and pH within kelp forests poses a key challenge for our understanding of impacts and for management. Given the high natural variability they experience, kelp forest organisms may be pre-adapted to tolerate the low-oxygen, acidic conditions expected under climate change (Booth et al., 2012). But the low oxygen and pH conditions these organisms experience might also be close to their physiological limits. In this case, climate change may push these organisms over a tipping point as these periodic exposures become more prolonged or extreme. Most studies on organism responses to hypoxia have used extended, constant exposures, which may not be a good representation of the patchy, repeated and periodic low-DO exposures that kelp forest organisms experience. In addition, managers often use single, static thresholds for assessing oxygen conditions, which may not be appropriate for an ecosystem with naturally high oxygen variability. This supports the need for studies that specifically address the effects of spatial and temporal variability of hypoxic conditions and how patterns of exposure may interact with other environmental stressors to impact macroalgae and associated fauna.

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8.3.7 References

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8.4 The significance of ocean deoxygenation for continental margin mesopelagic communities

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Summary

- Global climate models predict global warming will lead to declines in midwater oxygen concentrations, with greatest impact in regions of oxygen minimum zones (OMZ) along continental margins. Time series from these regions indicate that there have been significant changes in oxygen concentration, with evidence of both decadal variability and a secular declining trend in recent decades. The areal extent and volume of hypoxic and suboxic waters have increased substantially in recent decades with significant shoaling of hypoxic boundary layers along continental margins.
- The mesopelagic communities in OMZ regions are unique, with the fauna noted for their adaptations to hypoxic and suboxic environments. However, mesopelagic faunas differ considerably, such that deoxygenation and warming could lead to the increased dominance of subtropical and tropical faunas most highly adapted to OMZ conditions.
- Denitrifying bacteria within the suboxic zones of the ocean's OMZs account for about a third of the ocean's loss of fixed nitrogen. Denitrification in the eastern tropical Pacific has varied by about a factor of 4 over the past 50 years, about half due to variation in the volume of suboxic waters in the Pacific. Continued long-term deoxygenation could lead to decreased nutrient content and hence decreased ocean productivity and decreased ocean uptake of carbon dioxide (CO₂). Deoxygenation could also lead to increased oceanic release of nitrous oxide (N₂O), a powerful greenhouse gas that is microbially produced in suboxic conditions.
- There are few time series to evaluate the impact of declining oxygen on the mesopelagic fauna of continental margins. However, in the California Current a broad suite of mesopelagic fishes has declined ~77%, highly correlated with a 22% decline in midwater oxygen concentrations. Several tropical-subtropical taxa noted for their adaptations to hypoxic conditions have increased in dominance. The Humboldt squid, adapted to preying on mesopelagic fishes in the hypoxic boundary layer, has dramatically increased its range and apparent abundance. Mesopelagic micronekton is a key trophic link between the zooplankton and a variety of predators: squids, tunas, sharks and other fishes, and a number of marine mammals and seabirds of special conservation interest, so a widespread decline in mesopelagic fishes could have profound consequences for global marine ecosystems and fisheries.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen concentrations, expansion of suboxic and hypoxic waters.	<ul style="list-style-type: none"> Biogeochemical consequences: increased denitrification, leading potentially to loss of nitrate and decreased ecosystem productivity. Possible increased N₂O production, a powerful greenhouse gas, a positive feedback to global warming.
Shoaling of oxygen minimum zones and hypoxic boundary layers.	<ul style="list-style-type: none"> Potential shoaling of deep scattering layers, leading to possible increased predation risk and declining abundance; decreased carbon sequestration by diel migrators. Possible shifts in micronekton community composition toward taxa better adapted to suboxic conditions. Range expansion of predators, such as Humboldt squid, adapted to hypoxia.
Decreased abundance of mesopelagic micronekton not adapted to more extreme hypoxic and suboxic conditions.	<ul style="list-style-type: none"> Decreased prey available to a wide range of higher predators: fishes, squids, marine mammals and seabirds.

8.4.1 Introduction

Oxygen is a critical variable for the survival of marine organisms and as a determinant of the distribution and structure of marine communities. Declining oxygen concentrations are now a major issue in two somewhat distinct habitats: coastal waters subject to nutrient input from the land and hence to eutrophication and development of so-called “dead zones”, and along continental margins in regions of high productivity and

relatively sluggish circulation, which includes the major eastern boundary currents (EBC) and associated tropical oceans in the eastern Pacific, south-eastern Atlantic and northern Indian Oceans (Helly & Levin, 2004; Stramma et al., 2008) (Figure 8.4.1). The oxygen minimum zones (OMZ) in these regions along the continental margin are generally concentrated at mesopelagic depths, defined as 200 to 1000 m depth, where organic material settling out of the euphotic zone is predominantly consumed and metabolized (Robinson et al., 2010).

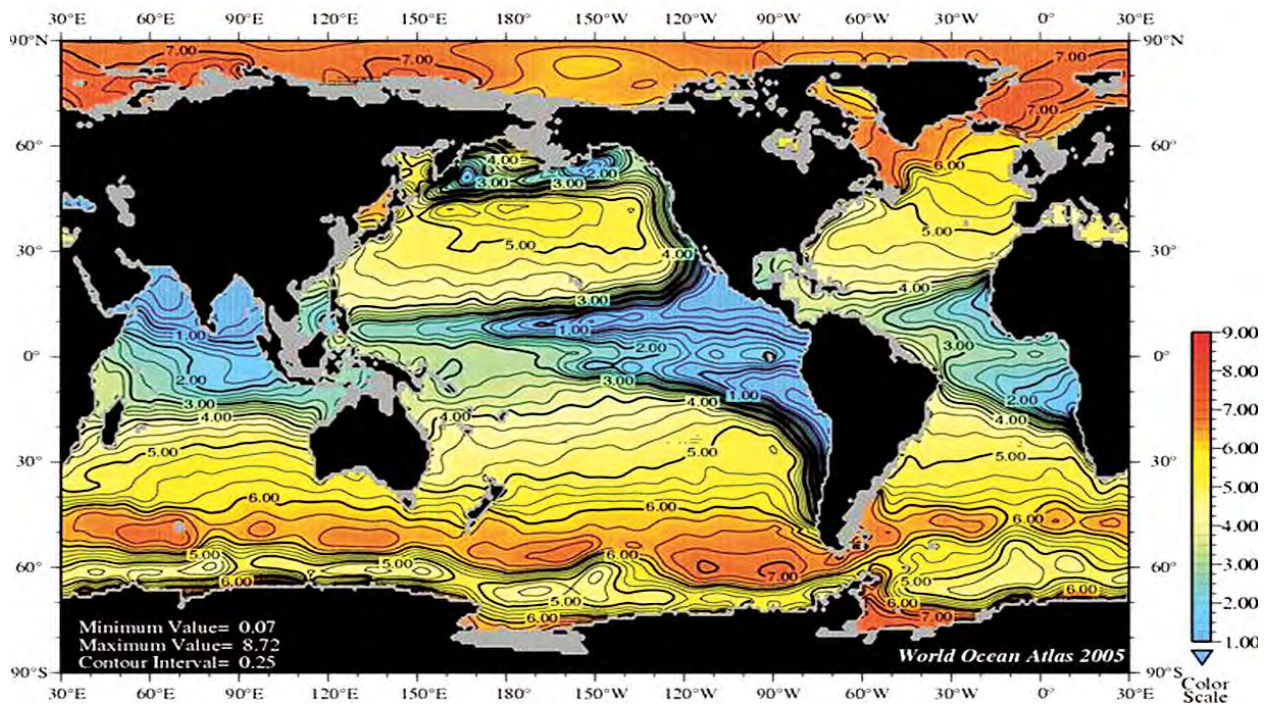


Figure 8.4.1 Annual mean oxygen concentration in ml L⁻¹ at 200 m depth, showing the distribution of major OMZs in the tropical Atlantic, Pacific and Indian Oceans and along the major eastern boundary currents. From the World Ocean Atlas (2005).

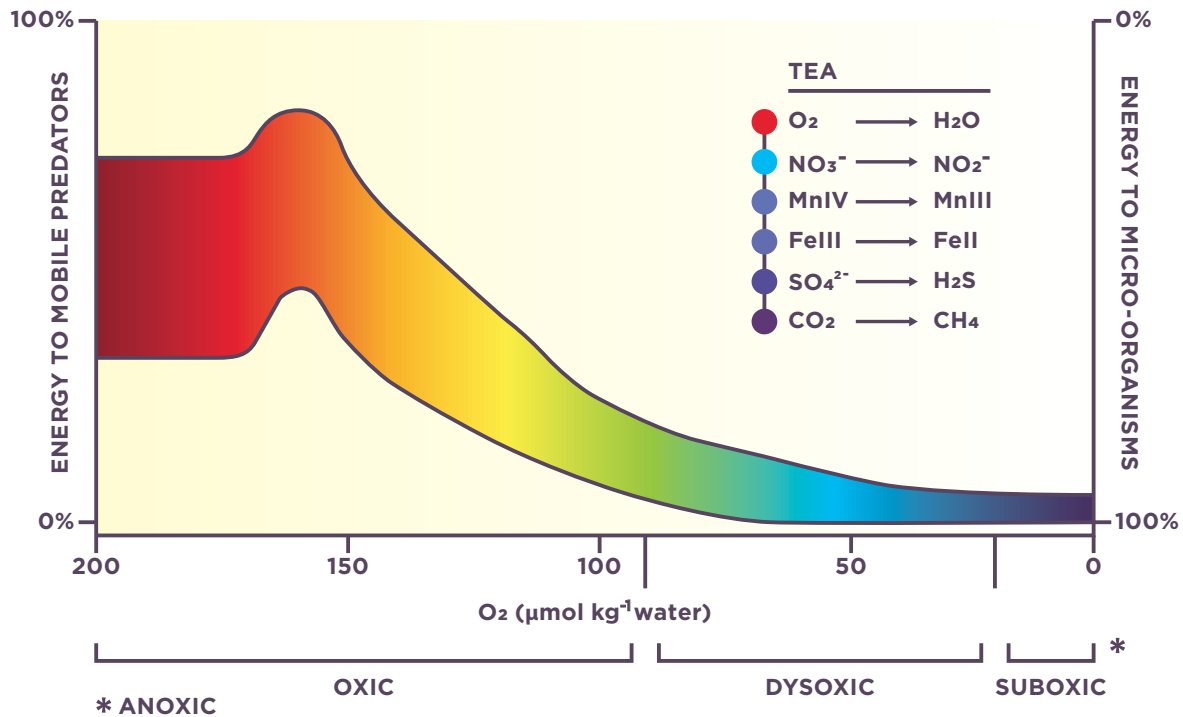


Figure 8.4.2 Oxidic, dysoxic (or hypoxic) and anoxic states of the ocean are defined in relation to oxygen concentration, along with the dominant energetic pathways at each state. From Wright et al. (2012).

Oxygen concentrations $< 2 \text{ ml O}_2 \text{ L}^{-1}$ are commonly defined as *hypoxic*, although many fishes, crustaceans and other metazoans exhibit physiological responses to oxygen concentrations considerably higher than this (Vaquer-Sunyer & Duarte, 2008). *Suboxic* conditions are often defined as oxygen concentrations $< 0.1 \text{ ml O}_2 \text{ L}^{-1}$, when microbial metabolism becomes predominantly anaerobic (Deutsch et al., 2011), whereas *anoxia* refers to the complete absence of oxygen (Figure 8.4.2). Classically, suboxia has been used as the criterion for determining the extent of OMZs (Paulmier & Ruiz-Pino, 2009), but higher organisms are strongly influenced by hypoxic conditions, so these waters will be considered in this review. Furthermore, there is considerable variation in the literature in defining the limits of hypoxia, suboxia, and OMZs, in large measure because organisms vary widely in their response to low-oxygen conditions (Vaquer-Sunyer & Duarte, 2008). OMZs are estimated to cover more than 1 million km^2 on the continental margins of the world ocean, defined as waters with oxygen concentration $< 0.5 \text{ ml L}^{-1}$ (Helly & Levin, 2004). On a volumetric basis, hypoxic waters are estimated to occupy 5% of the ocean's volume but are pervasive in the eastern Pacific and northern Indian Ocean between 100 and 1000 m depth (Deutsch et al., 2011), with a somewhat smaller, less intensely hypoxic zone in the upwelling regions of the eastern tropical Atlantic Ocean (Figure 8.4.1).

Deoxygenation of the global ocean is commonly predicted by global ocean climate models as the consequence of a decrease in oxygen solubility and deep-water ventilation in a warmer, more stratified ocean (Gruber, 2011; Keeling et al., 2010; Matear & Hirst, 2003; Oschlies et al., 2008). These predictions are consistent with the contraction and expansion of OMZs observed (based on proxies) during glacial-interglacial periods in the past 200 kyr (Falkowski et al., 2011; Galbraith et al., 2004), although the relationship may not be straightforward (Jaccard & Galbraith, 2012). However, recent climate models appear to underestimate the extent of deoxygenations due to climate warming, with projections of a 2-4% loss in oceanic oxygen content from 1870 to 2100 (Bopp et al., 2013; Levin, 2018). However, syntheses of global observations indicate an average 2% global loss of oxygen in the open ocean over just the past 50 years (Helm et al., 2011; Schmidtko et al., 2017), with substantially greater losses, in the order of 20%, in the eastern tropical Pacific, the North Pacific, and Southern Ocean (Levin, 2018) (Figure 8.4.3). The largest trends are often observed in the naturally oxygen-depleted OMZs along continental margins, where oxygen concentrations are at threshold levels for many organisms. The volume of anoxic water has quadrupled and the area of ocean with hypoxic water ($< 1.5 \text{ ml O}_2 \text{ L}^{-1}$) at 200 m depth has increased by 4.5 million km^2 , an area roughly the size of the European

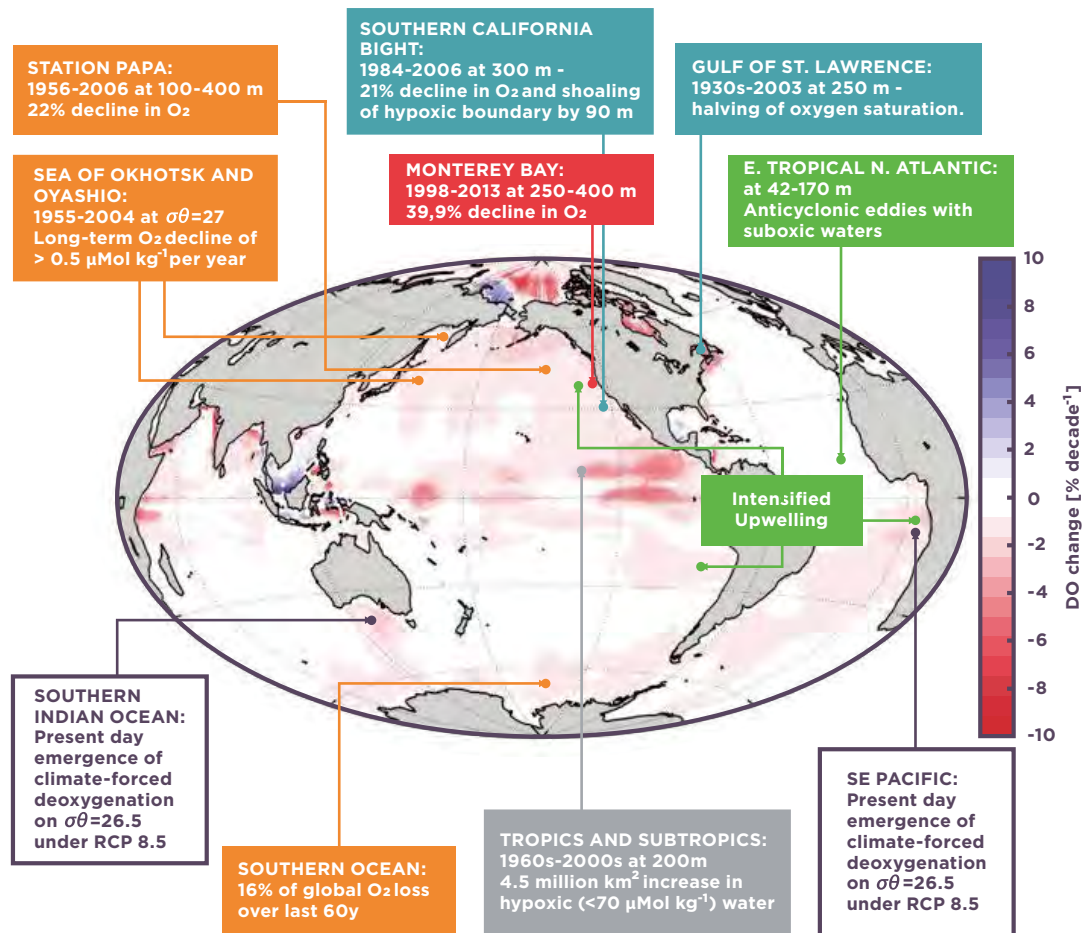


Figure 8.4.3 Summary findings of the primary long-term records of open ocean deoxygenation at mesopelagic depths superimposed on the percentage change in dissolved oxygen per decade since 1960 (from Schmidtko et al., 2017). The colour of the text boxes indicates the potential primary drivers: orange: solubility and stratification; red: oxygen decline in source waters; blue: circulation-driven changes; green: intensified upwelling; grey: uncertain causes; white: climate warming impact apparent due to low natural variability. Abbreviations: $\sigma\theta$, density surface; RCP, representative concentration pathway. From Levin (2018).

Union, over the past 50 years (Beitburg et al., 2018). Over this period, the hypoxic boundary layer (HBL) has shoaled approximately 100 m in the Gulf of Alaska and southern California Current, where midwater oxygen time series extend back more than 50 years (Bograd et al., 2008; Whitney et al., 2007).

Marine metazoans generally exhibit strong oxygen-level constraints, so it is expected that declining oxygen levels and the expansion of zones with critical oxygen levels will have significant impacts on the physiology, distribution, abundance and general ecology of the marine fauna in these regions (Ekau et al., 2010; Stramma et al., 2010; Vaquer-Sunyer & Duarte, 2008).

As Gruber (2011) notes, the ocean today faces a triad of threats: acidification, warming, and deoxygenation. These are linked causally – CO_2 build-up causes both global warming and ocean acidification and warming in turn leads to deoxygenation – and they may also work

synergistically in their ecological impacts. Deoxygenation and acidification also tend to be correlated in the ocean, since oxygen consumption by marine organisms produces CO_2 that in turn leads to a decline in ocean pH. However, each of these stressors has its own unique physiological and ecological impacts. This review will focus on the impact of deoxygenation, while noting potential synergistic impacts.

8.4.2 Definition of species groups

In considering the impacts of deoxygenation on the mesopelagic fauna of continental margins, the full range of the fauna from microbes to higher predators will be considered.

Microbial activity is closely associated with oxygen content, groups with differing metabolisms being found in well-oxygenated, hypoxic and anoxic waters. At suboxic concentrations ($[\text{O}_2] < 0.1 \text{ ml L}^{-1}$) anaerobic

processes dominate, such as denitrification and anaerobic ammonium oxidation. These processes in the OMZs are responsible for removing about a third of the fixed nitrogen in the global ocean, the remainder occurring in the anaerobic sediments (Sarmiento & Gruber, 2006). In nutrient-depleted ocean waters, certain photosynthetic cyanobacteria, such as *Trichodesmium* and *Prochlorococcus*, are able to fix atmospheric nitrogen (N_2) to ammonium and are responsible for approximately half of the ocean's photosynthetic production. However, the ocean's nitrogen cycle is in approximate balance, so an equivalent amount of nitrate and ammonium is converted back to gaseous nitrogen. This microbially-mediated process occurs only under suboxic conditions, either in the water column in OMZs or within the sediments.

This review will focus on the zooplankton, micronekton and nekton, particularly those mesopelagic taxa (principally crustaceans, squids and fishes) that interact with low-oxygen waters and are impacted by them. These groups are defined primarily along a size spectrum, with the zooplankton ranging in size from approximately 2 mm to 2 cm. As their name implies, they are largely advected by the ambient currents, although they are able to migrate on a diel or seasonal basis to depths of several hundred metres or more. The micronekton (roughly 2 – 20 cm in length) are dominated by small fishes, with squids and larger pelagic crustaceans comprising a significant fraction (Figure 8.4.4). They feed predominantly at the second trophic level and are able to carry out diel migrations of several hundred to 1000 m. The nekton (0.2 – 2 m) consist predominantly of fish and squid, predators on the micronekton.

The mesopelagic fauna is highly diverse with three-fold more mesopelagic than epipelagic fish taxa in the

global ocean (Koslow, 2007) (Figure 8.4.5). The most diverse family of mesopelagic fishes are the myctophids or lanternfishes (Figure 8.4.6), with some 240 species (Nelson, 2006). They are plankton feeders, but unlike the silvery plankton feeders in epipelagic waters (e.g. sardines, anchovies, mackerels), myctophids are highly adapted to life in the so-called “twilight zone,” with dark skins, large eyes, and numerous photophores or light organs (hence their name, “lanternfish”). However, the mesopelagic fauna encompasses a range of ecological and physiological strategies. A key family of mesopelagic fishes, the hatchetfishes (Figure 8.4.7), mostly inhabits the upper mesopelagic zone above ~500 m depth and typically has reflective scales as camouflage in these better-lit waters and has upward-directed eyes and mouth to pick out its prey against the downwelling light. On the other hand, one of the most abundant vertebrates on the planet, the fish *Cyclothone*, typically inhabits the deeper mesopelagic and bathypelagic, and its eyes are highly reduced (Figure 8.4.8).

The mesopelagic micronekton largely comprises the Deep Scattering Layer (DSL), so-called for its distinct signature on echo sounders. This is often, but not necessarily, associated with the HBL above the core of the OMZ and is noted for its diel migration into near-surface waters to feed at night (Bianchi et al., 2013; Netburn & Koslow, 2015) (Figure 8.4.9). However, a significant proportion of the DSL remains permanently at depth (Williams & Koslow, 1997), and these groups have markedly different physiological and life history strategies (Childress et al., 1980). Many lanternfishes are among the diel migrators whereas *Cyclothone* and hatchetfishes are generally among the non-migrators. In regions with the most strongly developed OMZ, where hypoxic waters may extend to within 200 m of the surface, a specialized mesopelagic fauna has evolved

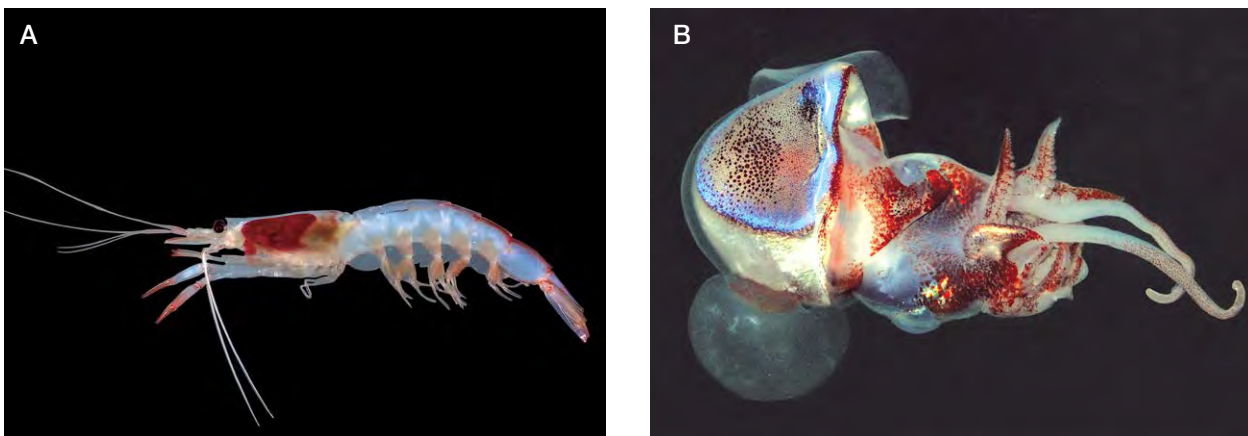


Figure 8.4.4 A) *Pasiphaea* sp. - a decapod shrimp; B) *Stoloteuthis* sp. - a bobtail squid. © Alex Rogers IUCN/NERC Seamounts Project.

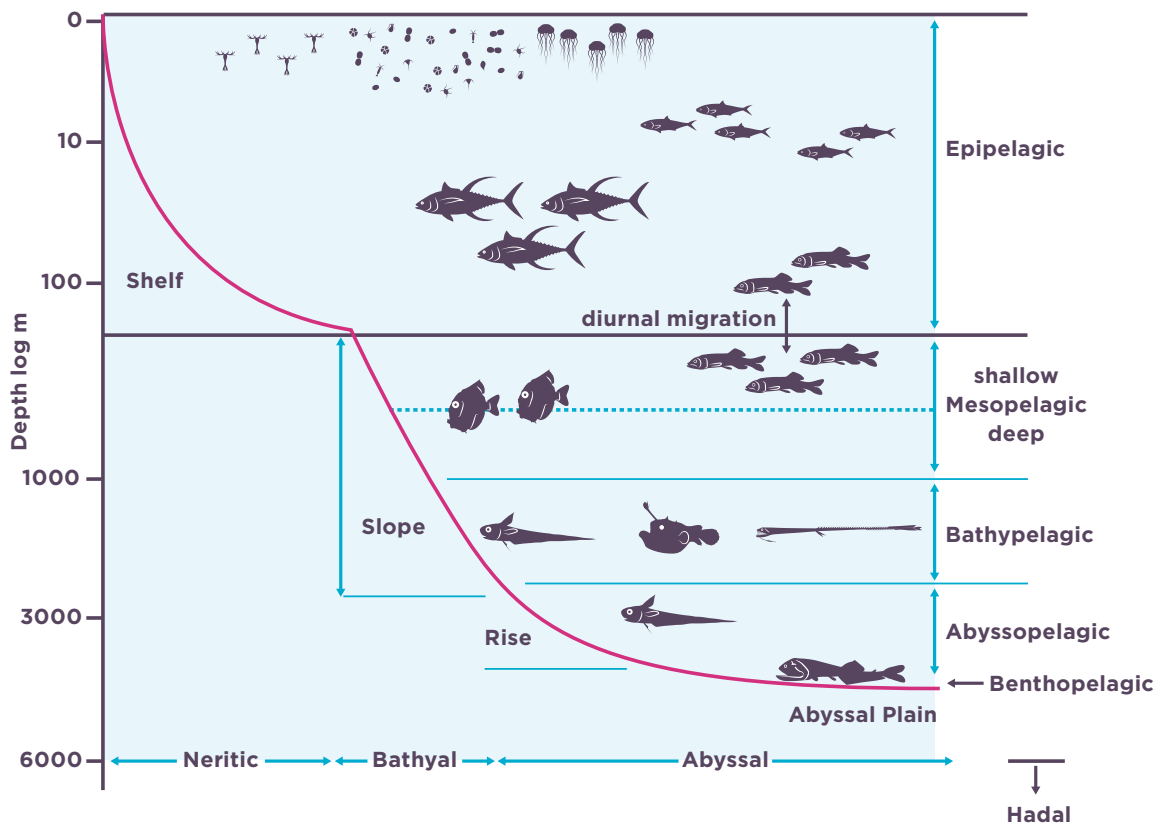


Figure 8.4.5 Schematic showing the zonation of pelagic and benthic faunas through the water column.

capable of descending into suboxic and anoxic waters during the day and migrating to the surface at night to re-oxygenate and feed (Childress & Seibel, 1998; Seibel, 2011). There does not appear to be a resident metazoan community in anoxic waters. However, mesopelagic zooplankton may be associated with the lower boundary of the OMZ as well as the upper boundary (Wishner et al., 2013).

8.4.3 Trends and impacts

8.4.3.1 Microbial communities

The mesopelagic zone has been termed the biogeochemical engine for the world's ocean: ~90% of the organic carbon that is exported from near-surface waters is consumed and metabolised back to CO_2 there, accounting for about 30% of the ocean's total CO_2 production (Robinson et al., 2010). A significant but still uncertain proportion of this water-column metabolism is carried out by the zooplankton and micronekton, but the bulk is generally considered to be carried out by the microbial community. The composition and metabolic functioning of the water-column microbial community is sensitive to ambient oxygen concentrations, with respiration dominated by dissolved oxygen where its

concentration is greater than $10 - 20 \mu\text{mol O}_2 \text{ kg}^{-1}$ sea water ($= 0.25 - 0.5 \text{ ml O}_2 \text{ L}^{-1}$), since oxygen provides the greatest free energy yield, followed progressively by nitrate (NO_3), manganese, iron, sulphate, and finally CO_2 (Figure 8.4.2; Wright et al., 2012).

These latter forms of microbial metabolism occur predominantly in the ocean's OMZs. Denitrification, the conversion of nitrate (NO_3), a key nutrient, to nitrite (NO_2) and then to gaseous nitrous oxide (N_2O) and finally



Figure 8.4.6 Lanternfish *Lepidophanes guentheri*. Note its various types of light organs, including photophores along its ventral surface that provide countershading so it can be seen less easily from below against downwelling light and its "flashlight" organs in front of its eyes. © Solvin Zankl / Alamy stock photo.



Figure 8.4.7 A hatchetfish, *Agryropelecus affinis*. Inhabiting the upper mesopelagic, it has reflective scales and upward-directed eyes and mouth to detect prey overhead against the downwelling light. © Paulo Oliveira / Alamy stock photo.

molecular nitrogen (N_2) is particularly critical to oceanic biogeochemistry, because it involves loss of NO_3^- , a limiting nutrient, from ocean waters, which must be balanced by nitrogen fixation if oceanic productivity is not to decline. The production of N_2O is also of interest because it is a powerful greenhouse gas, some 300-fold more powerful than CO_2 . The ocean accounts for about a third of natural N_2O emissions, much of which comes from the OMZs and HBLs. Expanding and shoaling pools of hypoxic and suboxic water could increase the ocean's production and release of N_2O (Codispoti, 2010). The OMZs account for approximately a third of the ocean's loss of fixed nitrogen (Sarmiento & Gruber, 2006).

Modelling studies indicate that the annual rate of denitrification in the eastern tropical North Pacific has varied by a factor of 4 over the past 50 years. About half of this is due to a two-fold variation in the volume of suboxic water in the Pacific, with the other half due to changes in microbial metabolism related to basin-scale variation in the depth of the thermocline, which affects microbial metabolism through the availability of organic matter (a shoaling suboxic layer contains more organic matter) and the influence of temperature on metabolic rates (Deutsch et al., 2011). Deutsch et al. (2014) use the $\delta^{15}N$ signal in sediment cores from anoxic basins off southern and Baja California to reconstruct a time series for denitrification in the California Current since 1850. (Denitrification preferentially removes the lighter ^{14}N isotope leaving behind nitrate enriched in ^{15}N , which is taken up by the phytoplankton and subsequently deposited in seafloor sediments.) The time series indicates that the OMZ and denitrification declined for much of the 20th century, prior to their expansion at the end of the century. This is linked to decadal



Figure 8.4.8 *Cyclothone acclinidens*, an abundant fish of the lower mesopelagic and bathypelagic with dark pigmentation and reduced eyes. © Welter-Schultes.

cycles in the intensity of the trade winds, which drive upwelling, productivity, and thermocline depth. This work indicates that variability in the trade winds, surface productivity and the depth of the thermocline, all of which influence oxygen consumption through microbial metabolism, may be as important as climate warming in their influence on oceanic oxygen concentration. Over the past several hundred thousand years, however, there has been a close correspondence between the $\delta^{15}N$ signal and glacial-interglacial cycles, with greater denitrification and apparently enhanced OMZs during periods of warming and contraction of OMZs during cooler periods. The trend over recent decades has been toward an expansion of the ocean's suboxic volume and hence greater denitrification. The potential long-term impact of this trend is a decline in the nitrate content of the world's ocean; as a key limiting nutrient, decreased nitrate could lead to a decrease in marine productivity and decreased uptake of carbon by the global ocean. Whether decreased nitrate regeneration in the ocean might be compensated by changes in oceanic nitrogen fixation remains unknown. Also uncertain are the relative impacts and interactions of trade wind/thermocline variability and climate warming on the pools of suboxic and hypoxic waters in the OMZs and HBLs of the world ocean, given that the tropical OMZs appear most sensitive to varying thermocline depth and its influence on microbial metabolism, whereas the extra-tropical HBLs may be most influenced by the effect of warming on oxygen solubility and water-column stratification, which inhibits the mixing of oxygen into deeper waters.

8.4.3.2 Zooplankton

Crustacean zooplankton, such as copepods and euphausiids, often carry out diel vertical migrations to avoid predators. Like fish, these crustaceans have varying tolerance for hypoxia: some taxa show little tolerance while others undergo metabolic suppression on the order of 40-80% and are able to vertically migrate in and out of hypoxic water in regions with a shallow HBL, such as the eastern Tropical Pacific or Humboldt Current (Seibel et al., 2016; Wishner et al., 2013). A distinct assemblage of crustaceans is also notable in

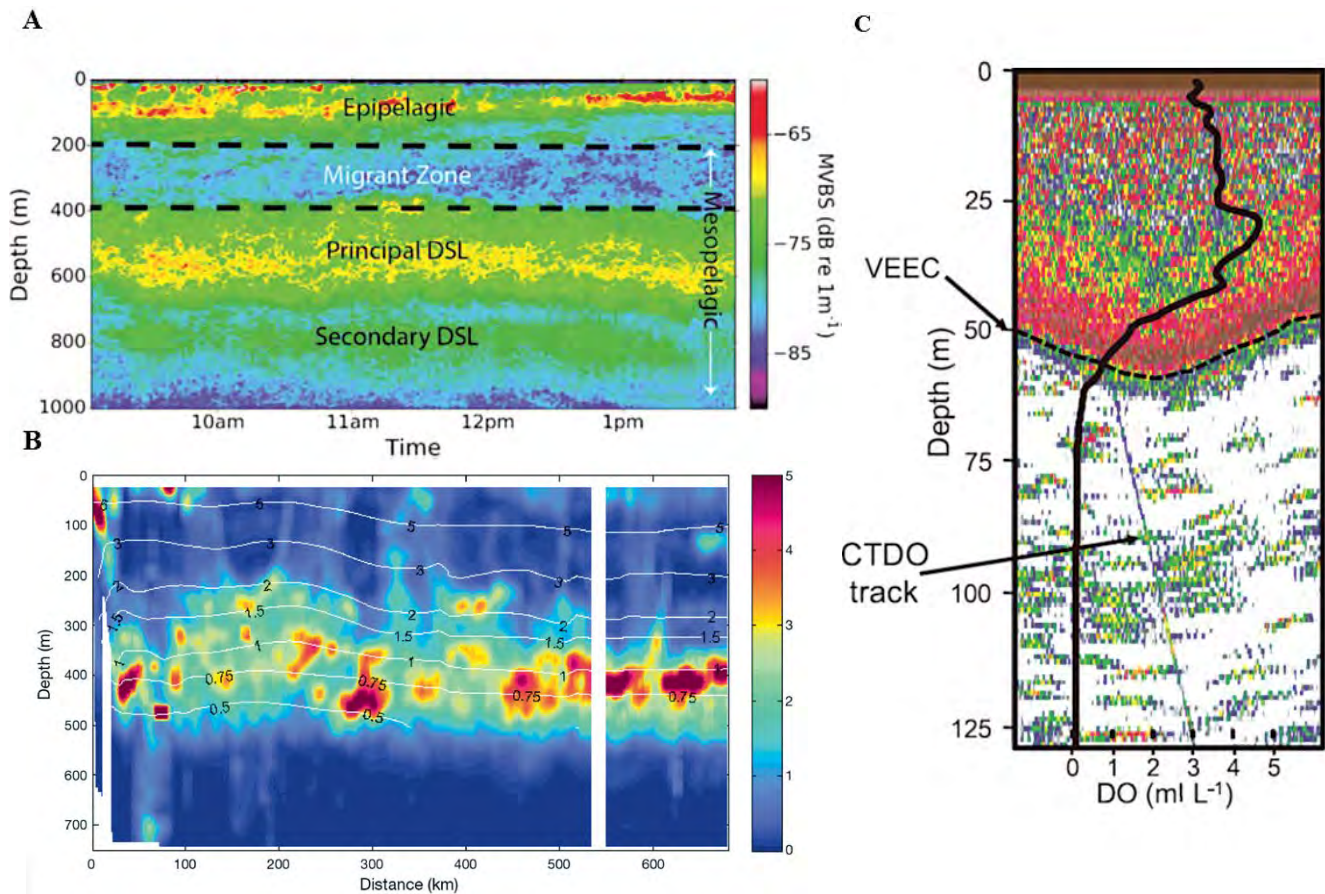


Figure 8.4.9 A) Echogram from the south-west Indian Ocean (28.8°S, 47.3°E). The colour bar is mean volume backscattering strength (MVBS, dB re 1 m⁻¹) (from Proud et al., 2017). B) Composite daytime echogram from 6 onshore-offshore transects of a CalCOFI cruises off southern California, with isolines of oxygen concentration (in ml O₂ L⁻¹). (From Koslow et al., 2011). C) Echogram from off Peru showing the vertical extent of anchovetta in relation to dissolved oxygen concentration. (From Bertrand et al., 2010.).

forming a secondary peak in biomass in the oxycline at the base of the OMZ (Saltzman & Wishner, 1997; Wishner et al., 1995, 2013). Although pteropods have been considered prime candidates to be affected by ocean acidification because of their aragonite shells, the physiology of pteropod taxa that migrate into the OMZ, unlike that of non-migrators, does not appear to be affected by elevated CO₂ (i.e. acidity) levels, presumably because they naturally encounter comparable conditions in the OMZ (Maas, 2012). However, while various authors have speculated how deoxygenation may affect crustacean or pteropod zooplankton (Ekau et al., 2010; Seibel et al., 2016; Stramma et al., 2010) (Figure 8.4.10), no studies have linked zooplankton time series of abundance with changing oxygen conditions.

Gelatinous zooplankton appear to be less stressed by hypoxic conditions than fishes and crustaceans, and several authors have speculated that jellyfish and ctenophore blooms may be facilitated by hypoxic conditions, as well as by other anthropogenic perturbations, such as overfishing (Purcell et al., 2013;

Richardson et al., 2009). Mesopelagic gelatinous plankton are typically too fragile to be sampled with nets and were very poorly known before developments in underwater video technology revealed that they play a major role in mesopelagic ecology (Robison, 2004) (Figure 8.4.11). However, time series of gelatinous zooplankton are few and often flawed, and the issue of current trends in their abundance remains uncertain (Condon et al., 2012).

8.4.3.3 Micronekton

Oxygen concentration is a critical factor influencing the physiology, behaviour, and ecology of metazoans within the mesopelagic. Although mass mortality events due to low-oxygen conditions are not observed offshore as in coastal regions (e.g. Chan et al., 2008), active swimming activity and high-cost physiological functioning, such as vision, are impaired at low oxygen concentrations (McCormick & Levin, 2017).



Figure 8.4.10 Deep-sea pteropod *Clio recurva*. © Solvin Zankl / Alamy stock photo.

In regions without an OMZ, the micronekton are predominantly distributed in DSLs throughout the mesopelagic zone down to approximately 1000 m depth (Proud et al., 2017; Williams & Koslow, 1997). However, in regions with a deep OMZ (depths > ~500 m), a primary DSL is situated in the HBL, above the core of the OMZ (Figure 8.4.9) (Bianchi et al., 2013; Koslow et al., 2011); DSLs are largely absent from within the OMZ. Thus, organisms apparently seek refuge from predation during daylight hours utilizing the lack of both light and oxygen within the HBL, and they avoid the suboxic conditions below the HBL (Netburn & Koslow, 2015). However, where the OMZ shoals above mesopelagic depths, epipelagic organisms, such as anchovy, are tightly constrained from entering suboxic waters, but mesopelagic taxa in these regions have evolved various adaptations to such conditions and enter the OMZ during daylight hours, migrating at night into



Figure 8.4.11 The mesopelagic siphonophore, *Praya dubia*, sometimes termed, “the curtain of death” can be several tens of metres in length. © S. Haddock, MBARI.

near-surface waters to oxygenate and feed (Cornejo & Koppelman, 2006).

The morphological, physiological and behavioural adaptations of mesopelagic organisms to low-oxygen conditions include increased gill area, respiratory proteins with high oxygen affinities, and the ability to reduce activity levels (e.g. observations of apparent torpor in certain myctophids (Barham, 1966)) and suppress metabolic activity (Seibel, 2011; Seibel et al., 2016). As a result of this suite of adaptations, the biomass and diversity of zooplankton and micronekton integrated through the water column is not significantly reduced until oxygen concentrations approach suboxic levels (Childress & Seibel, 1998). And while species richness can be markedly reduced in suboxic conditions, overall mesopelagic fish biomass may remain substantial (Gjøsaeter, 1984; Gjøsaeter & Kawaguchi, 1980). However, taxa differ markedly in their distributions in relation to oxic, hypoxic and suboxic waters and in their adaptations to such conditions. It should be noted that although many mesopelagic taxa conduct diel vertical migrations and can re-oxygenate at night in near-surface waters, many taxa do not, and non-migrators exhibit metabolic rates approximately an order of magnitude lower than migratory taxa (Childress et al., 1980).

Some of the dominant taxa that have evolved specialized adaptations to live within the HBL or partially within the OMZ have ranges that may extend over several water masses or biogeographic provinces where there is a contiguous OMZ. Thus, the ranges of the myctophid *Triphoturus mexicanus*, the gonostomatid *Cyclothone signata*, and the phosichthyid *Vinciguerria lucetia* extend from the southern California Current across the Eastern Tropical Pacific to the Humboldt Current (Moser, 1996). The hypoxia-tolerant euphausiid, *Euphausia exima*, and the copepod, *Rhincalanus nasutus* also follow this distributional pattern (Brinton, 1962; Castro et al., 1993; Ekau et al., 2010; Seibel et al., 2016).

There are few time series of mesopelagic fishes to assess the impacts of changing oxygen conditions on ecological time scales. However, using larval fish abundance as a proxy for spawning stock biomass, Koslow et al. (2011) report a strong correlation ($r = 0.75$) between mid-depth oxygen concentration and the abundance of 24 mesopelagic fish taxa, which dominated the first principal component (PC1) of the CalCOFI ichthyoplankton time series extending back to 1951. Since 1984, midwater oxygen concentrations

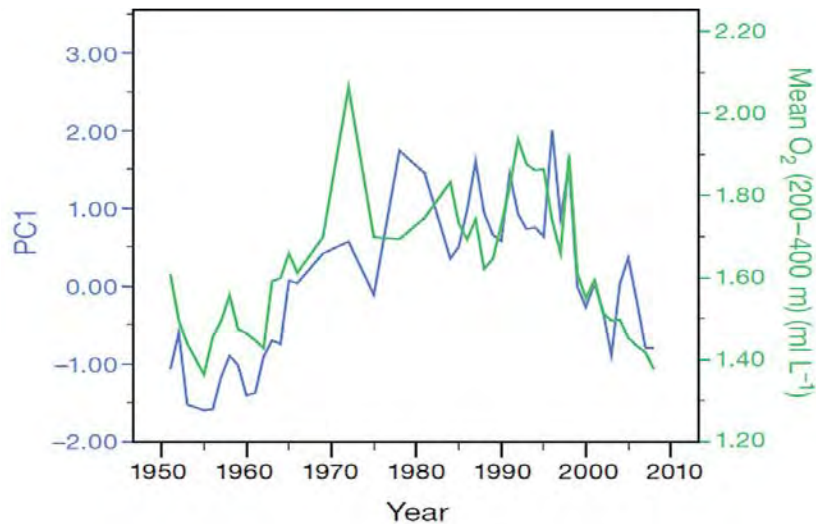


Figure 8.4.12 Time series, from the CalCOFI surveys (1951 – 2008) off southern California, of annual mean oxygen concentration at 200 – 400 m depth (green) and the first principal component (PC1) from analysis of the ichthyoplankton (blue). Twenty-four mesopelagic taxa loaded significantly on PC1. The correlation between the oxygen and PC1 time series is 0.75. From Koslow et al. (2011).

declined approximately 20%, leading to a concomitant shoaling of the OMZ by 41 m on average and up to 90 m in some regions of the Southern California Bight (Bograd et al., 2008). Over this period, the average abundance of the 24 mesopelagic fishes that loaded significantly on PC1 declined 63% (Figure 8.4.12). One hypothesized mechanism was increased predation, due to the mesopelagic fauna being more vulnerable to visual predation as the DSL followed the shoaling HBL: ambient light levels experienced by the DSL in the HBL would increase by an estimated 2.5 and 7-fold, respectively, with a 41 or 90 m shoaling of the HBL, assuming a constant light extinction coefficient with depth (Koslow et al., 2011). However, a recent study based on a circumglobal research cruise found that the depth of the DSL in the global ocean varied by about 400 m depending upon oxygen conditions (whether there was an OMZ or HBL and its depth and intensity) but that the DSL appeared to be tracking particular light levels rather than oxygen concentrations (Aksnes et al., 2017). Light extinction was significantly higher in hypoxic or suboxic waters, apparently due to bacterial production of coloured dissolved organic matter under low-oxygen conditions. The dramatic decline in abundance of mesopelagic fishes in the southern California Current (CC) may also be the result of a shift in the region's fauna. The southern CC is an ecotone, a region of mixing between two water masses and their associated mesopelagic faunas: the cool CC flowing equatorward and a warm water countercurrent extending northward from the equatorial tropical Pacific. The region has warmed in recent years, and the once-dominant cool-water mesopelagic fishes have substantially declined

while warm-water taxa, such as the Mexican lampfish (*T. mexicanus*) and Panama lightfish (*V. lucetia*) have dramatically increased (Koslow et al., 2019). This suggests that warming and deoxygenation may lead to a shift in the relative distributions of mesopelagic faunas more or less tolerant of hypoxic and suboxic conditions. Whether this will lead to an overall increase or decrease in mesopelagic fish biomass is an open question: a recent study found an increase in mesopelagic fish biomass off Baja California since 1998 concomitant with declining midwater oxygen levels, primarily due to increases in warm-water affinity taxa, such as the Mexican lampfish and Panama lightfish (Koslow et al., 2019).

8.4.3.4 Nekton

There appear to be winners as well as losers as a result of a shoaling HBL. The enhanced susceptibility to predation of small planktivorous mesopelagic fishes has led to increased populations of several of their predators. Two rockfish taxa (*Sebastes goodei* and *S. diploproa*) that prey on midwater fishes were virtually the only fishes that showed a significant opposite trend to the mesopelagic fishes off southern California (Koslow et al., 2011). Most striking has been the range expansion of the jumbo or Humboldt squid (*Dosidicus gigas*) over the entire California Current since the early 2000s and the dramatic expansion of its fishery from virtually non-existent 25 years ago to becoming the largest invertebrate fishery in the world (630,000 t in 2009) (Figure 8.4.13) (Gilly et al., 2013). The Humboldt squid has a number of physiological and behavioural adaptations that support its role as a particularly



Figure 8.4.13 Humboldt squid fishery © Amanda Cotton / Alamy stock photo.

active and voracious predator on mesopelagic fishes in the HBL, including reduced rapid jetting, metabolic suppression and having a form of haemocyanin that enhances oxygen binding (Gilly et al., 2012; Rosa & Seibel, 2010; Seibel, 2011; Stewart et al., 2014). Modelling indicates that enhanced availability of mesopelagic prey due to a shoaling HBL is likely a strong driver of the Humboldt squid's range expansion (Stewart et al., 2014).

A shoaling HBL appears to enhance the foraging of other visual predators on mesopelagic fishes. Prince and Goodyear (2006) show that the foraging depth of large, active predatory fishes, such as marlin and sailfish, is restricted by the HBL. Where there is a shallow HBL, such as in the eastern tropical Pacific, these fishes are significantly larger at age than in areas where such a layer is absent, such as in the western North Atlantic, presumably because foraging is more efficient where the foraging habitat is highly restricted. On the other hand, these fishes are more vulnerable to fishing gear where their habitat is compressed.

8.4.3.5 Ecosystem consequences

The biomass of mesopelagic fishes, and hence their role in marine ecosystems and biogeochemistry, were

substantially underestimated in the past when their abundance was estimated predominantly from sampling with small research trawls (e.g. Gjøsæter & Kawaguchi, 1980). Avoidance of such samplers by midwater fishes has now been clearly demonstrated (Kaartvedt et al., 2012), and recent studies based on acoustics (or, preferably, acoustics combined with net sampling) indicate that mesopelagic fish biomass is approximately an order of magnitude higher than previously estimated (Koslow et al., 1997), in the order of 10 billion tonnes globally (Irigoien et al., 2014), approximately two orders of magnitude greater than global marine fishery landings (Pauly & Zeller, 2016). The diel vertical migration of mesopelagic fishes, which involves a large fraction of this community feeding in near-surface waters and transporting and metabolising the material at midwater depths, may contribute significantly to carbon sequestration and the global carbon cycle and, indeed, to the metabolic processes leading to the HBL (Bianchi et al., 2013; Davison et al., 2013). A significant decline in the mesopelagic fish community due to climate warming and deoxygenation could diminish the ocean's rate of carbon sequestration, a potential positive feedback to climate warming. A shoaling of the DSL in response to a shoaling HBL could also influence carbon sequestration, since a shallower DSL increases the recycling of its

metabolic and waste products at mesopelagic depths and their potential return to near-surface waters.

Mesopelagic fishes are predominantly at the third trophic level and are key consumers of zooplankton production and key prey for a variety of squids, fishes, marine mammals and birds on continental margins and in the open ocean (Beamish et al., 1999; Brodeur et al., 1999; Brodeur & Yamamura, 2005). While much of mesopelagic fish production is consumed by other mesopelagic predators, such as squids, viperfishes and dragonfishes (Sutton & Hopkins, 1996) (Figure 8.4.14), it is not surprising given their enormous biomass that they comprise a significant component of the diet of many commercial species (e.g. tunas, salmon, and walleye pollock in the North Pacific) and species of special conservation interest such as a variety of marine mammals, including elephant and fur seals and whales (Beamish et al., 1999; Brodeur et al., 1999; Brodeur & Yamamura, 2005; Cherel et al., 2008). A significant decline in this group could therefore have a significant impact on global marine ecosystem productivity.

It should be noted that the observed decline in mesopelagic fishes associated with deoxygenation off southern California is counter to the recent prediction that mesopelagic fishes globally may significantly increase by approximately 17% over the coming century (Proud et al., 2017). This prediction, based on a simple model that examined the potential impacts of a warming ocean and a shoaling DSL, failed to assess the model against observed trends (e.g. Koslow et al., 2011) that ran counter to model predictions. Although the paper proposed a model for the biogeography of the global ocean's mesopelagic zone, there were no data from any of the ocean's major eastern boundary currents, OMZ regions or the northern North Pacific Ocean.

Few studies have examined changes in the biodiversity of mesopelagic communities in relation to deoxygenation. In the southern California Current, species richness in the CalCOFI ichthyoplankton time series was most closely correlated with the diversity of the mesopelagic community, which was in turn significantly correlated with temperature, due to the influx of the highly diverse warm-water affinity (tropical-sub-tropical) mesopelagic fauna during relatively warm periods (Koslow et al., 2017).

This influx of tropical-subtropical affinity mesopelagic fishes (e.g. *V. lucetia* and *T. mexicanus*) adapted to a shallow HBL has increased dramatically off southern California in recent years. Comparing the period 2011 – 2015 with the period prior to 2004, overall larval fish abundance declined by almost 50% due to the decline in cool-water dominant taxa, but the abundance of warm-water mesopelagic taxa increased 73%. The rank-order of abundance of the two most abundant warm-water affinity mesopelagic fishes, the Panama lightfish and Mexican lampfish, rose from 10 and 19 to six and seven, respectively, between these periods. The tropical-subtropical fish taxa that dominate the mesopelagic fish community in the region from Baja California to the northern Humboldt Current off Peru are thus becoming increasingly dominant off southern California as the OMZ there has shoaled (Koslow et al., 2019). These trends are consistent with predictions



Figure 8.4.14 (A) Sloane's viperfish *Chauliodus sloani* © Paulo Oliveira / Alamy stock photo; (B) Scaleless black dragonfish *Melanostomias biseriatus* © Nature Picture Library / Alamy stock photo.

based on palaeo-oceanographic patterns, that growing hypoxia will be associated with the increased dominance of fishes particularly well adapted to such conditions (Rogers, 2000).

This section has focused considerably on the California Current, in large measure because there are no time series for mesopelagic fish abundance and community dynamics from elsewhere. The extent to which patterns and trends in the southern California Current can be generalized is unclear; as noted, that region is an ecotone, where cool-water and warm-water affinity faunas meet, so changes in abundance may reflect distributional shifts at the edge of species ranges rather than large-scale trends. The ecosystem consequences of deoxygenation on continental margin mesopelagic communities are poorly understood, and comparative studies from other regions of the impacts of deoxygenation on mesopelagic fish communities is a high priority.

To date, ecosystem models have not adequately examined the potential impacts of deoxygenation on mesopelagic communities of continental margins in regions with OMZs. Ainsworth et al. (2011) stated as their objective to examine across five regions off the west coast of North America the impacts of deoxygenation, along with acidification, changes in primary production, range shifts and the size structure of the zooplankton. However, mesopelagic fishes were represented in only one of the five regional models, and even in that model the model domain only extended to ~1280 m depth. As a result, the biomass of mesopelagic fishes in that model (Field et al., 2006) was only about a third as high as in a model that treats the entire California Current domain (Davison et al., 2015). As noted above, Proud et al. (2017) failed to test and validate their recent model against existing time series and was based on few or no data from regions with significant OMZs. It is encouraging that recent models for the California Current (e.g. Marshall et al., 2017) have incorporated realistic biomass levels for mesopelagic fishes within an Atlantis modelling structure; the use of such a model to examine the potential impacts of deoxygenation would be extremely valuable. However, the value of such models would be considerably enhanced by a better understanding of the behavioural and physiological response of key taxa from different water types to varying OMZ and HBL characteristics. In regions, such as the California Current, where cool- and warm-water affinity mesopelagic faunas overlap, are they found at

similar depths and similar oxygen and light levels? What are the metabolic and productivity costs of descending into hypoxic or suboxic water? If fishes or other organisms undergo metabolic suppression when they remain during the day in suboxic water, does this limit their growth potential or, alternatively, does it enhance growth efficiency? Improved modelling of the impacts of deoxygenation must depend, at least in part, on a better understanding of the underlying physiology and ecology.

It is noteworthy that over the history of the planet, low-oxygen conditions appear to have considerably influenced the evolution of deep sea fishes, leading both to extinctions and the generation of biodiversity. Periods of highly anoxic conditions when the ocean was warm and highly stratified appear to be associated with extinction events in the deep sea, while the separation of populations by well-developed OMZs may also enable allopatric speciation over evolutionary time scales and hence the high species diversity at bathyal (mesopelagic) depths presently observed (Rogers, 2000; White, 1987).

8.4.3.6 Societal consequences

Societal consequences follow from the biogeochemical and ecosystem consequences. As described above, an expansion of the ocean's suboxic zones would have a significant impact on denitrification, leading potentially to decreased productivity in EBCs and tropical regions noted for their high levels of fish production.

The ecological consequences of deoxygenation appear highly complex, including the potential decline of a broad range of mesopelagic micronekton, the range expansion of certain OMZ specialist taxa including both mesopelagic fishes and predators (e.g. the Humboldt squid), which will influence both the abundance and availability of prey for a suite of visual predators. Some of these impacts could have further follow-on impacts. For example, the Humboldt squid feeds voraciously on commercial species, such as Pacific hake, as well as on mesopelagic fishes (Stewart et al., 2014). And today, the Humboldt squid is itself a valued commercial species. To evaluate the societal consequences of these ecological effects would require a reasonably sophisticated modelling exercise that can evaluate the influence of changing prey availability on predator feeding efficiency, and the flow-on to society of a number of first- and second-order effects and their

potential non-linear interactions. The recent Atlantis model that evaluated the impact of ocean acidification on the fisheries ecosystem of the California Current System would be a possible candidate for such a study if refocused on deoxygenation (Marshall et al., 2017): Atlantis models can potentially examine the flow-on of ocean change to biochemical, ecosystem, and societal impacts. To better address the impacts of deoxygenation and other aspects of climate change on mesopelagic communities, the deep sea should be recognized by the United Nations Framework Convention on Climate Change (UNFCCC) (Levin & Le Bris, 2015).

8.4.4 Conclusions

Distinct ecological communities of microbes, zooplankton, micronekton and predators are adapted to living within the oxygen-limited mesopelagic waters along continental margins, most notably in regions with OMZs. These organisms exhibit a variety of morphological, physiological and behavioural adaptations to inhabiting the HBL and even the OMZ in regions where the OMZ shoals above mesopelagic depths. Oxygen levels and the depth of the HBL and OMZ have exhibited strong fluctuations over the past ~70 years for which there are a few good time series.

Although these appear to be related in part to decadal-scale forcing, global climate models predict a secular decline in oxygen concentrations at intermediate water depths and there is already ample evidence of such a global trend. It is widely speculated that such changes could have significant consequences for the distribution and abundance of these and other marine mesopelagic communities. Off southern California, there is evidence that mesopelagic fishes have experienced several-fold changes in abundance since 1951, highly correlated with shifts in oxygen concentration and the depth of the HBL but also linked with sea temperatures, the ENSO cycle and Pacific Decadal Oscillation.

Based on current revised estimates for the abundance of the mesopelagic micronekton, this ecological community likely contributes far more to the global carbon cycle as well as to global food webs than previously recognized. Given the high level of uncertainty and its high global importance, high priority needs to be given to understanding the impact of global climate change and deoxygenation on mesopelagic ecosystems along continental margins, particularly where OMZs predominate. There is an urgent need for an expanded

network of time series for mesopelagic communities (Koslow & Couture, 2013) and for modelling studies that incorporate our best current understanding of these ecosystems.

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8.5 The significance of ocean deoxygenation for continental margin benthic and demersal biota

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Summary

- Continental margins in upwelling areas are exposed to naturally occurring hypoxia over an area of 1.1 million km²; the resulting oxygen gradients provide excellent natural laboratories for understanding adaptations, tolerances, thresholds and ecosystem responses to ocean deoxygenation.
- Expanding oxygen minimum zones will change the structure and function of benthic communities on continental margins through alteration of the taxonomic composition, body size, food-web structure, bioturbation and carbon cycling.
- Community diversity is especially sensitive to hypoxia, with decreases in diversity consistently observed under hypoxic conditions across all size classes of animals (from meiofauna to demersal fish). Loss of diversity can lead to reduced adaptive capacity and less resilience to various perturbations.
- Deoxygenation on continental margins is causing habitat compression for hypoxia-intolerant demersal and benthic species, and habitat expansion for hypoxia-tolerant species, leading to altered species interactions, including those with humans.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen concentrations and expansion of oxygen minimum zones on continental margins will lead to loss of invertebrate and fish biodiversity.	<ul style="list-style-type: none"> • Shift from complex organisms with high mobility to simple, soft bodied taxa. • Reduces the types and value of demersal fisheries species. • Loss of ecosystem adaptive capacity and resilience.
Deoxygenation on continental margins is causing habitat compression for hypoxia-intolerant demersal and benthic species and habitat expansion for hypoxia-tolerant species.	<ul style="list-style-type: none"> • Animals effectively experience habitat loss. • Altered species interactions including predation and competition for resources. • Forms high-density aggregations with increased susceptibility to overfishing. • Expanded ranges of some species have potential to alter community structure and fisheries resources.
In upwelling regions oxygen minima create strong oxygen gradients across continental margins; deoxygenation causes expansion of oxygen minima.	<ul style="list-style-type: none"> • Causes dramatic zonation of benthic fauna • Reveals oxygen tolerance thresholds that vary among size and taxonomic groups, providing clues about vulnerabilities to ocean deoxygenation • Bioturbation and carbon cycling decline with oxygen loss and exhibit distinct tipping points
Oxygen declines can shift trophic pathways (towards bacteria, protozoans and shorter food chains).	<ul style="list-style-type: none"> • Carbon reaching the sea floor, normally processed by metazoans is consumed by protozoans at very low oxygen levels, with potential for reduced trophic transfer. • Demersal fish shift from feeding in the water column (pelagic diets) to feeding on benthos under hypoxia, reducing benthic – pelagic coupling, increasing the length of the food chain, and reducing trophic transfer efficiency to top predators. • Chemosynthesis and the role of chemosynthetic symbionts can increase in importance.

8.5.1 Introduction

Continental margins, including subtidal shelf, slope and rise habitats (to about 3000 m) often exhibit very strong oxygen gradients with depth, and sometimes with distance from shore (Paulmier et al., 2011). On eastern boundary margins and in other areas, where upwelling enhances productivity, oxygen levels reach low values creating oxygen minimum zones, and such areas are expanding as a result of ocean deoxygenation (Levin, 2018; Stramma et al., 2008). Animals living in these low-oxygen zones are also subject to hypercapnic conditions, as oxygen minimum zone environments are also carbon maximum zones (Paulmier et al., 2011) and are characterized by carbonate undersaturation, and low pH conditions (Feely et al., 2008). On many upwelling shelves, for example off Oregon (Chan et al., 2008), southern California (Nam et al., 2015), Peru

(Graco et al., 2017), Namibia (Hamukuaya et al., 2001), Pakistan (Woulds et al., 2007) and India (Naqvi et al., 2006), there is pronounced oxygen seasonality, linked to winds and upwelling or in some cases fluctuating undercurrent strength. There are also oxygen variations associated with climate cycles such as El Niño-Southern Oscillation ENSO (Nam et al., 2011). People rely heavily on the ocean's continental margins, for food (fishing and aquaculture), energy, sand and minerals, shipping, recreation, and tourism (Levin & Sibuet, 2012). Human activities also modify the physical and biogeochemical environment through trawling, drilling, spills, and dumping, through river-borne nutrient inputs from watersheds, and through land-derived atmospheric inputs (Levin et al., 2015).

Eutrophication and associated algal blooms have created large, low-oxygen 'dead zones' on the sea

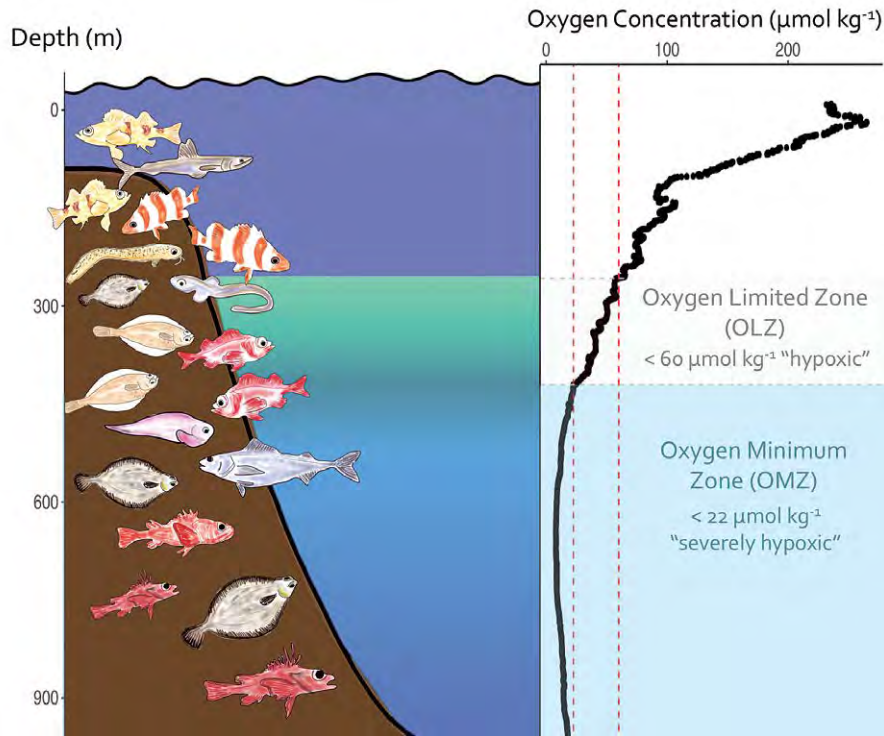


Figure 8.5.1 A conceptual diagram for the Southern California Bight on the US West Coast, showing how the depth distribution of the continental margin demersal fish community changes with depth and different oxygen conditions termed the oxygen-limited zone (OLZ) and the oxygen minimum zone (OMZ) (shown on the right). Community composition, density, diversity, and trophic interactions are all ecological metrics that can be sensitive to hypoxia, but changes occur under different oxygen thresholds in different regions. Note: drawing is not to scale.

floor of the Gulf of Mexico, Chesapeake Bay, the Baltic Sea, and many other areas (Diaz & Rosenberg, 2008) but this is distinct from the natural formation of hypoxic benthos on continental margins where oxygen minimum zones (OMZs $< 22 \mu\text{mol O}_2 \text{ kg}^{-1}$, Helly & Levin, 2004; Paulmier & Ruiz-Pino, 2008) and oxygen limited zones (OLZ = $22\text{--}60 \mu\text{mol O}_2 \text{ kg}^{-1}$, Gilly et al., 2013) impinge on the continental margin beneath upwelling sites. The oxygen concentrations cited above for the OMZ and OLZ are most often invoked for the Pacific and Indian Oceans and higher limits (45 and $90 \mu\text{mol O}_2 \text{ kg}^{-1}$, respectively) are sometimes applied to the Atlantic Ocean (Gilly et al., 2013). Conservatively, OMZs cover over $1.1 \times 10^6 \text{ km}^2$ of sea floor, primarily in the eastern Pacific, Northern Indian Ocean and off West Africa (Helly & Levin, 2004). The OMZ typically intercepts the sea floor between 100 and 1000 m , but the depth and thickness of hypoxia exposure varies regionally (affected by mixing, isolation and currents) (Helly & Levin, 2004) and seasonally (Paulmier & Ruiz-Pino, 2008) and these areas are expanding (Stramma et al., 2008). Records from the past 50 years reveal oxygen loss beyond oxygen minimum zones, in many other regions of the open ocean (Schmidtko et al., 2017). Regional differences and variability of oxygen minimum zone conditions, with a focus on continental

margins (hereafter margins), are reviewed in Gallo and Levin (2016). Strong temporal and vertical gradients in temperature, oxygen and carbon dioxide at the upper and lower boundaries of OMZs (Paulmier et al., 2011), make upwelling margins excellent natural laboratories for evaluating the influence of climate variables, including declining oxygen, on marine life (Sperling et al., 2016). However, ocean deoxygenation may also be manifested on other types of margins where eutrophication or water mass changes reduce oxygen availability (Breitburg et al., 2018). Because oxygen is required to sustain the majority of organisms (anaerobic microbes are an exception), the ocean deoxygenation-induced expansion of hypoxia on margins will have major consequences for organisms and communities on or near the sea floor.

8.5.2 Margin fauna

Here we consider the continental margin floor (primarily $> 200 \text{ m}$), and the benthic and demersal protozoans, invertebrates and fishes that live there. Most of the sea bed is covered with sediments, inhabited by meiofaunal- ($> 0.042 \text{ mm}$), macrofaunal- ($> 0.3 \text{ mm}$) and megafaunal-sized ($> 1 \text{ cm}$) protozoans and invertebrates that live in or on the substrate, and by benthic and demersal fishes

that may live on or interact with the sediment (Figure 8.5.1). There are also hard substrates in these settings – such as carbonates (which are a product of methane seepage), lithified continental sediment, or biotic substrates formed through accumulation of animal skeletons. These also host a wealth of biodiversity. Both single-celled organisms (Protozoa), and multi-celled animals (Metazoa) thrive on margins. Although this section focuses on the benthic and demersal communities, it is worthwhile to note that ecological processes mediated through the food web (i.e. benthopelagic coupling), ensure that impacts on pelagic and benthic communities do not occur in isolation, but are related and may be magnified through the ecological interactions of these scientifically defined zones.

8.5.3 Trends and impacts

There are relatively few modern studies that have documented directly the effects of changes in oxygen over time on the benthic and demersal biota of margins. Important exceptions involve temporal effects of ENSO cycles and seasonality on the Peru, Chile, and California margin faunas (Arntz et al., 2006; Sato et al., 2017). A greater body of knowledge exists about the effects of oxygen loss based on changes observed along cross-margin spatial gradients. The eastern Pacific and Arabian Sea margins in particular have yielded cross-margin studies of different animal size classes. These are often used to make predictions about the influence of deoxygenation in a ‘space for time’ translation, and to predict vulnerability of specific areas to changing conditions (e.g. Sperling et al., 2016). The results of these studies are discussed in the sections below.

8.5.3.1 Density

Oxygen effects on density over the full range of oxygen exposures are often not discernable in part because surface productivity or biological interactions appear to be more important drivers of density than oxygen. For small organisms (microbes, foraminifera, metazoan meiofauna) densities may peak at the lowest oxygen levels in OMZs due to an abundance of detrital food combined with an absence of predators (e.g. Levin et al., 1991; Neira et al., 2001, 2018). The density of larger taxa is generally reduced within OMZ core areas and increases downslope as oxygen levels rise. However, animal densities sometime exhibit a large maximum within or at the edge of the OMZ, at oxygen concentrations just above physiological thresholds

(Gallo et al., 2019; Gooday et al., 2010; Levin, 2003; Wishner et al., 1990). This has been termed an edge effect (Levin, 2003; Mullins et al., 1985). However, these density maxima sometimes occur at very low oxygen levels and give rise to density trends that appear to decrease as oxygen conditions continue to increase; other influences (e.g. food or predators) take precedence over dissolved oxygen conditions in determining faunal densities at higher oxygen levels. Off Peru, a study of benthic biomass changes across oxygen and depth gradients found that macrobenthic biomass peaked at $\sim 26.3 \mu\text{mol O}_2 \text{ kg}^{-1}$ and then declined as oxygen levels decreased (Rosenberg et al., 1983). In this study, demersal fish catches were positively correlated to high macrobenthic biomass, but negatively correlated to the occurrence of filamentous bacteria that occur in severely hypoxic environments (Rosenberg et al., 1983).

Dramatic changes in density can also occur with very minor changes in oxygen, where these gradients cross threshold levels. For example, in the eastern tropical Pacific, the Volcano 7 seamount rises into the oxygen minimum zone, resulting in steep gradients in oxygen availability for the benthic community. Here, the lowest density megafauna communities were observed at the lowest oxygen concentrations ($\sim 3.5\text{--}4 \mu\text{mol O}_2 \text{ kg}^{-1}$), while high-density communities were encountered 50 to 100 m deeper, where oxygen concentrations were only slightly higher ($\sim 5\text{--}7 \mu\text{mol O}_2 \text{ kg}^{-1}$) (Levin et al., 1991; Wishner et al., 1995). At oxygen levels higher than this, megafauna densities decreased again, showing a non-linear relationship between oxygen availability and density, and likely reflecting the influence of other factors. In coastal systems with eutrophication-driven hypoxia, the complicated nature of hypoxia occurrence and fisheries landings (arising from enhanced food availability and habitat compression) has also been documented (Breitburg, 2002; Breitburg et al., 2009; Craig et al., 2012). Changes in fisheries landings across oxygen gradients are further discussed in this report in Chapter 10.

Species tolerant of severe hypoxia can attain unexpectedly high densities under low oxygen conditions. Examples include crustaceans such as tuna crabs (*Pleuroncodes planipes*) off Panama (78 ind m^{-2} ; Pineda et al., 2014) or spider crabs (*Encephaloides armstrongii*) off Oman (47 ind m^{-2} ; Smallwood et al., 1999) (Figure 8.5.2), which can occur at oxygen concentrations of $2 \mu\text{mol O}_2 \text{ kg}^{-1}$ and $9\text{--}13 \mu\text{mol O}_2 \text{ kg}^{-1}$, respectively. Some demersal fish species also exhibit

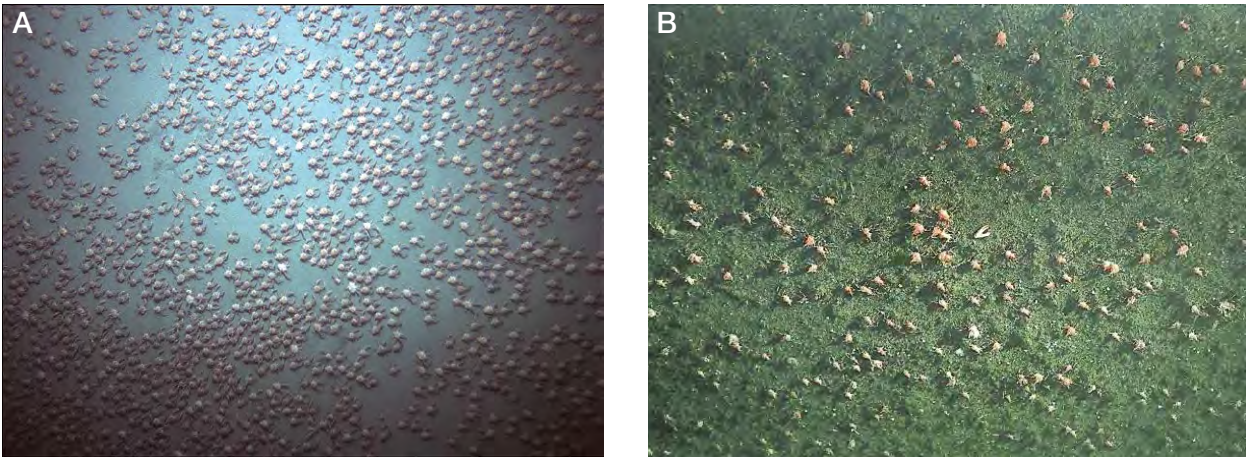


Figure 8.5.2 Examples of high-density crab aggregations within oxygen minimum zones. (A) Tuna crabs (*Pleuroncodes planipes*) off Panama (from Pineda et al. 2014) and (B): *Encephaloides armstrongii* off Oman. © Dr Brian J. Bett, National Oceanography Centre, UK.

remarkably high tolerance to hypoxia and can occur at very high densities. This has been observed in the Gulf of California for the cusk-eel, *Cherublemma emmelas* (3.5 fish m^{-2} at $1.6 \mu mol O_2 kg^{-1}$) (Figure 8.5.3) (Gallo et al., 2019) and on the Volcano 7 seamount summit for the grenadier, *Nezumia liolepis* (at $<4 \mu mol O_2 kg^{-1}$) (Levin et al., 1991; Wishner et al., 1990). While the occurrence of high-density communities of highly adapted species under low oxygen conditions are biologically and ecologically intriguing, most species are *not* able to thrive under oxygen-depleted conditions. A global review for benthic and demersal marine organisms found that the sub-lethal oxygen limit for demersal fish species ranges from 62–186 $\mu mol O_2 kg^{-1}$, while the sub-lethal limit for benthic invertebrates (including crabs, worms, and oysters) ranges from 15–124 $\mu mol O_2 kg^{-1}$ (Vaquer-Sunyer & Duarte, 2008). Most of these data were derived from studies carried out on Atlantic species with potentially limited adaptation to hypoxia; thresholds are much lower for species on upwelling margins that have evolved and adapted to hypoxia (Chu & Tunnicliffe, 2015).

An additional difficulty of interpreting the influence of oxygen conditions on density trends is that low-oxygen events can give rise to immediate habitat compression of sensitive species. This can result in temporary high-density aggregations that can increase susceptibility to overfishing. For example, in the Gulf of Mexico, aggregations of brown shrimp and demersal fishes occur along the edges of hypoxic areas (Craig, 2012). In the Sea of Oman, seasonal oxycline shoaling during the summer and autumn has also resulted in habitat compression for artisanal fisheries species, resulting in increased fisheries landings (Piontkovski & Al-Oufi, 2014).

Unfortunately, there is no simple, easily generalized relationship between oxygen conditions and density that can be used to predict the influence of deoxygenation on general community density patterns. However, regionally, some informative trends do exist. For example, the catch per unit effort (CPUE) for selected demersal fish species along the US West Coast is positively related to near-bottom oxygen concentrations, with CPUE decreasing more significantly as oxygen concentrations decrease (Keller et al., 2015). It should be noted that CPUE reflects the biomass as well as numbers of animals caught, and cannot be directly related to trends in density, as different species differ significantly in size. CPUE and density could show different relationships across oxygen gradients if larger-bodied species are replaced by numerous smaller-bodied species as oxygen conditions decline. Considering the different relationships between oxygen and density versus CPUE

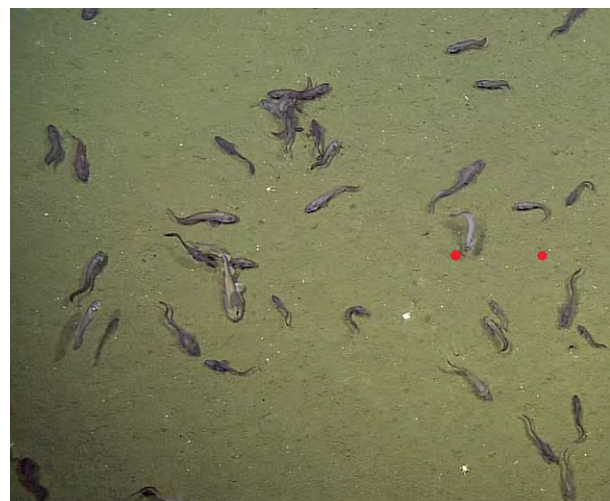


Figure 8.5.3 High density fish aggregations of cusk eel *Cherublemma emmelas* were observed in the Gulf of California at very low oxygen concentrations ($1.61 \mu mol kg^{-1}$) (from Gallo et al. 2019). Image from MBARI's ROV Doc Ricketts, red lasers are 29 cm apart.

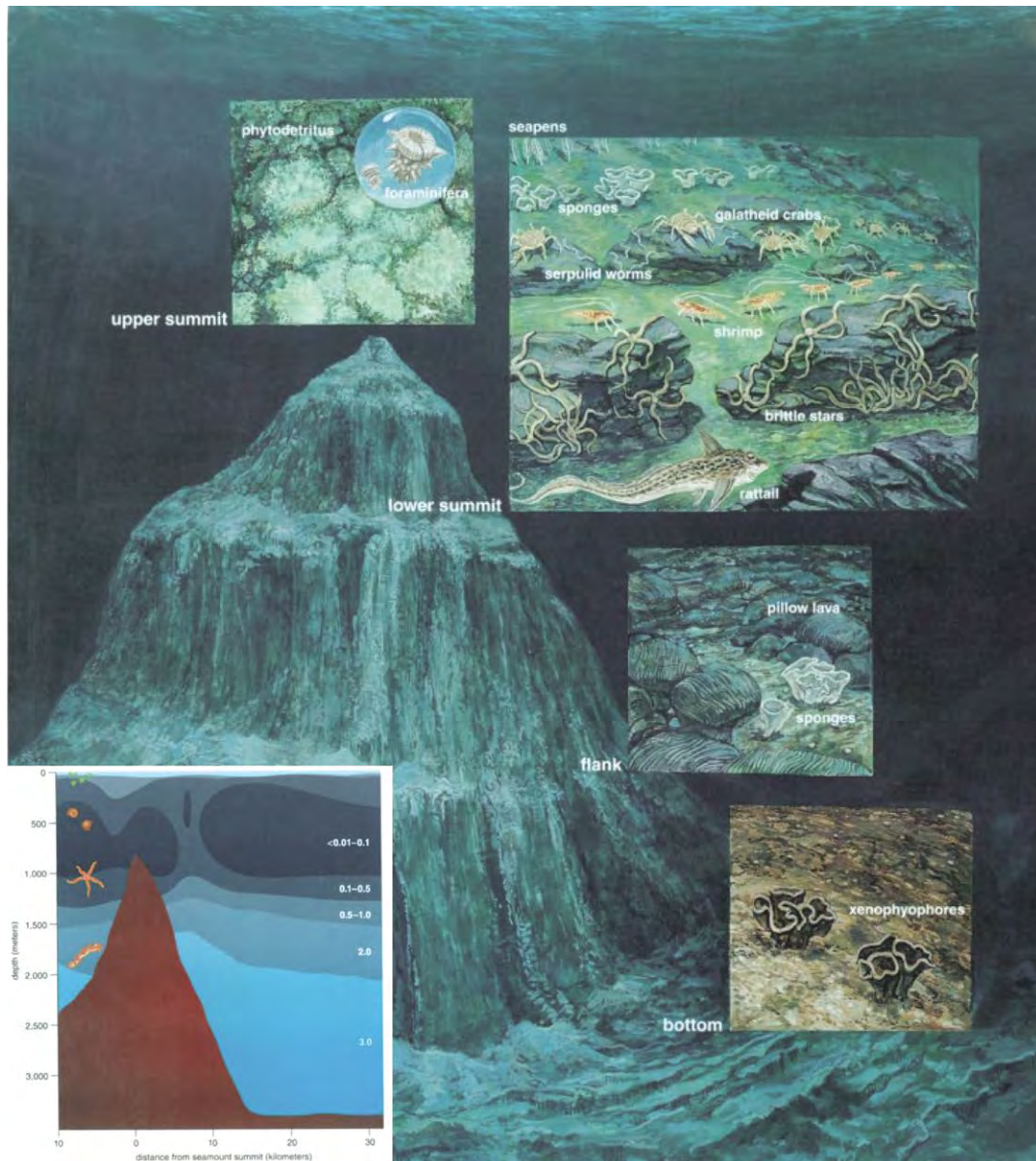


Figure 8.5.4 Strong faunal zonation occurs on Volcano 7 in the East Pacific west of Acapulco, Mexico in response to oxygen gradients. The upper and lower summit of this seamount protrude into the oxygen minimum zone (from Levin 1992).

or biomass, may be important from the perspective of food web interactions as well as fisheries efforts.

8.5.3.2 Depth distribution and zonation

Sharp faunal zonation across oxygen gradients on continental margins indicates the existence of strong tolerance thresholds for benthic biota. Such zonation was first noted for invertebrates and fish on the California continental margin (Thompson et al., 1985) and the flanks of the Volcano 7 seamount off Mexico (Levin et al., 1991; Wishner et al., 1990, 1995) (Figure 8.5.4), but has since been documented for macrofauna on the margins of Chile (Gallardo et al., 1995, 2004), Peru

(Levin et al., 2003), Oman (Levin et al., 2000), Pakistan (Hughes et al., 2009; Levin et al., 2009), India (Hunter et al., 2012; Raman et al., 2015) and for megafauna and demersal fish on the margins of Chile (Quiroga et al., 2009; Sellanes et al., 2010), Mexico (Papiol et al., 2017), India (Hunter et al., 2011), Pakistan (Murty et al., 2009), Central America (Bianchi, 1991; Stromme & Saetersdal, 1988), Namibia (Hamukuaya et al., 2001; Mas-Reira et al., 1990), and Oman (Piontkovski & Al-Oufi, 2014; Piontkovski et al., 2012), in submarine canyons off Hawaii (De Leo et al., 2012), and in a Canadian seasonally hypoxic inlet (Chu & Tunnicliffe, 2015). These gradients are maintained by species-specific oxygen tolerances but potentially also by the absence of larger predators at

each oxygen level (Levin, 2003). Dramatic differences in macrofaunal colonization potential, potentially reflecting larval availability and tolerances, were observed in short-term experiments conducted across oxygen gradients on the Indian continental margin (Levin et al., 2013). If hypoxia lengthens recovery time or reduces recolonization potential following disturbance, then ocean deoxygenation is likely to reduce ecosystem resilience.

Most of these studies reflect faunal response to oxygen gradients at a single point in time, and there are relatively few very long time series that document responses to changes in oxygenation. Several studies document a) changes in continental margin faunal composition and activity in response to seasonal changes in oxygenation (Gutierrez et al., 2008; Macpherson & Gordo, 1992; Sellanes & Neira, 2006; Woulds et al., 2007); b) responses to ENSO-related or episodic changes in oxygenation (Gutierrez et al., 2008; Hamukuaya et al., 2001; Levin et al., 2002); and c) long-term changes in species distribution on margins known to experience shoaling oxygen minimum zones (Sato et al., 2017). Studies on the Peru shelf (94 m) during oxygenation events associated with El Niño reveal successional

stages that range from nematode dominance under extreme oxygen deficiency, to *Thioploca* (bacterial) dominance at 10–20 $\mu\text{mol O}_2 \text{ kg}^{-1}$, to macrofaunal dominance at $> 40 \mu\text{mol O}_2 \text{ kg}^{-1}$ (Gutierrez et al., 2008) (Figure 8.5.5). Off central Chile, meiofaunal abundance was positively correlated with chlorophyll *a* and oxygen content over 1997–1998 during a major El Niño. On the Namibian shelf and margin, four clear demersal fish assemblages were identified that correlated with environmental variables, including oxygen (Hamukuaya et al., 2001; Mas-Reira et al., 1990). During the upwelling season when hypoxic conditions were more prevalent, the northern shelf assemblage expanded its distribution into deeper water (Mas-Reira et al., 1990); the northern and central shelf assemblages expanded into deeper water during the 1993 and 1995 Benguela Niño as well (Hamukuaya et al., 2001). These responses to changes in oxygenation indicate that these communities are sensitive to oxygen regimes, both on short and long timescales.

Across seasonal timescales, benthic communities also exhibit faunal composition changes in response to changes in oxygenation. The Saanich Inlet is a relatively shallow (230 m) fjord system in the Canadian N. Pacific

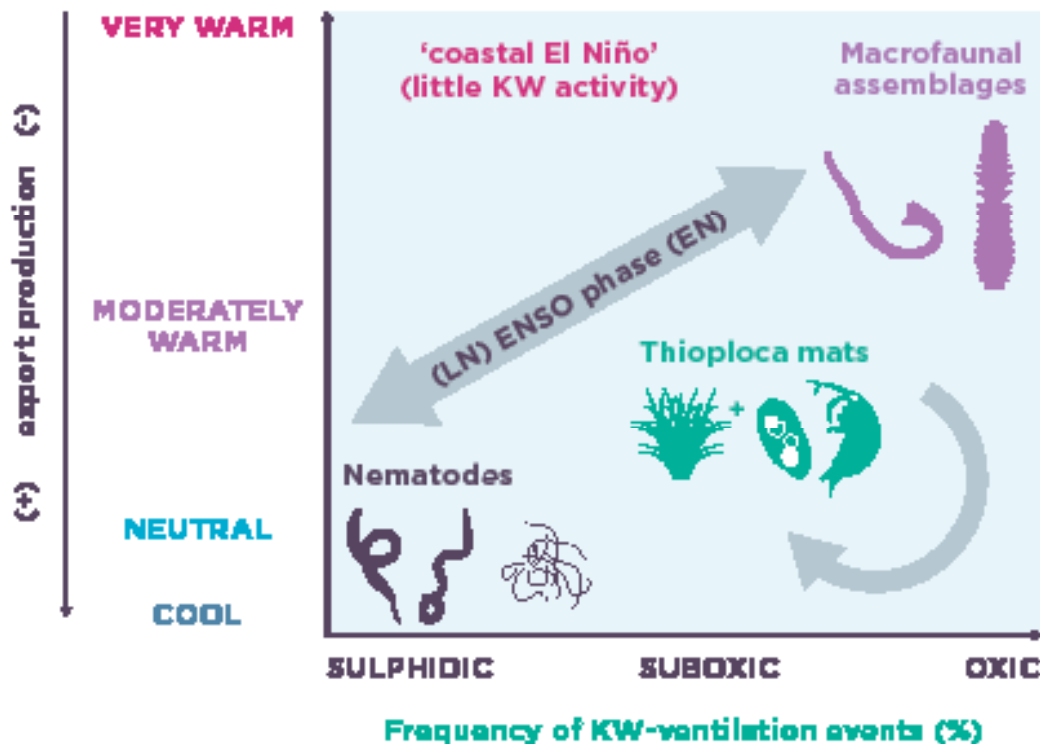
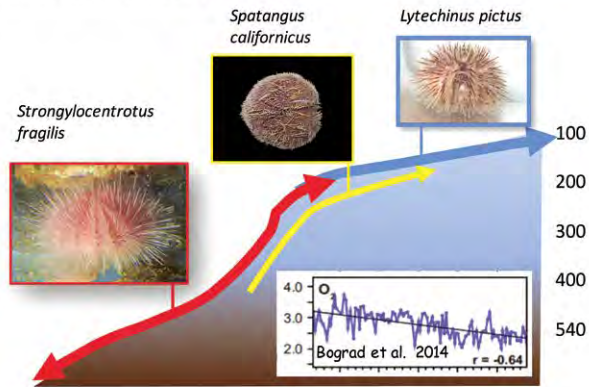


Figure 8.5.5 Shifts in benthic community dominance off Callao, Peru (93 m) as a function of oxygenation and export production. Macrofauna dominate under oxygenated conditions ($> 40 \mu\text{mol O}_2 \text{ kg}^{-1}$); Filamentous sulphide oxidizing bacteria dominate during weak El Niño ($20\text{--}40 \mu\text{mol O}_2 \text{ kg}^{-1}$); Nematodes dominate under lowest oxygen conditions ($< 20 \mu\text{mol O}_2 \text{ kg}^{-1}$). KW = Kelvin Wave; LN = La Niña, EN = El Niño. Based on Gutierrez et al. 2008; Figure courtesy of D. Gutierrez.

that goes seasonally hypoxic during the summer and is reoxygenated during the autumn and winter. Benthic communities exhibited consistent responses to changes in oxygenation across an eight-year study, with increases in the abundance of spot prawn, pink

shrimp, and sea whips under high-oxygen conditions, and increases in the abundance of slender sole and squat lobsters observed under low-oxygen conditions (Chu & Tunnicliffe, 2015). Community responses to seasonal and interannual changes in oxygenation can inform our understanding of species-specific tolerance limits to hypoxia.

Compression and expansion of sea urchins on the southern California Bight



Pronounced shoaling of the OMZ (which also has low pH waters) has occurred in the southern California Bight over the past 25 years (Bograd et al., 2008, 2015). Among echinoids, two burrowing, irregular urchins (*Brissopsis pacifica* and *Spatangus californicus*) common within the oxygen minimum zone (OMZ), have expanded their depth distributions from 2003-2013. The pink urchin, *Strongylocentrotus fragilis*, expanded upslope and increased in density, while the painted urchin *Lytechinus pictus* experienced habitat compression to shallower

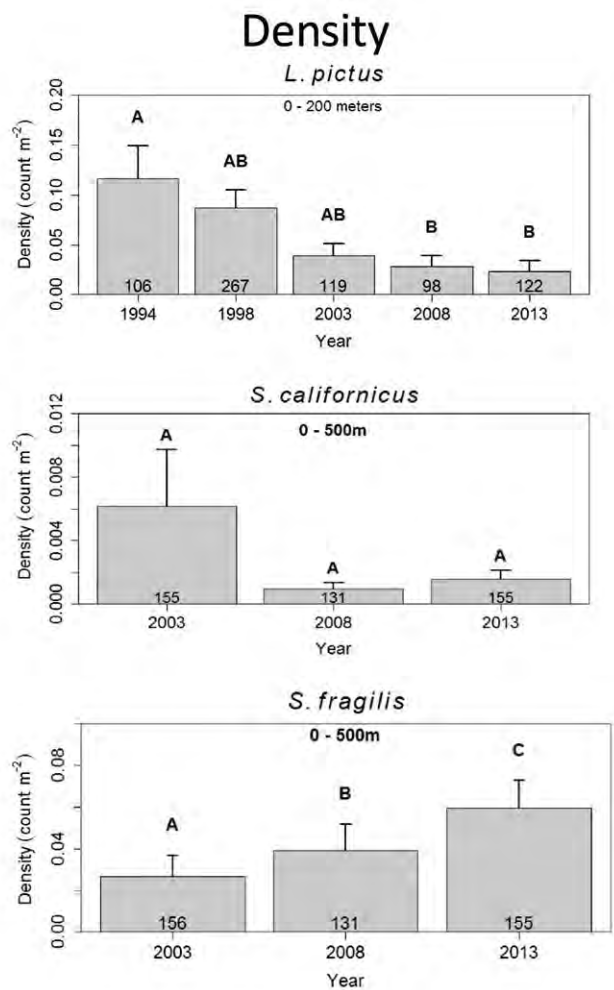
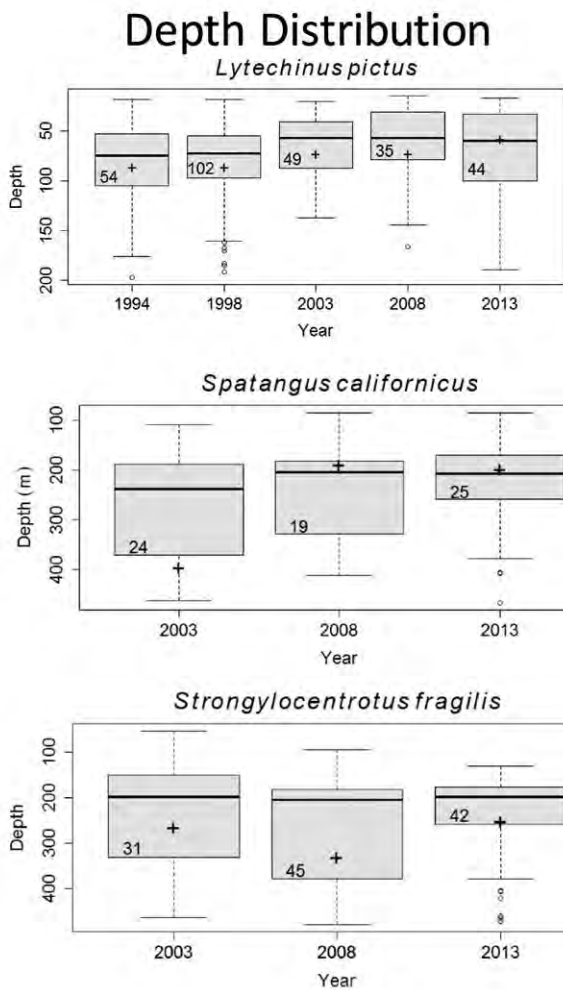


Figure 8.5.6 Changes in sea urchin distribution along the southern California Bight shelf and slope over the past 15-25 years as reported in Sato et al. (2017), based on data from the Southern California Coastal Water Research Project trawl surveys. Oxygen has declined by 20-30% at depths of 200-300 m (Bograd et al., 2014).

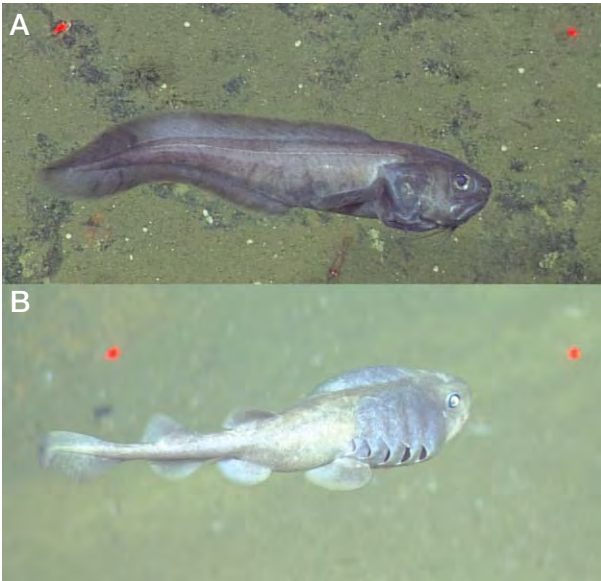


Figure 8.5.7 (A) The cusk eel, *Cherublemma emmelas*, and (B) the catshark, *Cephalurus cephalus*, represent some of the most hypoxia-tolerant fish species known. They live under suboxic and nearly anoxic conditions in the Gulf of California and their distribution extends throughout the eastern tropical Pacific (Gallo et al., 2019). Images from MBARI's ROV *Doc Ricketts*, red lasers are 29 cm apart.

depths and exhibited lower densities from 1994–2013 (Sato et al., 2017) (Figure 8.5.6). These species also appear influenced by ENSO, with stronger El Niño (associated with increased oxygenation) favouring *L. pictus* and negatively affecting *S. fragilis* and *B. pacifica* (Sato et al., 2017).

8.5.3.3 Taxonomic composition

Low oxygen availability on margins selects for a suite of hypoxia-tolerant, soft-bodied taxa such as nematodes, polychaetes, and some calcareous foraminifera. Most calcifying invertebrates tend to disappear in suboxic settings ($< 5 \mu\text{mol O}_2 \text{ kg}^{-1}$). There are, however, some notable exceptions such as the snail *Alia permodesta* and the mussel *Amygdallum politum*; these taxa tend to have very thin shells in suboxic or anoxic sediments (Levin, 2003; Moffitt et al., 2015b). *Bathybembix bairdii*, a deepwater sea snail, is a common inhabitant of the oxygen minimum zone core in the Southern California Bight and does not appear to have thin shells, although oxygen conditions do not reach suboxic conditions in this region (personal observation N. Gallo). The “core” of the OMZ refers to the depths with the lowest oxygen conditions observed within the water column, and oxygen levels increase both shallower and deeper than this core region. The most hypoxia-tolerant species can be found in the OMZ core. Among metazoan meiofauna

in OMZs, nematodes dominate in the lowest oxygen conditions and the ratio of nematodes to copepods steadily decreases with increasing oxygenation (Levin et al., 1991; Neira et al., 2001, 2018). Surprisingly, some fish can tolerate even lower oxygen concentrations than macro-invertebrates. The cusk eel, *Cherublemma emmelas* and the catshark, *Cephalurus cephalus* (Figure 8.5.7) live under suboxic ($[\text{O}_2] < 5 \mu\text{mol kg}^{-1}$) and nearly anoxic ($[\text{O}_2] < 2 \mu\text{mol kg}^{-1}$) conditions in the Gulf of California and their distribution extends throughout the eastern tropical Pacific (Gallo et al., 2019).

8.5.3.4 Diversity

Hypoxia associated with oxygen minimum zones or anoxic basins is known to reduce diversity of most animal groups ranging from foraminifera and metazoan meiofauna to invertebrate macrofauna and megafauna, as well as fishes (Levin, 2003; Rex & Etter, 2010). Reductions in species richness and elevated dominance occur at different oxygen thresholds, depending on animal size class; small taxa are generally more tolerant than large ones. But there are within-group differences. For example, among deep-sea metazoan meiofauna, nematodes are more tolerant of hypoxia than copepods (Levin, 2003). But even small forms like nematodes and foraminifera exhibit declines in diversity when oxygen availability is very low. Dramatic shifts in diversity can occur among macrofauna across small oxygen gradients. For example, on the Pakistan continental margin, where oxygen increases from 5 to 10 $\mu\text{mol O}_2 \text{ kg}^{-1}$ between 700 and 1100 m, the ecosystem moves from a single species assemblage with no bioturbation to a multi-species, highly bioturbated system (Levin et al., 2009) (Figure 8.5.8). Notably, the epibenthic community in a British Columbia fjord maintains high diversity despite annual exposure to $< 44 \mu\text{mol O}_2 \text{ kg}^{-1}$. This is potentially attributable to behavioural and physiological adaptations, periodic anoxia limitation of competitive dominants, and community evolution during low-oxygen periods of the Paleozoic (Chu et al., 2018; Tunnicliffe, 1981).

Diversity trends for the demersal fish community are also closely tied to bottom-water oxygen conditions, with diversity decreasing in a non-linear fashion with oxygen. This pattern holds true across different regions along continental margins in upwelling areas (Gallo & Levin, 2016). Off Oregon (Keller et al., 2010) and along the entire US West Coast (Keller et al., 2015) demersal fish and megafauna species richness is positively correlated

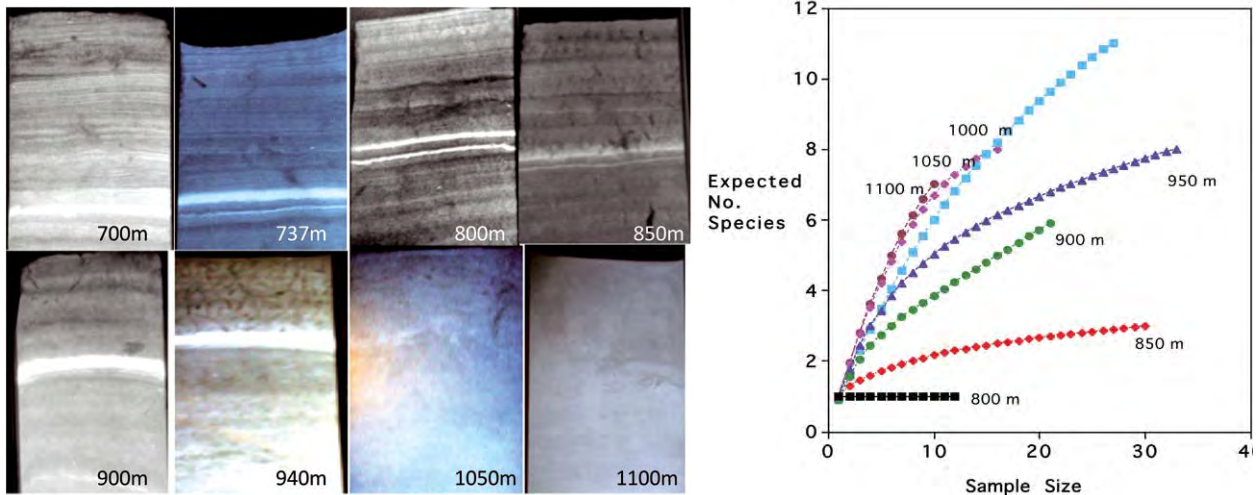


Figure 8.5.8 Abrupt changes in bioturbation as revealed by sediment x-radiographs (left) accompany increases in macrofaunal density (right) across the Pakistan margin. Bottom-water oxygen concentration increases with water depth from about $5 \mu\text{mol kg}^{-1}$ at 700 m to $10 \mu\text{mol kg}^{-1}$ at 1100 m (from Levin et al., 2009).

with near-bottom oxygen concentrations. In a Canadian seasonally hypoxic inlet, high single-species dominance (Matabos et al., 2014), increased homogenization and decreased species richness (Chu & Tunnicliffe, 2015) characterized the megafauna community during severely hypoxic periods. Off Namibia, the demersal fish assemblage that lived in the most hypoxic conditions on the central shelf, was characterized by lower diversity and higher dominance than other identified demersal fish assemblages in nearby areas (Hamukuaya et al., 2001). A demersal fish assemblage immediately adjacent to the Namibian low-oxygen shelf assemblage was found to have 2.5 times higher diversity than the low-oxygen assemblage (Mas-Reira et al., 1990), indicating the strong influence of oxygen on community diversity trends.

8.5.3.5 Body size

Smaller metazoans are more tolerant of low-oxygen conditions, in part because they have a larger surface area to volume ratio, facilitating oxygen diffusion. Thus, it is not surprising that larger animals (macrofauna and megafauna) are more vulnerable to deoxygenation than smaller fauna (metazoan meiofauna), and that small taxa dominate at the lowest oxygen levels (Gooday et al., 2009; Quiroga et al., 2005). However, among meiofaunal taxa, those species that are resilient to hypoxic conditions may attain relatively larger body size, presumably due to high food availability (Neira et al., 2001). In organisms that have specialized respiratory organs, higher respiratory surface area is needed under hypoxic conditions. This selective pressure on respiratory surface area is apparent in a number of highly adapted

oxygen minimum zone species that exhibit extensive gill surface areas (see examples in Levin (2003) and Gallo & Levin (2016)).

Foraminifera also become smaller under oxygen depleted conditions (Bernhard & Sen Gupta, 1999). However, their extreme hypoxia tolerance is likely linked to nitrate respiration and denitrification (Pino Ochoa et al., 2010).

Hypoxia is understood to reduce fish body size, but the underlying mechanism remains a scientifically contentious question and one that will require additional research. Pauly (2010) posits that given anatomical constraints related to respiratory surfaces, the growth and final size of fish is almost entirely determined by ambient oxygen concentration and temperature. This has led scientists to project that climate change will lead to a decrease in maximum fisheries catch potential, due to decreases in fish body size under lower oxygen conditions (Cheung et al., 2010, 2013). However, surface area to volume allometric relationships are typically described in terms of standard 3-dimensional shapes (spheres, cubes), whereas respiratory surfaces are folded surfaces that are not geometrically constrained in the same way (Wegner, 2011). As a result, physiologists have recently criticized this proposed relationship between fish size and environmental oxygen conditions as being based on erroneous assumptions (Lefevre et al., 2017), although some of these criticisms have been countered by Pauly and Cheung (2017). Deutsch et al. (2015) also found little relationship between body size and $\text{PO}_{2\text{crit}}$. Additional collaborations between fish physiologists, fisheries scientists and modelers are

needed to address this important question that may have critical implications for fisheries projections under future climate change.

8.5.3.6 Behaviour

Some species of benthic vertebrates and invertebrates inhabiting OMZs rely on vision for predator avoidance and prey capture at the sea floor, while most have highly visual larval stages that develop in lit waters. However, vision is a metabolically expensive process and has high oxygen requirements. This has led researchers to suggest that hypoxia impairment to the visual system may mediate changes in the vertical distribution of species (McCormick & Levin, 2017). Visual impairment of marine larvae can occur at oxygen concentrations much higher than physiological tolerance limits (P_{crit}) (McCormick et al., 2019), suggesting that sub-lethal impacts could occur at higher than expected oxygen concentrations. Pelagic fish, crustaceans, and cephalopods, and some benthic fish and crustaceans, exhibit a decline in metabolic rate with depth that has been linked to reduced locomotory capacity, but also corresponds to reduced light and visual activity (Childress, 1995). Future studies may therefore consider the interaction of light and oxygen gradients on the distributions of species, and how these may change under ocean deoxygenation.

Other forms of behaviour, including benthic-pelagic migrations, hypoxia avoidance, natal homing, foraging, chemotactic prey detection, and mating may be influenced by hypoxia, and further research in these areas is needed. The tuna crab *Pleuroncodes planipes* is reported to shift from a benthic to pelagic habitat under anoxic conditions (Boyd, 1967), but observations of high densities at $<2 \mu\text{mol O}_2 \text{ kg}^{-1}$ at depths of 380–400 m off Costa Rica (Cordes et al., unpublished) and Panama (Fig. 8.5.2A) (Peneda et al., 2014), combined with tolerance studies (Seibel et al., 2018) suggest that oxygen alone may not explain this behaviour.

8.5.4 Ecosystem-level consequences of deoxygenation on margins

8.5.4.1 Trophic pathways

One characteristic of systems subject to oxygen loss that accompanies change in diversity is a simplification of the food web. Among macrofauna for example, carnivory is nearly absent at very low oxygen levels (Sperling et al.,

2013), possibly because both capture and digestion of prey are highly oxygen-intensive. Infaunal taxa that are normally carnivorous can become phytodetritus feeders under severe oxygen stress (e.g. Jeffreys et al., 2012). Mat forming, filamentous sulphur oxidizing bacteria may provide a significant part of the *in situ* production; these may or may not be consumed by grazers such as snails (e.g. *Alia permodesta*) (Moffitt et al., 2015b; Myhre et al., 2017). A number of oxygen minimum zone animals host symbiotic chemo-autotrophic bacteria including lucinid and solemyid clams, phalodrilinid oligochaetes, nematodes, and frenulate polychaetes (Levin, 2003). Thus chemosynthesis-based trophic pathways can become more prevalent under severe oxygen limitation.

Seasonal comparisons of carbon processing during pre-monsoon (well oxygenated) and post monsoon (poorly oxygenated) periods on the Pakistan shelf, and across the lower OMZ (700–1100 m) on the Pakistan continental margin reveal that bottom-water dissolved oxygen concentrations exert a strong control over metazoan macrofaunal organic matter processing. Above oxygen thresholds between 5 and 7 $\mu\text{mol O}_2 \text{ kg}^{-1}$ (0.11 to 0.16 $\text{ml O}_2 \text{ L}^{-1}$) metazoans were primary carbon processors; below these levels protozoans (foraminifera) performed this role (Woulds et al., 2007).

Benthic-pelagic coupling may also be reduced on upwelling margins, as seawater oxygen concentration has been found to be the single best predictor of migration depth for diel vertical migrators on the global scale (Bianchi et al., 2013) and demersal fish communities are often reliant on midwater organisms and benthic-pelagic feeding (Trueman et al., 2014). Gallo (2018) reports that a predominance of demersal fish species on the southern California margin feed on pelagic resources above the oxygen minimum zone ($< 450 \text{ m}$) but those in the OMZ core are benthic feeders (Figure 8.5.9). In estuarine systems, seasonal hypoxia is known to influence the trophic structure of the benthic community by diverting energy from consumers to microbes (Baird et al., 2004; Diaz & Rosenberg, 2008). Similar trends may be expected in continental margin settings where filamentous bacterial mats are dominant, such as off Peru, Chile, and Central America (Gallardo & Espinoza, 2007).

8.5.4.2 Bioturbation and carbon burial

Hypoxia-induced reductions in diversity and in body size generally contribute to diminished bioturbation

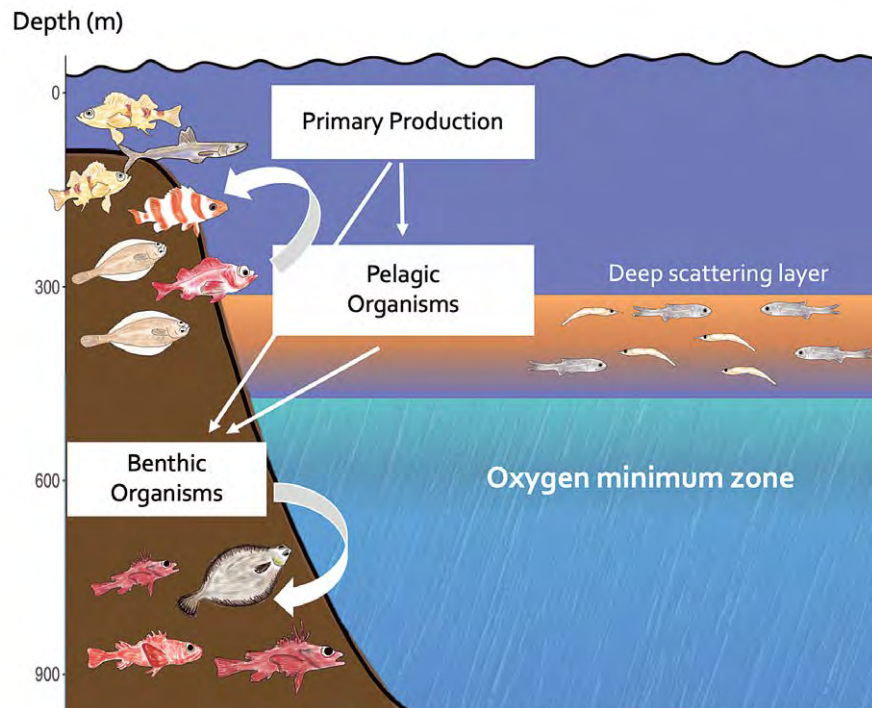


Figure 8.5.9 Conceptual diagram illustrating reduce benthic-pelagic coupling within the OMZ. Demersal fish above the oxygen minimum zone (OMZ) feed largely on pelagic prey whereas within the OMZ most demersal fish feed on benthic fauna (Gallo, 2018). Note: Drawing not to scale.

(particle mixing) and the generation of laminated or varved sediments (Calvert, 1964; Levin et al., 2009; Schimmelman et al., 2016; Smith et al., 2000) (Figure 8.5.8), although gutless, symbiont-bearing taxa can carry out bioturbation (Levin et al., 2003). Bioturbation normally mixes organic matter and particles deep into the sediments and can contribute to burial of carbon. It is likely that ocean deoxygenation will expand the regions of the continental slope where mixing of sediments is limited. Dysoxic/anoxic laminated sediments generally contribute less to nutrient recycling (due to absence of animals) and bioturbators that contribute to carbon burial are largely absent (Aller, 1994). Thus, more labile organic material remains unused.

8.5.4.3 O_2 influence on chemosynthetic ecosystems

Continental margin communities are highly heterogeneous and often include methane seeps dominated by large structure-forming taxa such as bathymodiolid mussels, siboglinid tubeworms, and vesicomid clams which are supported by sulphide and methane oxidizing symbionts (Tunnicliffe et al., 2003). Among these foundation species, both mussels and tubeworms are notably absent within severe oxygen minimum zones on the East Pacific margin ($< 8 \mu\text{mol } O_2 \text{ kg}^{-1}$), despite their occurrence in the better oxygenated

waters beneath the OMZ (Levin, pers. observation). Their absence is possibly due to insufficient oxygen to support their sulphide- or methane-oxidizing symbionts within the OMZ or the inability of their larvae to survive low-oxygen waters (e.g. Levin et al., 2016). Expanding oxygen minimum zones, or the creation of new hypoxic areas is likely to affect seep diversity and function by suppressing the occurrence of hypoxia-intolerant foundation species.

8.5.4.4 Thresholds and tipping points

Animal exposure history, and basin-wide differences in oxygenation appear to influence oxygen tolerance thresholds (Chu & Tunnicliffe, 2015). For example, oxygen thresholds that induce migration for demersal fish in the NE Pacific occur at $44\text{--}53 \mu\text{mol } O_2 \text{ kg}^{-1}$ ($1.0\text{--}1.2 \text{ ml } L^{-1}$) (Chu & Tunnicliffe, 2015; Vaquer-Sunyer & Duarte, 2008,) but are several times higher in the Atlantic (Chu & Gale, 2017). There is also considerable variation in tolerance related both to taxonomic group and mobility; mobile fish and crustaceans that can move away from hypoxia exhibit higher thresholds (greater sensitivity) (Vaquer-Sunyer & Duarte, 2008). Tolerance thresholds for most infaunal invertebrates (macrofauna) occur at much lower oxygen concentrations, with values between $5\text{--}10 \mu\text{mol } O_2 \text{ kg}^{-1}$ (0.1 and $0.2 \text{ ml } L^{-1}$) (Levin et al., 2009; Sperling et al., 2016), or in some cases less

than 20 $\mu\text{mol O}_2 \text{ kg}^{-1}$ (Levin & Gage, 1998). However, some fish and invertebrate species can survive at 1–2 $\mu\text{mol O}_2 \text{ kg}^{-1}$ (Gallo & Levin, 2016; Gallo et al., 2019; Levin, 2003).

8.5.4.5 Lessons from the past

Oxygen regimes in the ocean have changed multiple times through geological history, providing a record to help understand how periods of high and low oxygen influence marine communities (Sperling et al., 2015). Changes in global oxygen conditions are associated with major extinctions or radiations of benthic marine fauna (Moffitt et al., 2015a) and the expansion and contraction of oxygen minimum zones through time are hypothesized to have played an important role in the modern-day distribution and diversity patterns of deep-sea species (Rogers, 2000; White, 1988). During the Cretaceous/Paleogene Event, bottom waters underwent severe oxygen depletion due to accumulation of organic matter (de Oca et al., 2013), at the same time aerobically active predatory fishes exhibited particularly large losses (Friedman, 2009). However, fishes in the open ocean, far from coastal oxygen minima, appeared to be more resilient to the extinction event (Sibert et al., 2014).

8.5.4.6 Changes over the last 25–50 years

Long-term records documenting changes in species distributions over the past 25–50 years on deep margins are rare. Catch records for hypoxia-intolerant groundfish off British Columbia show they have moved shallower by 2–3 m each year over a decade (Whitney et al., 2009) as hypoxia has expanded on the British Columbia coast (Whitney, 2009). Off Southern California, echinoid distributions have expanded for some species and contracted for others (Sato et al., 2017) (Figure 8.5.6). Where long-term, fisheries independent survey data exist (e.g. Sato et al., 2017) or detailed catch records are kept, data could be mined for this type of information to better understand the influence of changing oxygenation on margin ecosystems and their services.

8.5.4.7 Variability, tolerance and adaptation potential

There is a general belief that those ocean ecosystems subject to greatest variability in climate drivers will host species most adaptable and least vulnerable to negative climate impacts (Henson et al., 2017). Continental shelf and slope settings subject to seasonal, wind-driven

upwelling are among the most variable and many taxa already experience low oxygen conditions seasonally or permanently. The East Pacific, North Indian Ocean and West Africa are such regions, as they are subject to major interannual and multi-decadal climate cycles as well as wind events that influence oxygenation (Nam et al., 2011). Communities that have evolved under these conditions usually have several species that are highly adapted to living under severely hypoxic conditions. A recent review found that at least 77 representative demersal fish species have been reported living in oxygen minimum zones (Gallo & Levin, 2016), and this group includes several species important for demersal fisheries, such as *Sebastes* spp. (thornyhead), *Microstomus pacificus* (Pacific Dover sole) and *Anoplopoma fimbria* (black cod) (Figure 8.5.10). Due to the fact that these are long-lived species, it is unlikely that increased fishing effort on these species could compensate for losses from hypoxia-intolerant fisheries species. In regions that are more highly oxygenated and less variable, declining oxygen levels could exhibit (anthropogenic) signal emergence above background variability sooner (Long et al., 2016). Oxygen loss on better-oxygenated margins such as in the Atlantic could be of greater concern as there may be less phenotypic plasticity in hypoxia response, conferring reduced adaptation capacity. On the other hand, communities in areas that already exhibit low oxygen conditions seasonally or permanently may also be closer to their tolerance limits, and therefore in some cases more vulnerable under deoxygenation scenarios.

Beyond the survival potential of hypoxia-tolerant species, physiological adaptations to declining oxygen levels may include increased concentration of blood pigments such as haemoglobin, enhanced respiratory surface areas, slowed metabolic rates, increased ventilation rates, altered muscle composition, enzymatic adaptations and energy-conserving behaviours (Gallo & Levin, 2016; Levin, 2003). A detailed listing of adaptations in fishes can be found in Gallo and Levin (2016).

8.5.5 Ecological and societal consequences

Oxygen declines (or oxygenation events) on continental margins can lead to mortality (or redistribution) of key invertebrate and vertebrate fisheries (Arntz et al., 2006; Grantham et al., 2004). Sperling et al. (2016) predict future biodiversity loss for macrofaunal invertebrates at 500–1000 m on continental margins due to combined stressor effects. As these are key to feeding demersal

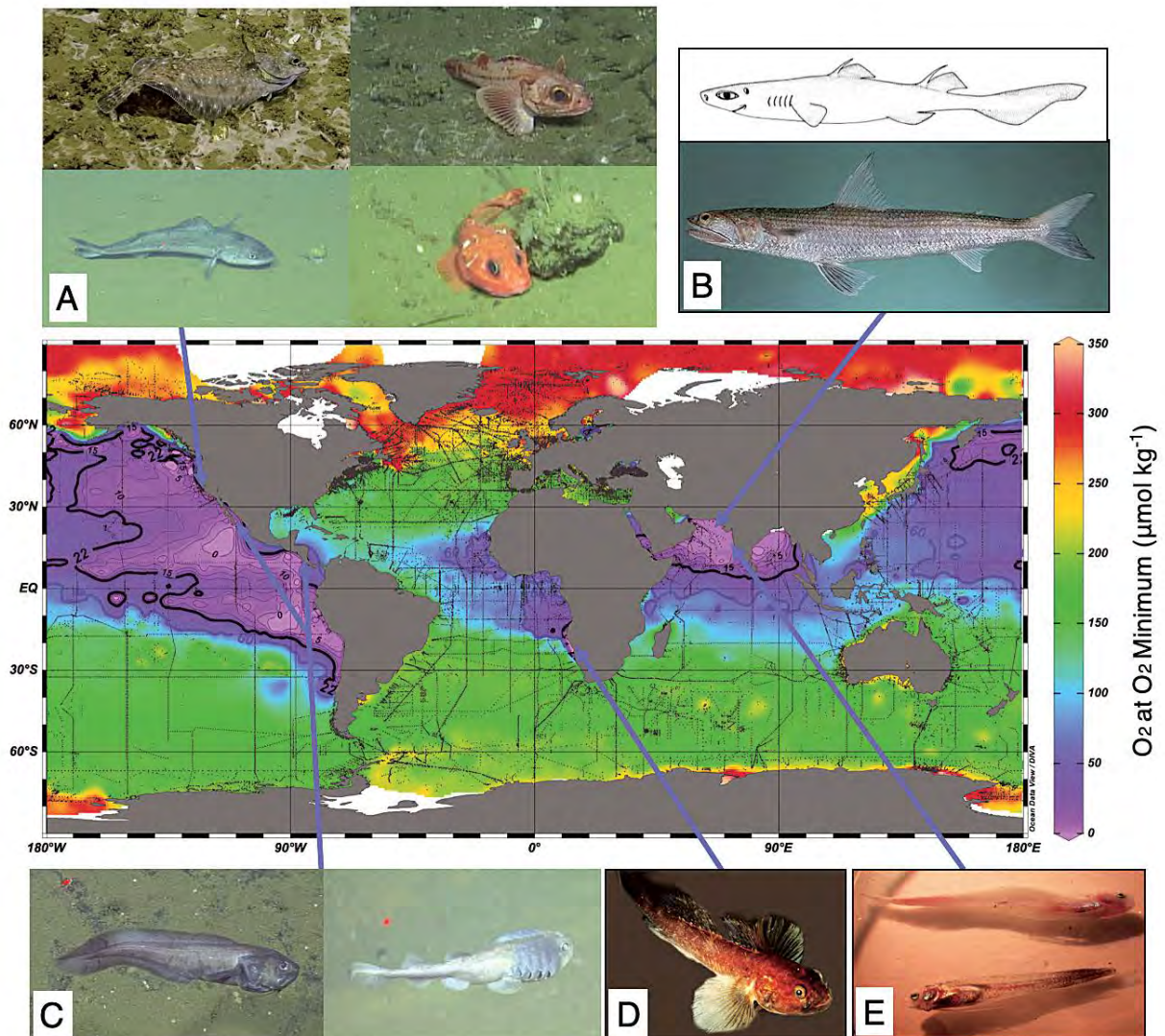


Figure 8.5.10 Global minimum oxygen concentrations within the water column and dominant demersal fish species in oxygen minimum zones (purple). Representative fish in oxygen minimum zones are shown. Modified from Gallo and Levin (2016). OMZ-adapted demersal fish species include: (A) in the Northeast Pacific—*Microstomus pacificus* (upper left), *Careproctus melanurus* (upper right), *Nezumia liolepis* (lower left), *Sebastolobus alascanus* (lower right); (B) Pakistan margin—*Centroscyllium ornatum* (upper) and *Saurida tumbil* (lower); (C) Gulf of California and central America *Cherublemma emmelas* (left)—*Cephalurus cephalus* (right); (D) Namibian margin—*Sufflogobius bibarbatus*; (E) west Indian margin—*Bregmaceros* sp.

fishes, there may be negative food web effects for demersal communities. Many demersal fish species may also rely heavily on pelagic production, which also will be influenced by changes in oxygenation (Gilly et al., 2013; see Section 8.4). Decreasing oxygen levels in the California Current Ecosystem were associated with a 63% decline in the region's mesopelagic fish larvae (Koslow et al., 2011); these species act as an important trophic linkage to seafloor communities.

Demersal fisheries on continental margins are economically valuable and deoxygenation will likely negatively affect demersal fishery catches. Catch per unit effort (CPUE) of demersal fish species along the US West Coast is tied to near-bottom oxygen concentrations

(Keller et al., 2015), which can explain up to 84% of the variation in biomass of individual fisheries species along a hypoxic gradient off Oregon (Keller et al., 2010). In other upwelling areas of the world including Peru, India, and Pakistan, the CPUE of demersal fisheries decreases when bottom oxygen levels decline (Gallo & Levin, 2016). Reductions in habitable area with warming are predicted for fish by Deutch et al. (2015) based on their metabolic index. Studies in the Southern California Bight have used projections of current trends in oxygen loss in concert with known physiological thresholds for sensitive species to project an 18% loss of habitat for rockfish (*Sebastes* sp.) in the Cowcod Conservation Area by 2030 (McClatchie et al., 2010). A number of important fisheries species in upwelling areas are not

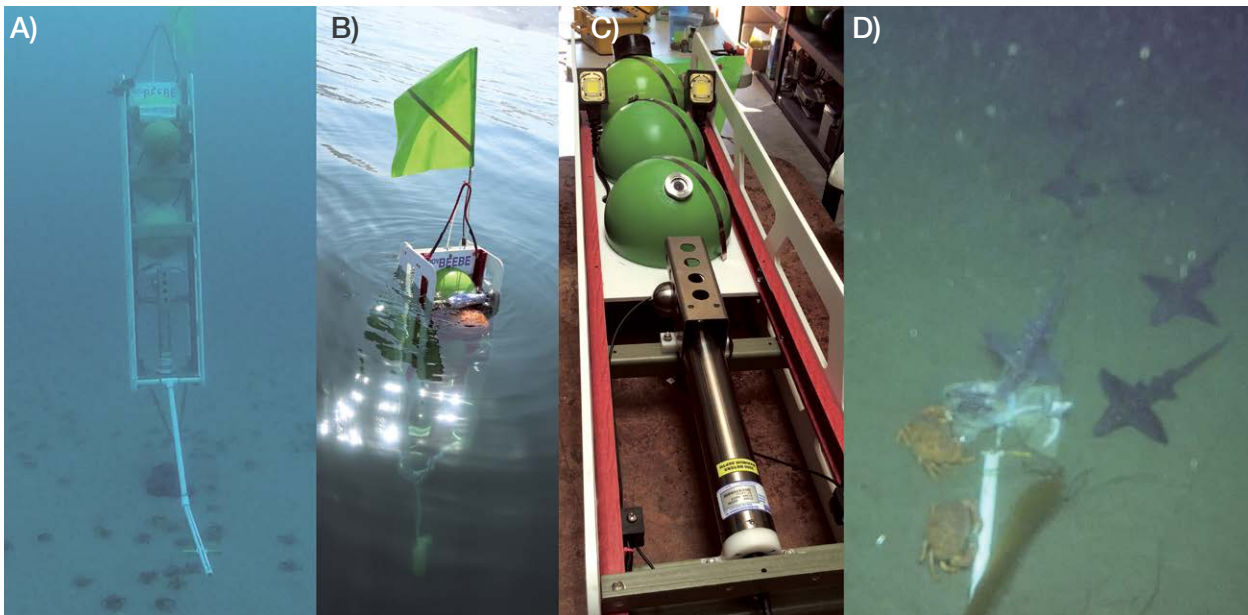


Figure 8.5.11 Autonomous landers with coupled environmental sensors and camera systems provide a low-cost framework for studying how environmental oxygen conditions affect continental margin communities. Pictured is Deep Ocean Vehicle (DOV) BEEBE, which is rated to 1000 m and collects data on environmental conditions (temperature, oxygen, salinity, and pressure) with a SBE MicroCAT ODO sensor and collects video data on the seafloor community with a pre-programmed camera system. A) DOV BEEBE deployed on the sea floor; B) DOV BEEBE at the surface during recovery; C) DOV BEEBE in the lab, showing the position of the SBE sensor and the camera sphere; D) image of seafloor community during a deployment with crabs and chimeras attracted to the bait on the drop-arm. Lander design courtesy of Kevin Hardy (Global Ocean Design).

hypoxia-tolerant and would likely be negatively impacted by deoxygenation trends (Gallo & Levin, 2016). These include *Sebastes* spp. and *Cancer magister* along the US West Coast (Grantham et al., 2004; McClatchie et al., 2010). During the 1997-1998 El Niño, local fisheries for hake, octopus, and scallop off Peru expanded in response to a significant increase in oxygen along the sea floor (Arntz et al., 2006). This suggests that future trends in hypoxia expansion may lead to reductions in these fisheries in coming years.

8.5.6 Implications of continuing ocean deoxygenation and vulnerabilities

In some developing countries, including Mexico, Peru, and India, severely hypoxic conditions can be found at upper slope and shelf depths, sometimes as shallow as 20 m (Banse, 1968). In the US, severely hypoxic conditions can also be found seasonally at inner shelf depths (20-50 m) off Oregon (Grantham et al., 2004; Keller et al., 2010). These regions, where severely hypoxic waters already occur at shallow depths, may be particularly vulnerable to continued deoxygenation trends and should be monitored closely (Hofmann et al., 2011). This is especially pertinent given that decreases in oxygen in the Southern California Bight have been most pronounced closer to shore at depths between 100-400 m (Bograd et al., 2008). These nearshore,

shallow areas are particularly vulnerable because they are likely more utilized by coastal communities for fishing. Shallower marine communities are exposed to warmer conditions which increase oxygen demand. At the same time, they likely experience habitat compression from shoaling oxyclines (Rosa & Seibel, 2011), making them more concentrated and thus susceptible to overfishing. Likely, benthic communities in areas with shallow OMZs in tropical parts of the world where water temperatures are warmer will be those most impacted by deoxygenation trends.

Most developing countries do not have good oxygen monitoring networks in place to document declines in oxygen and impacts to marine communities, nor do they have good baseline data against which to compare future conditions. Relative to other climate impacts, deoxygenation remains an under acknowledged climate impact within the international climate policy community (Gallo et al., 2017).

8.5.7 Approaches to monitoring deoxygenation on margins

Long-term time-series are an important tool in monitoring oxygen loss and consequent biological responses. Time-series data can reveal: (i) the timing, intensity and duration of hypoxic events and the rate and

magnitude of the response in the animal communities, or (ii) the influence of the various oceanographic phenomena operating on different time scales (e.g. ENSO, seasonality, abrupt events) that can mask the long-term decline imposed by climate change. Long-term monitoring programmes such as the California Cooperative Fisheries Investigation (CalCOFI) have shown the potential importance of oxygen trends in influencing the abundance of mesopelagic fishes (Koslow et al., 2011). However, compared to pelagic time-series, benthic time-series are more limited. Key contributions have come from the VENUS Observatory in Saanich Inlet off Canada that actively monitors both environmental oxygen conditions and collects video imagery of the benthic community (e.g. Matabos et al., 2014). Additionally, landers with coupled environmental sensors and camera systems can be used to collect high-frequency data on oxygen conditions and community responses at more locations (though usually for shorter periods) than possible with cabled observatories (Figure 8.5.11; Gallo, 2018). Existing benthic time-series programmes should include oxygen monitoring if they do not do so already. Fisheries-relevant trawl studies that sample across latitudes and depths (e.g. Bianchi, 1991; Hamukuaya et al., 2001; Keller et al., 2015) can also provide important insight into the influence of oxygen on community characteristics, provided that they collect paired high-quality environmental and community data. The use of satellite archival tags that can measure dissolved oxygen concentrations *in situ* (Coffey & Holland, 2015) will also be informative in determining the oxygen niches of species and observing any changes in environmental characteristics through time. All of these monitoring tools will prove useful in attribution of ecological change to specific climate drivers (whether oxygen, temperature, pH or other) in an ocean increasingly subject to multiple stressors.

8.5.8 Conclusions / Recommendations

Although anthropogenic access to deep margins for fishing, energy extraction and scientific research has intensified significantly over the past quarter century (Levin & Sibuet, 2012; Ramirez-Llodra et al., 2011), there are relatively few seafloor observations made on appropriate long time and space scales that document the consequences of changing environmental conditions, including ocean deoxygenation. Notably, benthic ecosystems have received much less attention with regards to deoxygenation than pelagic systems; the majority of long-term coastal monitoring

programmes focus on water column measurements and do not encompass the sea floor.

Research across natural gradients on margins in space and time indicates there are dynamic and rapid responses to oxygen change at all levels of organization, from the ecosystem to the gene, on both ecological and evolutionary time scales. Deoxygenation drives changes in species distributions, assemblage composition, body size, biomass (productivity), biodiversity, and food webs. Sublethal impacts take place at much higher thresholds than lethal impacts (Hofmann et al., 2011; Vaquer-Sunyer & Duarte, 2008), so we should be conservative in identifying thresholds of concern, especially since sublethal impacts are harder to observe but impact organismal fitness. Marine environments only appear to be viable if they support metabolic indices (the ratio of O_2 supply to resting metabolic O_2 demand) of 2 to 5 (Deutsch et al., 2015), suggesting that sublethal impacts begin occurring at oxygen concentrations much higher than experimentally-determined physiological limits. To advance understanding of how deoxygenation impacts on benthic communities will affect ecosystem services, it will be necessary to understand species-specific environmental niches and physiological tolerances and predict changes in the densities of key species of interest, expanding beyond the use of broader groupings such as the meiofauna, macrofauna, or megafauna. However, species-specific information will need to be interpreted within an ecosystem-based framework, considering the role each species occupies in the food web and in mutualistic and competitive interactions with other species. Some metrics, such as carbon sequestration, will require whole community metrics.

8.5.9 References

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8.6 The significance of ocean deoxygenation for estuarine and coastal plankton

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Summary

- Seasonal deoxygenation of estuarine and coastal ecosystems leads to a variety of impacts on zooplankton including: lower overall abundance; altered community structure with smaller, egg carrying taxa and gelatinous zooplankton increasing with decreasing dissolved oxygen; shallower vertical distributions and reduced vertical migration extent; sub-lethal impacts including reduced size at adulthood; and reduced growth rates.
- Pelagic predator-prey interactions can be altered if zooplankton prey utilize hypoxic waters as a refuge from fish predation. Conversely, avoidance of low oxygen bottom waters can result in zooplankton aggregations at the interface of hypoxic waters which can be sought out by zooplankton predators.
- In coastal ecosystems with shears and differential flow between surface and deep layers, avoidance of low oxygen bottom waters can influence spatial dynamics of zooplankton populations by altering emigration and immigration patterns, and residence times.
- Ecosystem models of estuarine and coastal seas should incorporate seasonal hypoxic bottom waters to better understand the impacts of current and future deoxygenation on pelagic food webs.

Low oxygen effects on estuarine and coastal zooplankton	Potential consequences
Low oxygen bottom waters may result in lower overall zooplankton abundances.	<ul style="list-style-type: none"> • Lower grazing pressure on phytoplankton. • May result in limiting food levels for zooplankton-feeding fish.
Low oxygen waters may result in zooplankton species changes with a shift to smaller sized individuals.	<ul style="list-style-type: none"> • Different zooplankton species may be less nutritious to their fish predators. • Smaller zooplankton prey may require that more zooplankton be consumed by fish to meet their nutritional needs.
Zooplankton may use mild hypoxic bottom water as a refuge from predation.	<ul style="list-style-type: none"> • Zooplankton-feeding fish may avoid the low oxygen bottom waters and thus have reduced consumption of zooplankton. • Zooplankton-feeding jellyfish can tolerate low oxygen waters more than fish and thus may replace fish as the dominant consumers of zooplankton.
Zooplankton may avoid severe hypoxic bottom waters and aggregate at the depth interface of rapidly decreasing oxygen.	<ul style="list-style-type: none"> • These zooplankton aggregations in surface waters may result in enhanced feeding zones for zooplankton predators.
The differences between environmental supply of oxygen and the organism's demand for oxygen drive the response of plankton to deoxygenation.	<ul style="list-style-type: none"> • The definition of hypoxia as a concentration does not account for the decreasing solubility of oxygen and increasing metabolic rate of organisms with increasing temperature. • At high temperatures organisms may be in stressful or lethal conditions even when the concentration of dissolved oxygen is above levels defined as hypoxic ($< 2 \text{ mg L}^{-1}$). • The actual effect of hypoxia is very likely species and temperature specific, related to each species oxygen demand.

8.6.1 Definition of species group

Hypoxia exerts widespread and expanding stress on coastal ecosystems worldwide, triggered in large part by eutrophication. Hypoxia is often defined as dissolved oxygen concentrations $< 2 \text{ mg O}_2 \text{ L}^{-1}$ (at $18 \text{ }^\circ\text{C}$ in sea water $= 1.5 \text{ ml L}^{-1} = 62.6 \text{ } \mu\text{M L}^{-1} = 5.6 \text{ kPa}$ oxygen partial pressure), although more biologically relevant definitions are required to define its impacts (Breitburg et al., 2009; Elliott et al., 2013; Vaquer-Sunyer & Duarte, 2008; Verberk et al., 2011). Physiologists usually express dissolved oxygen (DO) in terms of partial pressure because oxygen availability to aquatic organisms is dependent on the rate of diffusion across integuments or gills and is controlled by the partial pressure of O_2 (mm Hg or kPa). Oceanographers usually express DO in terms of concentration (mg L^{-1} , ml L^{-1} , or $\mu\text{M L}^{-1}$). Temperature and salinity directly influence the oxygen solubility in

sea water and thus DO concentration and oxygen partial pressure, and temperature affect the metabolic demand of aquatic ectotherms. In order to effectively assess the impacts of hypoxic stress, it is therefore necessary to consider the effects of temperature on both oxygen availability and animal metabolism.

Hypoxic water formation is driven primarily by nutrient stimulation of largely ungrazed phytoplankton blooms. These blooms sink or are eaten and processed by zooplankton, and are subsequently decomposed by microbial activity, consuming much of the available oxygen in the lower water column (Diaz & Rosenberg, 2008; Howarth et al., 1996; Malone, 1991; Nixon, 1995). The type of deoxygenation that is addressed in this section is seasonal and confined to coastal bottom waters which are separated from the surface waters and contact with the air by a density interface (Figure 8.6.1).

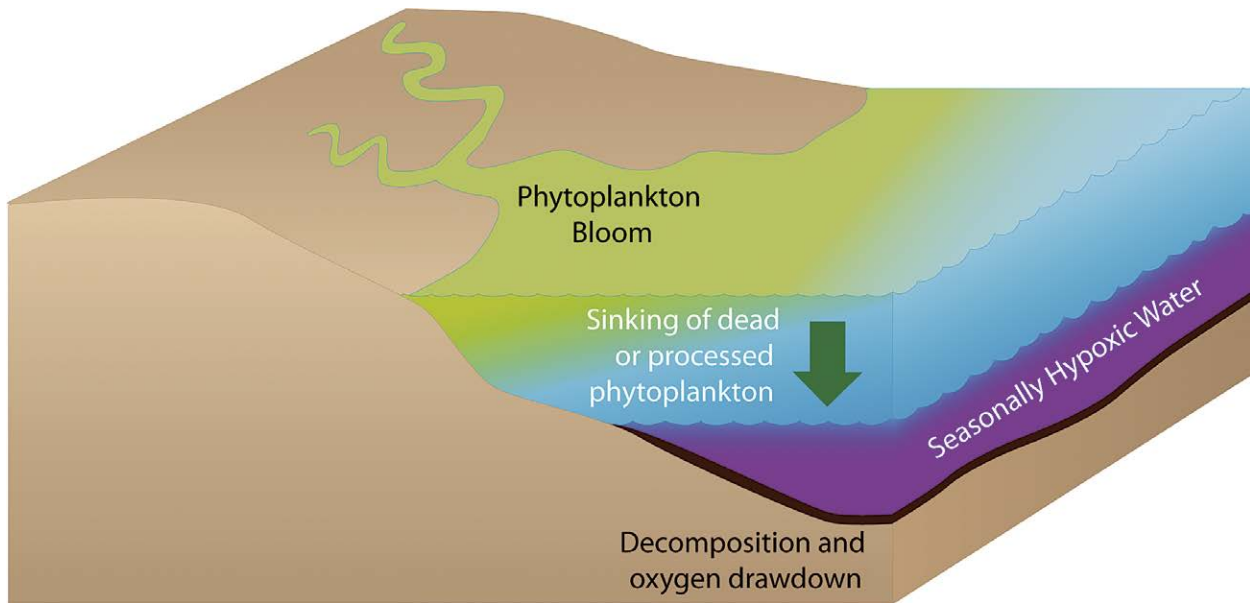


Figure 8.6.1 The formation process for coastal and estuarine deoxygenation. Graphic Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

The focus of this section is to review the effects of seasonal hypoxia on estuarine and coastal plankton. Plankton includes both the autotrophic phytoplankton and heterotrophic zooplankton. We focus on the animal zooplankton that require oxygen for their metabolic functions. These zooplankton include both the “temporary” meroplankton which are planktonic larval stages of benthic organisms (e.g. oysters, barnacles, polychaete worms, etc.) (Figure 8.6.2) and the “permanent” holoplankton, largely dominated by crustaceans (e.g. copepods, mysids, euphausiids) (Figure 8.6.3) and jellyfish but including members of a wide variety of other phyla. Copepods are a diverse group of crustaceans that predominate zooplankton communities, in terms of both numerical abundance and biomass. They can be classified with respect to reproduction: those that carry their eggs until hatching and those that release their eggs (broadcast spawners). Copepod eggs are denser than sea water and thus sink to bottom waters where they can be affected by low oxygen conditions.

8.6.2 Trends and impacts

8.6.2.1 Effects of low oxygen waters on zooplankton metabolism

When considering the potential biological and ecological effects of hypoxia on coastal zooplankton, reduced rates of oxygen uptake are ultimately responsible for adverse effects such as reduced growth and increased mortality.

Oxygen solubility, partial pressure and diffusivity all can influence the rate of oxygen uptake (Verberk et al., 2011). Under low oxygen environmental conditions (relative to oxygen demand), aerobic respiration may not be fully supported by the consequent lower oxygen uptake rates, and respiration becomes oxygen limited (Childress & Seibel, 1998; Elliott et al., 2013; Gnaiger, 1991; McAllen et al., 1999; Pörtner & Knust, 2007; Seibel, 2011). As a



Figure 8.6.2 Barnacle larva © Papilio / Alamy stock photo.



Figure 8.6.3 Mysid shrimp © Daniel L. Geiger / SNAP / Alamy stock photo.

result, zooplankton residing in hypoxic water must either implement specific adaptations to maintain the rate of oxygen uptake, make up the energy deficit through anaerobic respiration, or reduce their energy demand and oxygen requirements by decreasing metabolic rate (Childress & Seibel, 1998; Elliott et al., 2013; Gnaiger, 1991; McAllen et al., 1999; Seibel, 2011). In aquatic ectotherms, temperature controls these respiration and metabolic rates.

Specific adaptations that help maintain oxygen uptake under low DO (or increasing oxygen demand) include increased ventilation of the respiratory surfaces (e.g. gills), increased heart rate, reduced activity, and production of high affinity oxygen uptake molecules (Childress & Seibel, 1998; Herreid, 1980; Pörtner & Knust, 2007; Seibel, 2011). These types of responses are common among organisms in oceanic oxygen minimum zones, which likely have co-evolved with low oxygen concentrations for thousands of years. However, among coastal organisms, exposure to hypoxia is generally more ephemeral (seasonal) and in many cases is a relatively new stressor associated with cultural eutrophication. Since 1950, more than 500 sites in coastal waters have reported DO concentrations $< 2 \text{ mg O}_2 \text{ L}^{-1}$, with fewer than 10% of these systems known to have hypoxia prior to 1950 (Diaz & Rosenberg, 2008; Isensee et al., 2015). Consequently, estuarine and coastal zooplankton do not appear to have developed specific physiological adaptations to hypoxia in coastal systems (Childress & Seibel, 1998; Dam, 2013; McBryan et al., 2013). Instead, these organisms must either avoid hypoxia through behavioural mechanisms or reside in hypoxic water and tolerate some deleterious effects.

Two useful thresholds can be defined to evaluate effects of low environmental oxygen on zooplankton. These are the critical (P_{crit}) and lethal (P_{leth}) oxygen thresholds

(Childress & Seibel, 1998; Connett et al., 1990; Elliott et al., 2013; Gnaiger, 1991; McAllen et al., 1999; Pörtner & Knust, 2007; Seibel, 2011). Both of these thresholds reflect the balance between oxygen *supply* to the organism, a function of the rate of molecular diffusion, and oxygen *demand* by the organism, a function of respiration rate (and ultimately metabolic rate). As such, both thresholds are temperature dependent, and are expressed in terms of oxygen partial pressures. However, according to Fick's First Law of Diffusion across a membrane, oxygen uptake, and thus maximum potential aerobic respiration rate, will depend on oxygen supply as governed by the external (environmental) oxygen solubility, partial pressure, and diffusivity (Verberk et al., 2011). Thus, corresponding critical and lethal oxygen supply thresholds can be defined that account for oxygen solubility, partial pressure and diffusivity. These thresholds will depend on an organism's non-oxygen-limited (target) respiration rate, and the lowest sustainable (basal) respiration rate, respectively (Elliott et al., 2013). When maximum potential respiration rate drops below an organism's "target" respiration rate (P_{crit}), respiration rate becomes limited by oxygen supply, and sub-lethal effects of hypoxia can be expected. When the oxygen supply drops below an organism's "basal" respiration rate (P_{leth}), acute lethal effects of hypoxia can be expected. Thus, for coastal zooplankton lacking specialized adaptations to low environmental oxygen, oxygen uptake is more-or-less constant at the target level when PO_2 is above P_{crit} , then declines linearly as DO declines below the P_{crit} level (Figure 8.6.4). Because zooplankton lack gills, their oxygen uptake is a function of diffusion through their body surface. Under low oxygen conditions relative to copepod oxygen requirements, species with a higher surface/volume ratio would be favoured because of their greater oxygen diffusion potential.

Deoxygenation reduces the survival of copepods under controlled laboratory conditions (Marcus et al., 2004; Richmond et al., 2006; Roman et al., 1993; Stalder & Marcus, 1997; Vargo & Sastry, 1977). In laboratory experiments Marcus et al. (2004) and Richmond et al. (2006) showed that *Acartia* egg production and population growth rate were reduced in low-oxygen waters (0.7 and $1.5 \text{ mg O}_2 \text{ L}^{-1}$) compared to normoxic ($\text{DO} > 2 \text{ mg L}^{-1}$) controls. Low oxygen conditions have also been shown to reduce the ingestion rates of copepods in laboratory experiments (Elliott et al., 2013), as well as reduce their escape response (Decker et al., 2004). Copepod survival, growth rate, egg production

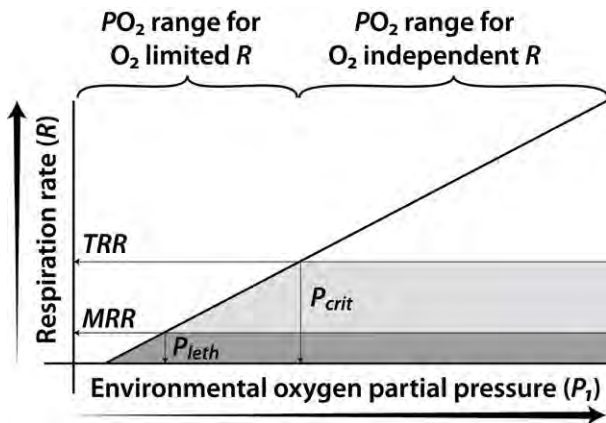


Figure 8.6.4 Relationship between an organism's respiration rate and the environmental oxygen partial pressure. Target Respiration Rate (TRR); Minimum survivable Respiration Rate (MRR), critical oxygen partial pressure (P_{crit}) and lethal oxygen partial pressure (P_{leth}) are shown. Adapted from Elliott et al. (2013).

and ingestion rate all decline with oxygen availability as predicted by the relationship given in Figure 8.6.4.

8.6.2.2 Effects of low oxygen on copepod egg hatching

Copepods in estuarine and coastal waters produce two types of eggs: diapause (resting) eggs which must complete a dormancy (refractory) period before hatching and subitaneous eggs which hatch within hours-days of being spawned, depending on temperature (Grice & Marcus, 1981). Low oxygen has been shown in laboratory experiments to severely reduce the hatching success of subitaneous copepod eggs (Invidia et al., 2004; Lutz et al., 1992; Marcus & Lutz, 1994; Marcus et al., 1994, 1997; Roman et al., 1993; Richmond et al., 2006). The eggs of dominant coastal copepods have sinking rates which range from 15 to 35 m d⁻¹ (Jiang et al., 2006; Knutsen et al., 2001; Uye, 1980). Thus, if hatching times are longer than the time it takes eggs to sink to bottom waters, subitaneous (ready to hatch) copepod eggs will be subjected to low oxygen conditions (Jiang et al., 2006; Tang et al., 1998). For example, assuming an egg hatching rate of 24h and a sinking rate of 20 m d⁻¹, if the deoxygenated conditions begin 10 m below the surface and eggs are released at the surface, most would already be well within the low oxygen waters by the time they would have hatched. But if low oxygen conditions were more than 40 m below the surface, most eggs would hatch before sinking to the low oxygen waters. Low oxygen conditions can sometimes induce dormancy in these subitaneous eggs, which is reversed with increases in oxygen (Katajisto,

2004). Thus, the potential exists for subitaneous eggs to hatch if hypoxia dissipates or they are resuspended into normoxic waters. The length of time that subitaneous eggs can withstand hypoxia/anoxia and still remain viable to hatch varies with copepod species and abiotic conditions such as temperature and hydrogen sulphide levels (Broman et al., 2017; Hansen & Drillet, 2013; Katajisto, 2004).

Copepod diapause eggs have an obligatory "refractory phase" and sink to the sediment which is typically anoxic below a depth of several millimetres. Diapause eggs can withstand considerable periods of anoxia and toxic hydrogen sulphide (Marcus, 2001). In general, subitaneous eggs are less able to withstand prolonged exposure to low oxygen than diapause eggs because of their higher metabolic demand (Hansen & Drillet, 2013).

Coastal and estuarine waters which experience seasonal hypoxia in bottom waters may develop a significant "egg bank" of copepod eggs which if reaerated could hatch and make important contributions to copepod populations and their predators. A combined laboratory and modelling study by Broman et al. (2017) demonstrated that re-oxygenation of anoxic sediments activated copepod egg hatching which could make a substantial contribution to copepod populations in the Baltic, and perhaps in other similar systems (Figure 8.6.5). However, reduced hatching success of subitaneous eggs that do not have induced diapause may significantly affect copepod production during periods of hypoxia due to egg mortality (e.g. Roman et al., 1993). This was observed in the Chesapeake Bay, where copepod biomass was lower both within the region where hypoxia was present compared to outside of that region, and during the period of hypoxia compared to before and after hypoxia occurred (Roman et al., 2005).

8.6.2.3 Effects of low oxygen waters on zooplankton distributions

The general observation of reduced copepod abundances (integrated over the entire water column) in hypoxic water columns (Keister et al., 2000; Kimmel et al., 2012; Roman et al., 1993) suggests lower population growth, greater copepod mortality, predation and/or emigration in water columns with hypoxic bottom waters.

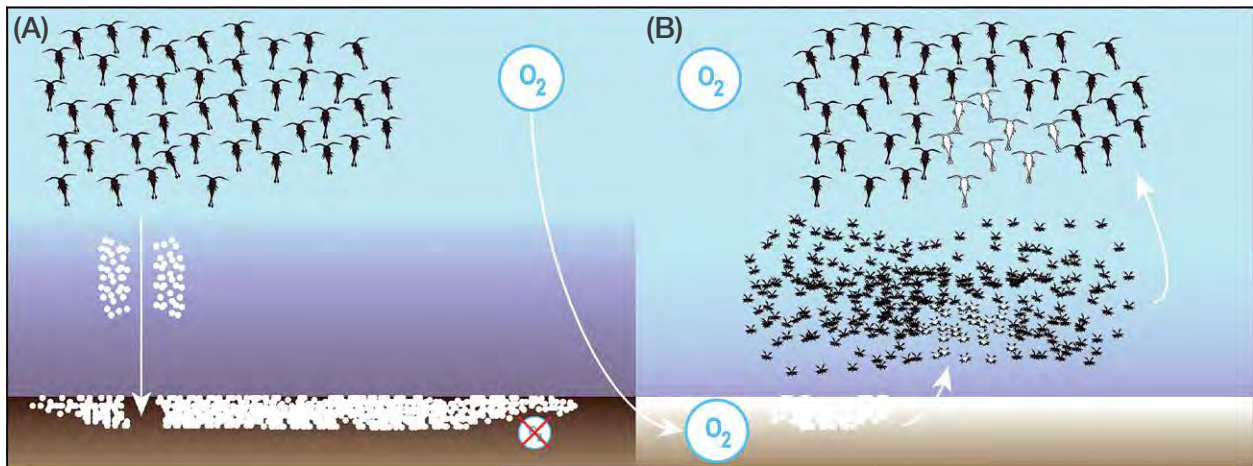


Figure 8.6.5 Showing how diapause eggs deposited by copepods in anoxic sediments can later contribute to a copepod population following re-oxygenation of sediment containing the diapause eggs. (A) sediments and bottom water are deoxygenated, and eggs are dormant. (B) the sediments are reoxygenated and eggs hatch, contributing up to 20% of the copepod population. Symbols Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). Adapted from Broman et al. (2017).

Zooplankton are able to change their vertical position in the water column to avoid low oxygen bottom waters. However, the vertical compression of their distribution to the upper water column can make them more vulnerable to predation by visually feeding fish and thus alter food-web processes. In general, depth-stratified zooplankton sampling has shown that copepod abundances are higher in the surface mixed layer and within the pycnocline compared to hypoxic bottom water in coastal environments (Keister & Tuttle, 2013; Keister et al., 2000; Kimmel et al., 2009; North & Houde, 2004; Pierson et al., 2009b, 2017; Roman et al., 1993). This is not always the case (Qureshi & Rabalais, 2001; Taylor & Rand, 2003) and, even if most zooplankton are above the oxycline, significant amounts often occur in hypoxic bottom water for part of the day (Keister & Tuttle, 2013; North & Houde, 2004; Pierson et al., 2017; Roman et al., 1993; Taylor et al., 2007).

In most coastal and estuarine waters copepods exhibit diel vertical migrations, presumably to reduce predation by visual feeders by residing at depth during the day, and returning to the surface layer at night (Cahoon, 1981; Roman et al., 1988). Bottom-water hypoxia can clearly disrupt vertical migration behaviour. For example, when a wind event mixed the water column and reaerated hypoxic bottom water, copepods migrated to a deeper depth during the day (Roman et al., 1993). Generally, hypoxic bottom waters truncate zooplankton vertical migration behaviours, reducing the excursion distance (Keister & Tuttle, 2013; Pierson et al., 2009b, 2017; Roman et al., 1993, 2012). For example, zooplankton in the Gulf of Mexico avoided hypoxic bottom waters in their diel vertical migrations and the median depth

of their daytime distribution was 7 metres higher in the water column compared to daytime distributions of zooplankton in water columns with no hypoxic bottom waters (Roman et al., 2012). In Hood Canal and the Neuse River system, migration behaviour and vertical distribution of fish was more directly affected by bottom water hypoxia than zooplankton, creating a potential refuge for zooplankton (Parker-Stetter & Horne, 2009; Taylor & Rand, 2007). Thus, along with food levels (Hays et al., 2001; Huntley & Brooks, 1982; Pearre, 2000; Roman et al., 1988) and predators (Bollens & Frost, 1989; Frost & Bollens, 1992; Ohman, 1988), the presence of hypoxic bottom waters can influence diel shifts in the vertical distribution of neritic copepods (e.g. Keister et



Figure 8.6.6 Male (upper left) and female (lower right) adults of the copepod species *Acartia tonsa* from the Chesapeake Bay. © J. Pierson.

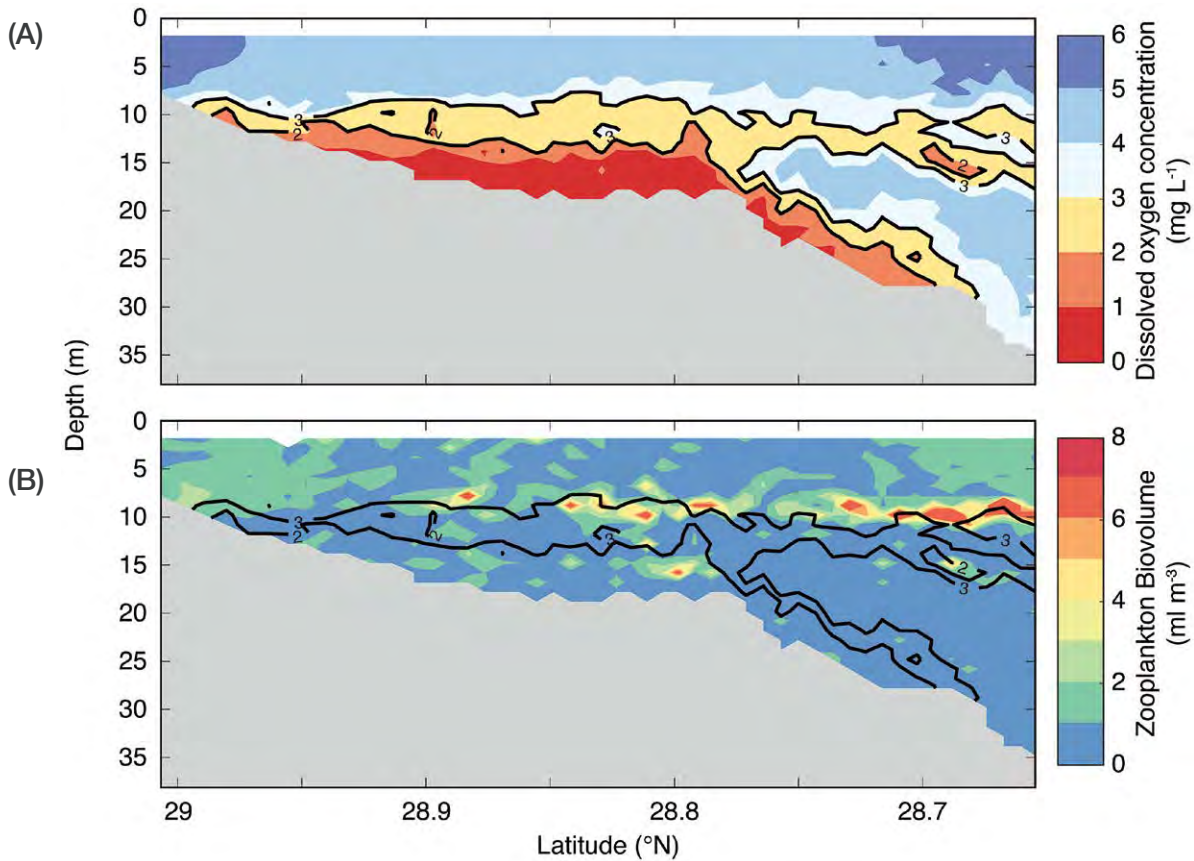


Figure 8.6.7 (A) Dissolved oxygen concentration and (B) zooplankton biovolume data shown as contour plots from a cross-shelf transect in the Gulf of Mexico in July 2004. The black lines on both plots are contours of the 2 and 3 mg L⁻¹ dissolved oxygen conditions, and on (B) they are shown to illustrate the close association between the oxygen gradients and the zooplankton biovolume.

al., 2000; North & Houde, 2004; Qureshi & Rabalais, 2001; Roman et al., 1993). Decker et al. (2003) reported that behavioural responses of copepods to hypoxia may differ depending on environmental history: *Acartia tonsa* (Figure 8.6.6) from Chesapeake Bay appeared to avoid hypoxic bottom waters in laboratory mesocosms while *A. tonsa* from Florida, not typically exposed to hypoxia, did not avoid low-oxygen concentrations in the same mesocosms. In addition, temporal analysis of vertical distributions of copepods has suggested that individuals display considerable variation in their vertical movements, often taking brief (hours) excursions between the surface mixed layer and sub-pycnocline depths (Hays et al., 2001; Pearre, 2000; Pierson et al., 2009a). Thus, it may be common for copepods in coastal waters with hypoxia to experience a range of oxygen concentrations over the day.

Oxygen gradients between hypoxic and normoxic waters can be abrupt, sometimes only centimetres thick (Breitburg et al., 1999, 2003; Donaghay et al., 1992). As a result of these sharp gradients, acoustic and optical sampling technologies can provide insights

into the fine-scale distribution of zooplankton in relation to oxygen concentrations. Sharp gradients of oxygen embedded within the pycnocline can serve as loci for enhanced predator-prey interactions. Transects sampled with an optical plankton counter (OPC) in Chesapeake Bay and the northern Gulf of Mexico indicate significant amounts of zooplankton occurring in hypoxic waters, and often concentrated at the oxycline (Kimmel et al., 2009; Roman et al., 2012) (Figure 8.6.7). The food of copepods may also be concentrated within the oxycline. Microbial communities and micro-zooplankton are often aggregated at oxic/hypoxic interfaces in the water column (Coats & Revelante, 1999; Detmer et al., 1993; Fenchel et al., 1990, 1995). Thus, copepods could find food “hot-spots” within the oxycline which have higher food but lower oxygen concentrations.

8.7.2.4 Effects of low oxygen on zooplankton community composition

Low oxygen waters have been associated with changes in zooplankton species assemblages. These zooplankton species changes could be due to direct

effects of low oxygen on the metabolic functions of the animal or indirect effects due to selective predation by zooplankton consumers. Long term increases in bottom water hypoxia may favour copepod species that carry their eggs as compared to broadcast spawners whose eggs would sink into anoxic/hypoxic bottom waters. For example, increased eutrophication and low oxygen bottom waters have resulted in an increase in the abundance of the small egg-carrying copepod *Oithona davisae* (Figure 8.6.8) in Tokyo Bay and decline in the occurrence of *Acartia omorii* and *Paracalanus* sp.; both of which release their eggs into the water column (Uye, 1994). A similar decline in the broadcast egg spawner, *Acartia tonsa* has been associated with the increase in bottom water hypoxia in Chesapeake Bay (Kimmel et al., 2012). Egg-carrying copepods showed more relative abundance in water columns with hypoxic bottom waters in the Gulf of Mexico as compared to nearby normoxic water columns (Elliott et al., 2012).

Smaller copepods have a higher surface to volume ratio which would favour their oxygen uptake over larger copepods in hypoxic waters and warmer waters where oxygen solubility is lower and oxygen demand (respiration) is higher. In laboratory experiments, Stalder and Marcus (1997) showed that the smaller copepod, *Acartia tonsa*, survived low oxygen conditions better than the larger *Labidocera aestiva* and *Centropages hamatus*. In similar types of laboratory experiments, Roman et al. (1993) found that the smaller copepod *Oithona colcarva* survived low oxygen conditions better than the larger *Acartia tonsa*. The same copepod species, *Acartia tonsa*, was smaller when reared under low oxygen conditions compared to fully oxygenated waters (Richmond et al., 2006) suggesting that decreased oxygen conditions favours smaller animals.

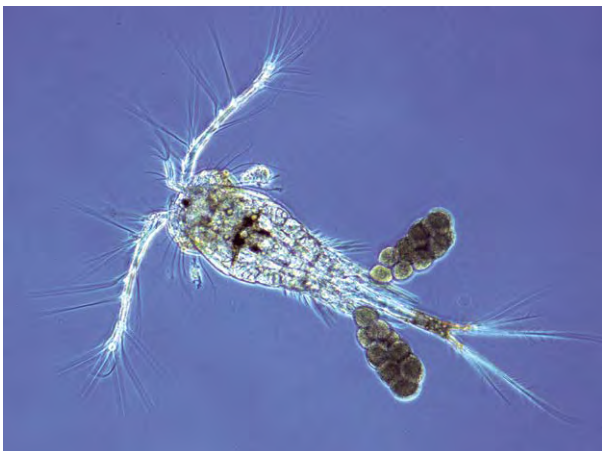


Figure 8.6.8 *Oithona davisae* © Albert Calbet.

Field observations on zooplankton species assemblages in/out of hypoxic areas have shown a variety of patterns. In both the Gulf of Mexico and Chesapeake Bay, the size distribution of zooplankton as measured with an Optical Plankton Counter (OPC) was shifted to smaller individuals in surface normoxic waters as compared to bottom hypoxic waters where there was larger zooplankton (Kimmel et al., 2009). The investigators interpreted these patterns as a consequence of larger copepods being removed from surface waters by visual predators (fish) which could not tolerate the hypoxic bottom waters. Analysis of depth-stratified zooplankton collections in the Gulf of Mexico confirmed OPC results, with larger copepod species relatively more prevalent in low oxygen bottom waters and smaller copepod species assemblages more prevalent in the oxygenated surface waters where selective predation by fish would likely reduce the abundance of larger copepod species (Elliott et al., 2012). In addition to species differences there may be sex differences in tolerance to hypoxia. Pierson et al. (2017) reported that male *Acartia tonsa* were found in lower oxygen waters than females in Chesapeake Bay. Males are smaller (Pierson et al., 2017; Figure 8.6.6), and thus have a higher surface/volume ratio than females which may also have a higher respiratory demand because of egg production (e.g. Castellani & Altunbas, 2014). Thus, in water columns with hypoxic bottom waters, female copepods may be restricted to the upper water column throughout the day and be more susceptible to predation by visual feeders. Not only are individual copepods smaller under deoxygenated conditions, but the assemblage of copepods that can exist in low oxygen conditions is smaller. This means that the overall amount of food available for predators feeding on zooplankton is reduced in hypoxic conditions, and these factors will propagate both through the food web and over time. Copepod egg production rate is partly controlled by female size, and so smaller copepods will produce fewer eggs, leading to population level effects. Also, the smaller, more deoxygenation tolerant species may or may not have the same nutritional value for predators, so the overall ecosystem trophic health and trophic dynamics can be severely altered by hypoxia.

8.6.2.5 Hypoxic impacts on planktonic food web interactions

Several lines of evidence suggest that the presence of low-oxygen bottom waters affects food-web interactions in coastal waters. Hypoxia may favour gelatinous over fish predators of copepods. For



Figure 8.6.9 Sea walnut jellyfish *Mnemiopsis leidyi* © aquapix / Shutterstock.com.

example, the ctenophore, *Mnemiopsis leidyi* (Figure 8.6.9), and scyphomedusan, *Chrysaora quinquecirrha*, have been shown to be more tolerant of low-oxygen water than fish (Breitburg et al., 1994; Purcell et al., 2001). Thus, gelatinous zooplankton are often found in greater abundance lower in the oxycline than fish larvae (Keister et al., 2000; North & Houde, 2004). Modelling research has demonstrated how complex interactions between bay anchovy and zooplankton prey, controlled by DO levels, may affect consumption and production of bay anchovy in Chesapeake Bay (Adamack, 2007; Kolesar, 2006) and potentially control consumption by predators on bay anchovy (Costantini et al., 2008). Peak concentrations of jellyfish in the main stem of Chesapeake Bay occur during summer, the peak period for bottom-water hypoxia. Decker et al. (2004) found that the copepod, *Acartia tonsa*, escape response was significantly reduced in hypoxic waters, and clearance of zooplankton by the ctenophore, *Mnemiopsis leidyi* was elevated at low-oxygen levels. Increases in the abundance of gelatinous zooplankton has occurred in the Gulf of Mexico along with the expansion of bottom water hypoxia (Graham, 2001) where seasonal low oxygen bottom waters can enhance the survival of jellyfish polyps (Miller & Graham, 2012). Grove and Breitburg (2005) suggest that jellyfish are favoured to assume a dominant trophic role in coastal waters experiencing deoxygenation.

Analysis of long-term records of copepods in Chesapeake Bay going back to the 1950s suggests a decline in the summer abundance of the dominant copepod, *Acartia tonsa*, is associated with the increase in bottom water hypoxia (Kimmel et al., 2012). Similarly, the abundance of the mysid, *Mysis mixta* has decreased by up to 50% with increasing hypoxia in the Baltic Sea off Sweden (Ogonowski et al., 2013). Increased eutrophication and low oxygen bottom waters have resulted in an increase in the abundance of the small egg-carrying copepod *Oithona davisae* in Tokyo Bay and decline in the occurrence of *Acartia omorii* and *Paracalanus* spp. both copepods which release their eggs into the water column (Uye, 1994). As more long-term time series are reported for coastal waters experiencing bottom water hypoxia, we will likely learn of more examples of changing coastal food webs experiencing deoxygenation.

8.6.2.6 Physiological and genetic adaptations

While a variety of physiological adaptations to low oxygen conditions have been described for open ocean zooplankton with permanent low oxygen zones, coastal zooplankton experience hypoxia which varies on daily to seasonal time scales. Without gills or haemoglobin, coastal zooplankton have limited options for adapting to low oxygen conditions. Oxygen binding proteins that

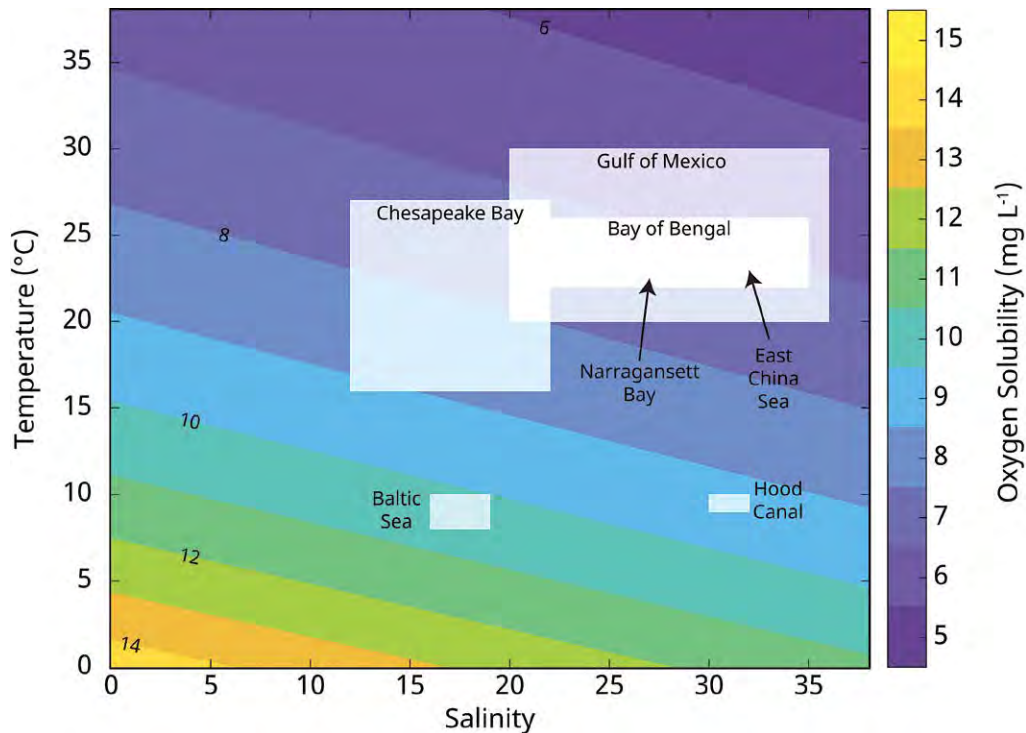


Figure 8.6.10 Oxygen solubility (mg L^{-1}) is shown by the colour scale at different salinity and temperature ($^{\circ}\text{C}$) conditions, with boxes indicating the range of salinity and temperature during periods of seasonal deoxygenation for different coastal and estuarine bodies of water around the world. Oxygen solubility calculated using the equations of Benson and Krause (1980, 1984), assuming surface water pressure.

have the potential to enhance survival at low oxygen conditions have not been identified in copepods (Thuesen et al., 1998). However, some biochemical adaptations to low oxygen may help zooplankton adapt to periods of hypoxia. Invertebrates that experience conditions of hypoxia with diel migrations to low oxygen bottom waters may enhance their antioxidant potential to deal with a physiological stress during the transition from hypoxic to normoxic conditions (Hermes-Lima & Zenteno-Savin, 2002). Mysids in the Gulf of Finland which migrated in/out of bottom hypoxic waters had higher antioxidant than conspecifics that remained in normoxic waters throughout the day, with no sign of oxidative damage (Webster et al., 2015).

8.6.2.7 Regional comparisons of hypoxia impacts on coastal zooplankton

Global comparisons of how bottom water hypoxia affects the habitat space of estuarine and coastal zooplankton reveal a variety of spatial and temporal patterns. While taxa-specific differences in hypoxia tolerance likely exist, the primary reason investigators have not found clear geographic and seasonal differences in the spatial distributions and physiological responses to low DO by zooplankton is the failure to consider and evaluate the role of temperature in

controlling oxygen availability, metabolic demand, and organism behaviour. For example, temperatures of hypoxic ($< 2 \text{ mg O}_2 \text{ L}^{-1}$) bottom water in the Gulf of Mexico can exceed 28°C in contrast to the Baltic where hypoxic water temperatures are $8\text{--}10^{\circ}\text{C}$ (Figure 8.6.10). Such differences in bottom temperatures not only affect oxygen availability (partial pressure and solubility) for organisms, but also drive differences in respiratory demands of zooplankton which increase exponentially with temperature. This is illustrated by the Q_{10} value for respiration, which for most zooplankton and is around 2. This means that for every 10°C temperature increase, the respiration rate is doubled and so zooplankton require twice as much oxygen for every 10°C increase in temperature. Thus, all “hypoxic” bottom waters, do not pose the same stress on zooplankton and their fish predators, and deoxygenation can generate different responses in spatial ecology and predator-prey interactions depending on other factors, especially temperature. For example, using the predictive response to decreasing oxygen (P_{crit}) developed for the copepod *Acartia tonsa* by Elliott et al. (2013), $2 \text{ mg O}_2 \text{ L}^{-1}$ bottom water in the Baltic (9°C) would have an oxygen partial pressure of 4.24 kPa, which is slightly below the limiting P_{crit} of *A. tonsa* predicted for this temperature (5.07 kPa). In contrast, $2 \text{ mg O}_2 \text{ L}^{-1}$ bottom water in the Gulf of Mexico (30°C)

would have an oxygen partial pressure of 6.37 kPa, which is significantly below the limiting P_{crit} of *A. tonsa* predicted for this temperature (18.31 kPa) and approximately the same as the predicted lethal oxygen concentration ($P_{leth} = 6.77$ kPa). These predicted differences in oxygen availability and demand are a useful way to assess how low oxygen waters determine habitat availability for estuarine and coastal zooplankton. Thus, field surveys have shown that zooplankton generally avoid the warmer low oxygen waters of the Gulf of Mexico (e.g. Qureshi & Rabalais, 2001; Roman et al., 2012) but reside in the colder low oxygen waters of the Baltic for significant portions of the day, affording the zooplankton a potential refuge from predation (e.g. Appeltans et al., 2003; Webster et al., 2015). Because of the higher oxygen demand by estuarine and coastal zooplankton in warmer waters of the tropics and subtropics, the loss of habitat space by low oxygen bottom waters would be expected to be more severe in these regions because the zooplankton are already living near their upper limit of thermal tolerance.

8.6.3 Ecosystem consequences

The presence of low oxygen bottom waters can have ecosystem consequences in estuarine and coastal waters by altering spatial and temporal predator-prey relationships, changing the size structure and species composition of zooplankton communities which will affect foraging, consumption and growth of fish species. Living under sub-optimum oxygen conditions can reduce temperature-dependent metabolic efficiencies, prey capture efficiency, growth and reproductive potential, and thus impact individual zooplankton fitness and population production. Hypoxic bottom water can reduce or eliminate low-temperature thermal refuges for organisms, increasing energy demands and respiration rates, and potentially reduce overall fitness. Thus, an important issue related to bottom water hypoxia in estuarine and coastal waters is whether zooplankton use the lower oxygen area as a critical habitat to avoid predation or must avoid it and remain in the upper water column where they are subject to greater predation (Figure 8.6.11). In theory, zooplankton could reside in hypoxic bottom waters if the oxygen supply is greater than its critical oxygen demand (P_{crit}) but not if the oxygen availability is well below P_{crit} or the lethal oxygen partial pressure (P_{leth}). Avoidance of low DO bottom waters can influence spatial dynamics of zooplankton and fish populations. For example, more hypoxia-tolerant zooplankton may use hypoxic

waters as a refuge from fish predation. Conversely, zooplankton avoidance of hypoxic bottom waters can result in prey aggregations at oxyclines which are used by fish predators. In coastal ecosystems with shears and differential flow between surface and deep layers, avoidance of low oxygen bottom waters can influence spatial dynamics of zooplankton populations by altering emigration and immigration patterns, and residence times. As more information becomes available on the oxygen demand of dominant estuarine and coastal zooplankton at different temperatures, we will be able to better assess if low oxygen bottom waters result in a loss of critical habitat.

Hypoxic conditions that affect spatial ecology and population dynamics can drive taxonomic and size shifts in the zooplankton community which will affect foraging, consumption and growth of fish species. Smaller zooplankton may be favoured in low oxygen conditions because their higher surface/volume ratio would be advantageous to oxygen uptake under hypoxic conditions. If hypoxic conditions resulted in a community shift to smaller zooplankton, there may be negative consequences for larval fish species feeding on smaller prey items. Similar food web consequences from changing of zooplankton species could occur if there was a succession to copepods that carry their eggs in water columns with hypoxic bottom waters (Uye, 1994). As mentioned previously, low oxygen waters may favour jellyfish over planktivorous fish because of the higher oxygen requirements of fish. Thus, shifts in the zooplankton food available to fish and greater competition by jellyfish can work together to alter pelagic food webs in estuarine and coastal waters experiencing seasonal bottom water hypoxia.

8.6.4 Societal consequences

The root cause of seasonal deoxygenation in estuarine systems is excess organic production that is decomposed in the bottom water, removing oxygen faster than it is replaced. That excess productivity is a result of cultural eutrophication, which can have its own societal consequences, ranging from harmful and nuisance algal blooms, poor water quality that limits use of water ways, and even the presence of human pathogens borne from run-off. Additionally, increasing water temperatures as a result of anthropogenic climate change can exacerbate the effects of deoxygenation by increasing the metabolic demand of organisms,

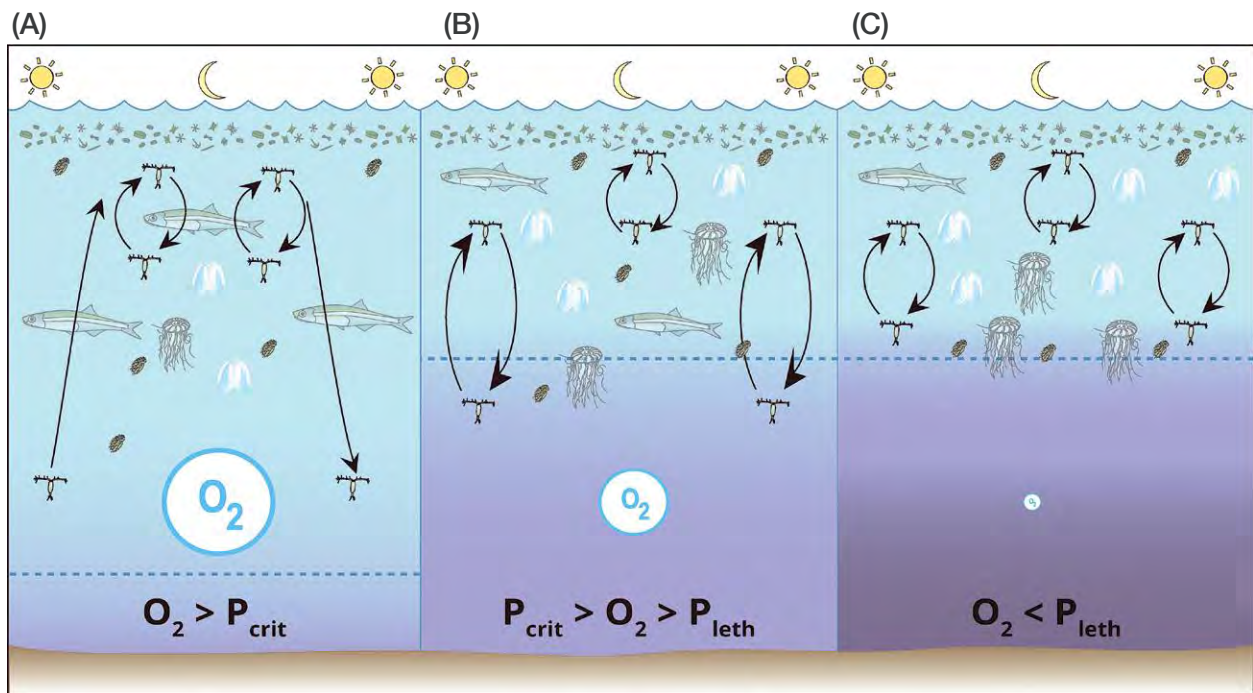


Figure 8.6.11 Conceptual diagram of food web changes that occur over diel cycles between (A) normoxic conditions, (B) sub-lethal deoxygenation conditions, and (C) lethal conditions. The size of the symbol for O_2 and the colour indicates the relative amount of dissolved oxygen under each condition (with light blue indicating high oxygen concentration and purple indicating lower oxygen concentration). With decreasing oxygen concentration comes reduced habitat, truncated magnitude of copepod vertical migration (shown by length of arrows), increased gelatinous zooplankton abundance, and decreased forage fish abundance. Symbols Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

making the severity of the impacts greater than they would be at lower temperatures.

Plankton are able to change their vertical position in the water column and thus would not face imminent mortality under hypoxic conditions, unlike sessile benthic organisms such as oysters, worms and crabs which are unable to move or are severely limited in their mobility when faced with deoxygenated bottom water. However, negative consequences for plankton biodiversity, productivity, and sub-lethal biological effects are projected to result from expanding hypoxic bottom waters. Additionally, individuals growing in oxygen deficient waters would have reduced respiration rates, slower growth rates, and diminished escape responses, amongst other non-lethal effects. These effects are likely to cascade through the food web, ultimately impacting higher trophic levels including economically important fish species that rely on plankton as prey. The changing zooplankton species composition and the use of hypoxic bottom waters as a refuge from predation could directly impact the larval forms of commercially important fish species, as well as small pelagic fish that are a critical food resource for piscivorous fish. Indirect effects from the diminished escape responses could mean that predation mortality of plankton is increased

in the presence of predators that are tolerant of hypoxia. But in the case of hypoxia, there are likely to be some winners and some losers. Planktivorous fish are likely to be replaced with more hypoxic-tolerant gelatinous zooplankton, which can in turn increase their own predation on the plankton that are impacted by the low oxygen. This could result in more shortened, “dead-end” food chains, where the highest trophic levels are the gelatinous zooplankton and not the higher trophic levels that include commercially important fish species that rely on the replaced planktivorous fish as prey. Additionally, expanding hypoxic regions can alter the location of viable fishing grounds, and the added costs of longer transit times from dock to fishing areas can be a major impact on the fishing community.

8.6.5 Implications of continuing ocean deoxygenation

Warming estuarine and coastal waters will exacerbate the deleterious effects of low oxygen zones by increasing the respiration and oxygen demand of zooplankton, while decreasing the solubility of oxygen at the same time. Climate warming has the potential to increase the seasonal period and spatial extent of bottom-water hypoxia thus having longer term impacts on pelagic food

webs. While zooplankton may tolerate periods in low oxygen waters that limit their metabolic functions ($DO < P_{crit}$ but $> P_{leth}$), greater eutrophication and warming seas may increase the severity of low oxygen waters to lethal levels ($DO < P_{leth}$) for estuarine and coastal zooplankton. Zooplankton would lose habitat, distributions would be concentrated in more oxygenated surface waters and with greater predation mortality and zooplankton populations would decrease. Deoxygenation in coastal waters may be more severe in lower latitudes where higher temperatures and respiration already create oxygen limiting conditions for zooplankton.

8.6.6 Conclusions / Recommendations

- Seasonal deoxygenation of estuarine and coastal ecosystems leads to a variety of impacts on zooplankton including: Lower overall abundance; altered community structure with smaller, egg carrying taxa and gelatinous zooplankton increasing with decreasing dissolved oxygen; shallower vertical distribution and reduced vertical migration extent; sub-lethal impacts including reduced size at adulthood and reduced growth rate.
- Continuing ocean deoxygenation will be accompanied by warmer temperatures and decreasing pH, thus estuarine and coastal zooplankton will experience multi-stressors that will impact their fitness, life histories and population dynamics.
- Management efforts to reduce eutrophication in estuaries and coastal seas should be increased to reduce organic loads which cause oxygen depletion in bottom waters.
- Global plans to reduce greenhouse gas emissions which are causing global warming and increased deoxygenation should be increased and implemented.
- Ecosystem Based Management (EBM) of estuarine and coastal seas should incorporate the seasonal hypoxic bottom waters to better understand the impacts of current and future deoxygenation on pelagic food webs and fisheries.
- To assess effects of the globally expanding coastal low oxygen zones, we need to determine if generic models can be developed to evaluate and

predict how low DO imposes temporal and spatial limitations on metabolic functioning of zooplankton. Because oxygen availability to these organisms is a function of the rate of diffusion across their integument, allometric relationships such as surface/volume, body mass, etc., can be developed for similar groups of zooplankton to predict oxygen limitation and its consequences, e.g. reduced growth or alteration of vertical distribution in hypoxic coastal waters. Allometric models for predicting temperature-dependent oxygen supply and demand in zooplankton and planktivorous fish will lead to improved size-structured models that serve to predict impacts of increasing coastal hypoxia on pelagic food webs and allow common, quantitative comparisons across coastal ecosystems.

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8.7 The significance of ocean deoxygenation for estuarine and coastal benthos

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Summary

- Mobile benthic invertebrates migrate away from water masses with less than 2 mg L⁻¹ dissolved oxygen.
- Diversity in benthic assemblages decreased 13-fold; abundance of benthic infauna, 25-fold; and biomass, 10-fold as dissolved oxygen approached levels of 0.05 mg L⁻¹ in a seasonally severe coastal low oxygen zone.
- As much as 343,000 to 734,000 MT carbon in the form of secondary production is lost from ecosystems annually over 245,000 km² when bottom waters are severely deoxygenated.
- Recovery of benthic communities under improved oxygen conditions may take years to decades and may not approach pre-impact conditions.

Estuaries and coastal hypoxia effects	Potential consequences
Severe deoxygenation on a seasonal basis in coastal waters alters benthic community composition.	<ul style="list-style-type: none"> • Deeper-burrowing infauna are replaced by mostly small, opportunist, surface deposit feeders that live in the upper 2 cm of the sediment. • Diversity, number of taxonomic groups, abundance, and biomass decrease as the dissolved oxygen concentration decreases. • Sediments do not become azoic (multi-cellular organisms are mostly depleted except a few acclimated to severe hypoxia or anoxia). • Microbial communities thrive.
Levels of severity of deoxygenation affect benthos differently.	<ul style="list-style-type: none"> • Developmental life stages are more sensitive to deoxygenation than adults are. • Pericaridean crustaceans will be exterminated before many polychaete worms and sipunculans. • Of the meiofauna, harpacticoid copepods are more sensitive than nematodes.
Loss of infauna from deoxygenation affects ecosystem functioning.	<ul style="list-style-type: none"> • Loss of benthos that are bioturbators allows the redox potential discontinuity to move closer to the sediment-water interface. • Loss of benthic organisms and secondary production decreases food availability to higher consumers. • At severely low oxygen levels, there are effluxes of ammonium and ortho-phosphates from the sediments that generate a negative feedback to further deoxygenation.
Areas of deoxygenation reduce suitable habitat for commercially important species.	<ul style="list-style-type: none"> • Migration of organisms to suitable habitats is prevented and results in reduced growth. • Market prices are affected.

8.7.1 Introduction

There is little doubt that the number of human-caused coastal ocean areas of deoxygenation has increased since the 1960s (Diaz & Rosenberg, 2008) with an approximate doubling of the number of areas every decade since the 1960s through 2007 (see Section 3.2). In the case of many estuaries and coasts, the development of deoxygenation paralleled the increase in nutrient loads (nitrogen and phosphorus) and other pollutants, an increase in human population, overfishing, and dramatic habitat restructuring among others (Breitburg, 2002). Many of the watersheds and airsheds contribute two to three times more nitrogen and phosphorus to receiving water bodies since the 1950s, when landscape alterations expanded, especially for agriculture, high use of artificial fertilizers prevailed, and consumption of fossil fuels increased.

Estuarine waters from the head of tide continuing to the coastal waters of the inner and mid continental

shelf are especially affected by multiple stressors including deoxygenation. These waters are the focus of this section. Compilation of their occurrence through literature citations (Diaz & Rosenberg, 2008) and recent compilations of academic and government data in coastal areas of the Baltic Sea (Conley et al., 2011) brings the global total of estuarine and coastal areas of low oxygen to about 500. The formation of human-caused deoxygenation has occurred in the last seven decades (see Section 3.2) while oxygen minimum zones that impinge on continental margins have existed for millennia (see Section 8.6). Benthos, organisms associated with the sea bed, in the former situation have been exposed to a dramatic change in environmental conditions over the last 50 to 100 years and the consequences have been mostly death and replacement by opportunistic species, rather than evolutionary adaptation in the latter situation. Estuarine and coastal benthos are adapted to changes in salinity and temperature, but the increase in conditions of low oxygen is mostly a recent phenomenon.

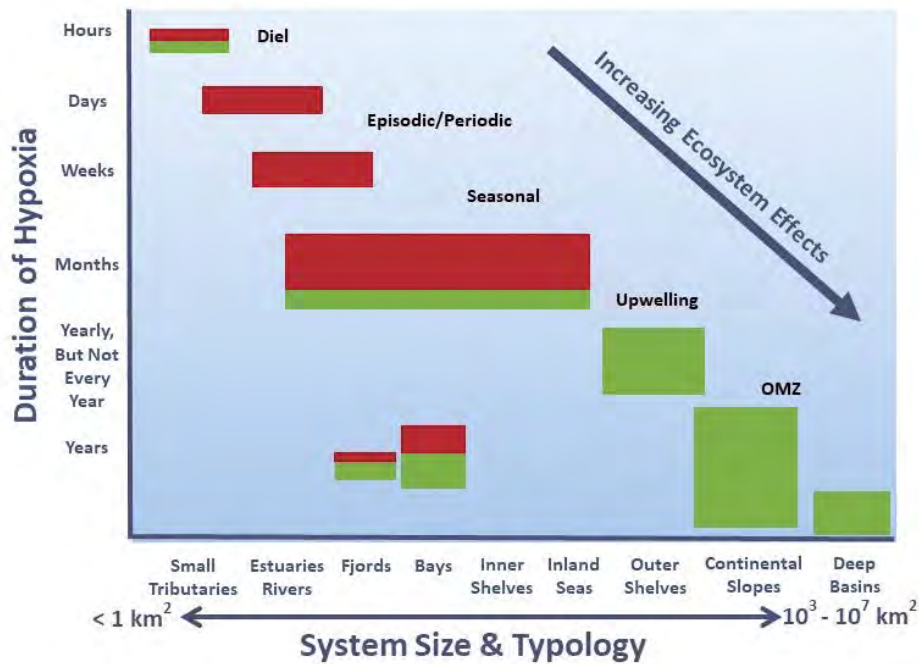


Figure 8.7.1 A synthesis of the variability of temporal, spatial, and typological categories for environments with deoxygenation (modified from Rabalais et al., 2010). The scales are without units but go from lower to higher. The red and green colours represent the relative ratio of human versus natural influences, respectively.

The additional nutrient loads stimulate primary production, the excess carbon from which falls to the lower water column and sea bed and is decomposed by aerobic bacteria that utilize oxygen in the process. The resupply of oxygen is prevented most often because of a temperature- or salinity- (or both) driven density difference (pycnocline). In some instances, a bathymetric shallow feature or sill prevents horizontal renewal of oxygenated waters into those basins that are depleted of oxygen. Estuaries may be microtidal or macrotidal, with the former more likely to have longer water residence times than the latter (Warwick et al., 2018). Coastal waters with a long residence time support the development of stratification, high primary production, and flux of carbon. Circulation or tidal cycles may push the low dissolved oxygen water mass laterally or onshore and offshore, periodically worsening low oxygen conditions or encroaching into better-oxygenated waters. Many shallow estuarine waters host stands of rooted seagrasses or attached macroalgae. The diel cycle in these systems involves high photosynthetic activity and generation of dissolved oxygen during daylight hours, then a period of respiration in the dark results in an oxygen-deficiency occurring late in the night or early morning (Tyler et al., 2009).

Amidst the milieu of physical, chemical and biological processes that generate deoxygenation in estuarine and coastal waters are living biota. The increasingly higher

loads of nutrients and development of deoxygenation, however, have put living resources at risk, including commercially important ones, such as penaeid shrimp, cod, and striped bass. The worsening of eutrophication and hypoxia have been blamed for shifts in community structure and/or declines in abundance of phytoplankton, benthos and fishes (Caddy, 1993; Hagerman et al., 1996; Turner et al., 1998). Benthic organisms reflect the environmental parameters to which they are exposed because of their relative inability to move great distances (e.g. polychaetes, molluscs, and echinoderms) or not at all (e.g. sponges, corals, burrowing crabs, and shrimp). Infauna, living in the sediments, are useful in studies of polluted waterways (Tweedley et al., 2015), and as indicators of ambient dissolved oxygen concentrations. Indicators of stress include community composition changes, food web alterations, loss of biodiversity, and shifts in functional groups.

8.7.2 Definitions and scope

This section addresses the benthos, those organisms living in, on, or associated with the sea bed, and covers primarily multicellular invertebrates, although some information on demersal fishes is appropriate for inclusion. Benthic foraminiferans are amoeboid protists with mineral or calcium carbonate tests that allow for consistent taxonomic identification. Several species maintain unicellular algal endosymbionts or chloroplasts

from ingested algae to conduct photosynthesis, i.e. generation of oxygen, but others succumb to severely low oxygen concentrations ($\sim 0.05 \text{ mg O}_2 \text{ L}^{-1}$) (Gooday et al., 2009). Because of their complex metabolic processes (LeKieffre et al., 2017), they will not be considered here but are good indicators of dissolved oxygen concentrations over millennial time scales or more recent decades or centuries (see Chapter 5). Demersal fishes are mostly excluded from this section because of their ability to escape, but they face other sublethal effects (see Section 8.5). Benthos may be exposed permanently or over extended periods to extremely low oxygen conditions in anoxic ocean basins or semi-enclosed seas, e.g. Black Sea or Cariaco Basin, Baltic Sea proper, deep fjords, and upwelled oxygen minimum zones (OMZs) (Section 8.4; Levin et al., 2009).

The benthos in estuaries and coastal waters are exposed to deoxygenated waters on either (1) a short time period, e.g. days to weeks, (2) a seasonal basis where there are strong pycnocline(s) that prevent reoxygenation; these may be perennial or seasonal, (3) seasonally intermittent deoxygenation where physical forces disrupt longer periods of seasonal deoxygenation, or (4) a diel cycle in areas with subaquatic vegetation. Many of the deoxygenation trends in estuaries and coastal waters are expressed following eutrophication (the increase in the production and accumulation of carbon in an aquatic ecosystem). The responses to either may be similar but can be identified, especially in studies of Foraminifera in accumulated sediments where multiple productivity and deoxygenation indicators can each be identified along with biogeochemical indicators (Chapter 5; Gooday et al., 2009). As human influences increase in shallower waters of the coastal ocean, there are more ecosystem effects (Figure 8.7.1). Upwelling areas and OMZs are primarily natural, but human activities that indirectly affect global climate change are also affecting these areas. OMZs are the largest, most persistent and natural oxygen-depleted areas in the world's ocean and have the greatest ecosystem changes relative to oxygen conditions, but these are the result of adaptation over geological time.

Studies of benthos exposed to lower dissolved oxygen conditions than what is sustainable for life processes take many approaches: use specific groupings by body size (e.g. meiofauna versus macrofauna, dependent on sediment sieve size for collection), employ different collection techniques (e.g. sediment corers, trawls, dredges, video or photographic transects, and digital

imagery), assign isotopic signatures to infer food web changes, apply categories of functional groups or the ratio of one functional group to another, and many others. Measurements of stress may be determined from taxonomic composition changes over time, metabolic stress under hypoxic conditions, behavioural changes, and reproductive physiology. Necessary data to complement studies of benthos responses to lower oxygen levels are the actual dissolved oxygen concentrations. Depending on logistics and resources, records may be for the duration of the experiment, minimal oxygen measurements at the time of study, inferred levels from other studies, or quality-controlled, long-term *in situ* deployed instrumentation. The more ancillary data that are available, the better is the understanding of the results and their implications.

Most multicellular aquatic organisms require dissolved oxygen to live. Physiologists often measure the partial pressure of oxygen available for transfer to tissues (measured in milli-atmospheres, matm , or kPa) to determine the effects of lower than optimal oxygen conditions (Hoffman et al., 2011; Seibel, 2011). Environmental data for aquatic systems, however, measured in units of $\text{ml O}_2 \text{ L}^{-1}$ or $\text{mg O}_2 \text{ L}^{-1}$ are often converted to percentage oxygen saturation to compensate for temperature and salinity (Rabalais et al., 2010). The most commonly used and agreed-to value of dissolved oxygen for estuarine and coastal waters that affects the benthos is 2 mg L^{-1} (equivalents are 1.4 ml L^{-1} , $63 \mu\text{M}$, or 30% saturation).

8.7.3 Range of responses

While the typical value for responses of benthic organisms to oxygen deficiency is 2 mg L^{-1} , there is a continuum of decreasing dissolved oxygen concentrations starting at about 5 mg L^{-1} down to 0 mg L^{-1} where organisms succumb to insufficient oxygen or are affected physiologically or behaviourally (Gray et al., 2002; Vaquer-Sunyer & Duarte, 2008). There is variability in these responses according to the severity, the duration of the exposure, the presence of toxic hydrogen sulphide, the taxon or taxonomic group, the life history stage, and the organism's physiological capacity. Effects on a species are not all the same, but on average result in population effects, and eventually community effects. These responses are mostly determined by the duration and severity of the decrease in oxygen concentration.

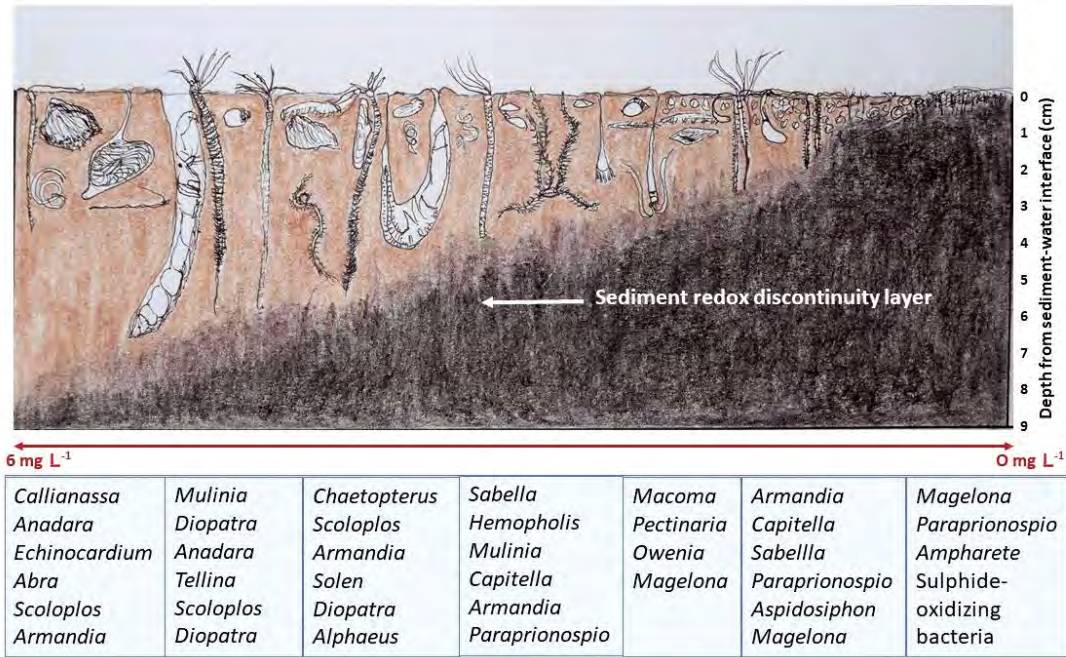


Figure 8.7.2 Diagram of changes in fauna and sediment structure including redox discontinuity layer from no oxygen on the right to well-oxygenated waters on the left. Source: N.N. Rabalais, based on benthic fauna in Rabalais et al. (2001b) and Baustian and Rabalais (2009) in a decline of dissolved oxygen similar to the organic pollution gradient originally in Pearson and Rosenberg (1976).

Benthic assemblages exposed to seasonally low dissolved oxygen over extended periods, i.e. weeks to months (Figure 8.7.1) become a less diverse species mixture, often shift species composition, experience decreased abundance of most organisms and, therefore, decreased biomass and secondary production, and shift from more mature, deeper burrowing groups of organisms to smaller forms associated with the upper few centimetres of the sediment.

This progression of benthic community responses along a gradient of decreasing oxygen concentration follows the classic model described by Pearson and Rosenberg (1978) resulting from organic loading of paper mill effluents (Figure 8.7.2). Advanced stage benthic communities with deep burrowing infauna and high diversity were replaced by less diverse communities of low oxygen-tolerant infauna or early successional communities of small-sized individuals. Following prolonged hypoxia over an area of several thousands of km², benthic communities in a Danish estuary transitioned from slower growing, burrowing species to fast-growing, surface-dwelling species (Conley et al., 2007). The gradient in the Pearson and Rosenberg (1978) model is distance from a polluting effluent; in the case of benthos affected by deoxygenation, the model follows a decline in oxygen levels. Recovery usually follows the opposite trend, but the recovered community is not necessarily the same as

the original community (Duarte et al., 2015; Rosenberg et al., 2002).

The following sections provide examples of how benthic assemblages change depending on how severe the deoxygenation becomes and for how long.

8.7.3.1 Migration from low oxygen

Benthic invertebrates, such as penaeid shrimp and nephropid lobsters, are well known for their ability to migrate away from oxygen-deficient waters, either laterally or vertically (Baden et al., 1990; Craig, 2012; Craig & Crowder, 2005; Rabalais et al., 2001a). Hypoxic conditions, occasionally observed in the Kattegat and the Adriatic can cause severe disruption of the natural emergence patterns and even mass mortality in Norwegian lobsters *Nephrops* populations (Hallbäck & Ulmestrand, 1990). At oxygen saturation levels <50% *Nephrops* are forced from their burrows, and at <25% oxygen saturation are dead within 24 h, particularly the juveniles that are more sensitive to low oxygen compared to adults. Emergence of *Nephrops* under low oxygen conditions may result in higher catches in bottom-dragging trawls and give a mistaken impression that stock density is increasing or sustainable (Hallbäck & Ulmestrand, 1990).

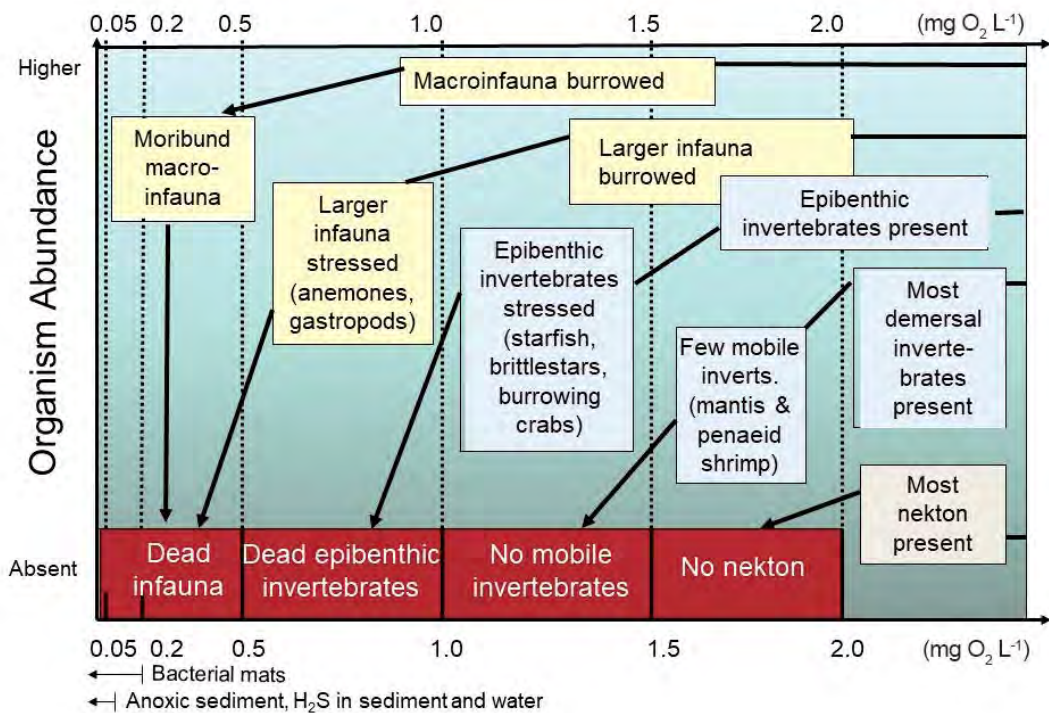


Figure 8.7.3 Progressive changes in fish and invertebrate fauna as oxygen concentration decreases from near 2 mg L⁻¹ to anoxia (0 mg L⁻¹). Source: generated from data and illustrations in Rabalais et al. (2001a).

Brown shrimp *Farfantepenaeus aztecus* catch per unit effort in trawls on the Louisiana continental shelf west of the Mississippi declined dramatically at a threshold of 1.3 ± 0.10 mg O₂ L⁻¹ (Craig, 2012), but Rabalais et al. (2001a) documented no brown shrimp in night-time remotely operated vehicle (ROV) videotapes at oxygen concentrations less than 2 mg O₂ L⁻¹ in the same area. The latter value is representative of the concentration of dissolved oxygen below which mobile fauna will move away from the area (Rabalais et al., 2001a; Renaud, 1986) (Figure 8.7.3).

The diagram begins just above 2 mg L⁻¹ dissolved oxygen on the right, because most demersal fish move out of the area before the oxygen becomes that low. Dead fish were not observed on the sediment surface and were not seen swimming in and out of the bottom area. Some penaeid shrimp and stomatopods (mantis shrimp) were observed at oxygen levels as low as 1.7 to 1.8 mg L⁻¹, but never below 1.5 mg L⁻¹. Stomatopods remaining in hypoxic waters down to 1.5 mg L⁻¹ is consistent with the results of Pihl et al. (1991) who indicated that the mantis shrimp *Squilla empusa* first adapted physiologically to hypoxia and then migrated as hypoxia became more severe, which is consistent with its more stationary and territorial behaviour. The blue crab *Callinectes sapidus* (Figure 8.7.4), however, in the York River (Pihl et al., 1991), migrated from hypoxic waters as soon as

the oxygen concentration fell below 2 mg L⁻¹ and then returned when conditions improved. Large aggregations of rock shrimp (*Sicyonia dorsalis* and *S. brevirostris*) and portunid crabs (*Portunus gibbesii*, *Callinectes sapidus*, and *C. similis*) were observed swimming at the surface above bottom waters on the Louisiana shelf that were severely oxygen depleted (0.1 to 0.2 mg L⁻¹) (N.N. Rabalais, personal observation).

8.7.3.2 Death of attached epibenthos

The northern Adriatic Sea is a shallow, semi-enclosed sea with a history of seasonal hypoxia and anoxia due to long-term eutrophication and increasing frequency, duration and severity of oxygen depletion since the mid-20th Century (Barmawidjaja et al., 1995; Danovaro, 2003; Justić, 1987). The epibenthic community there, specifically those organisms living attached to the sea bed usually on shells or shell hash amidst a fine-grained sediment surface, are subject to varying levels of low dissolved oxygen over extended time (Riedel et al., 2008; Stachowitsch et al., 2007). The foundations for these bioherms are typically sponges and ascidians (tunicates). Multiple brittlestars, anemones, living gastropods, hermit crabs in gastropod shells, amphipods, and crustaceans add levels of complexity. The eutrophication process of high carbon production in the form of phytoplankton begins the process of epibenthic habitat destruction and



Figure 8.7.4 Blue crab (*Callinectes sapidus*) © Mark Conlin / Alamy stock photo.

deoxygenation. The sinking senescent phytoplankton form a mucous-like detritus, called mucilage, that falls and settles on the sea bed and covers the bioherms (Figure 8.7.5). The subsequent decomposition of the mucilage results in oxygen depletion that causes further mortality in the sediment fauna that in turn decomposes reducing oxygen concentrations further.

Similar to bioherms, coral reefs can be exposed to low oxygen events. A massive coral mortality event caused by deoxygenation affected corals and other reef-associated organisms such as sponges (Figure 8.7.6) in Bahía Almirante in the Bocas del Toro region of Panama (Altieri et al., 2017). In a well-oxygenated area only $3 \pm 2\%$ of corals were bleached, whereas $76 \pm 11\%$ of the corals were bleached in the severely deoxygenated area. The likelihood of coral reefs being exposed to deoxygenation in the future is high given the trends in resource use by developing countries in tropical regions.



Figure 8.7.5 Mucilage on bioherms of the Northern Adriatic Sea © Open source Google, Francesca Malfatti.

8.7.3.3 Seasonally severe hypoxia

8.7.3.3.1 Northern Gulf of Mexico continental shelf west of the Mississippi River delta

Low oxygen conditions that occur over weeks to months most often are exposed to shifts in sediment-water biogeochemical processes including the release of toxic hydrogen sulphide (H_2S) from sediments (Vaquer-Sunyer & Duarte, 2010; Villnäs et al., 2012). Gulf of Mexico hypoxic waters on the continental shelf off Louisiana and eastern Texas are most prevalent from late spring through late summer. Low oxygen waters occur from shallow depths near shore (4 to 5 m) to as deep as 60 m but more typically between 5 and 30 m. When the dissolved oxygen level falls below 2 mg L^{-1} , it often reaches less than 1 mg L^{-1} or severely depleted levels of less than 0.2 mg L^{-1} for periods of two to eight weeks (Rabalais et al., 2007).

The stages of this decline were documented with ROV showing severely hypoxic bottom sediments on the inner continental shelf of the northern Gulf of Mexico west of the Mississippi River (Rabalais et al., 2001a) (Figure 8.7.3). This area is hypoxic for extended periods in mid-summer recorded at a frequency of 75 to 100% during mid-summer shelf-wide hypoxia mapping cruises (Rabalais et al., 2018) (Figure 8.7.7).

As the oxygen level decreases from 1.5 to 1 mg L^{-1} , bottom-dwelling organisms exhibited stress behaviours. Crabs (*Libinia* sp. and *Persephona* sp.) and sea stars (*Astropecten* sp.) climbed on top of 'high' spots, such as burrow excavation mounds (Figure 8.7.8). Hermit crabs clustered on top of shells lying on the bottom. Brittlestars

emerged from the sediment and used their arms to raise their disks off the substrate. Burrowing shrimp (*Alpheus* sp.) emerged from their burrows (Rabalais et al., 2001a). Gastropods (*Oliva sayana*, *Terebra* sp., *Cantharus cancellarius* and *Distorsio clathrata*) moved through the surface sediments with their siphons extended directly upward. Large burrowing anemones (*Cerianthus* sp.) became partly or completely extended from their tubes and laid on the substrate, in a flaccid and non-responsive condition. Polychaete worms emerged from the substrate and laid motionless on the surface (e.g. *Chloëia viridis* and *Lumbrineris* sp.). These behaviours were presumed to position the organisms in higher oxygen content waters, even though moving from the safety of the sediments exposed them to greater risk of predation. Jørgensen (1980) also found that many of the organisms seen lying on the bottom in hypoxic areas were moribund, not dead. The presence of large typically infaunal organisms on the sediment surface supported the idea that bottom-feeding fish were excluded from the hypoxic lower water column.

At oxygen levels of 1 to 0.5 mg L⁻¹, even the most tolerant burrowing organisms, principally polychaetes, emerged partially or completely from their burrows and lay moribund on the bottom. Below oxygen



Figure 8.7.6 Extremely low oxygen levels (<0.5 mg L⁻¹) near the bottom of a coral reef in Bahia Almirante, Panama killed the bottom half of erect sponges © Andrew Altieri / PNAS.

concentrations of 0.5 mg L⁻¹, there was a linear decline in species richness, abundance and biomass of benthic

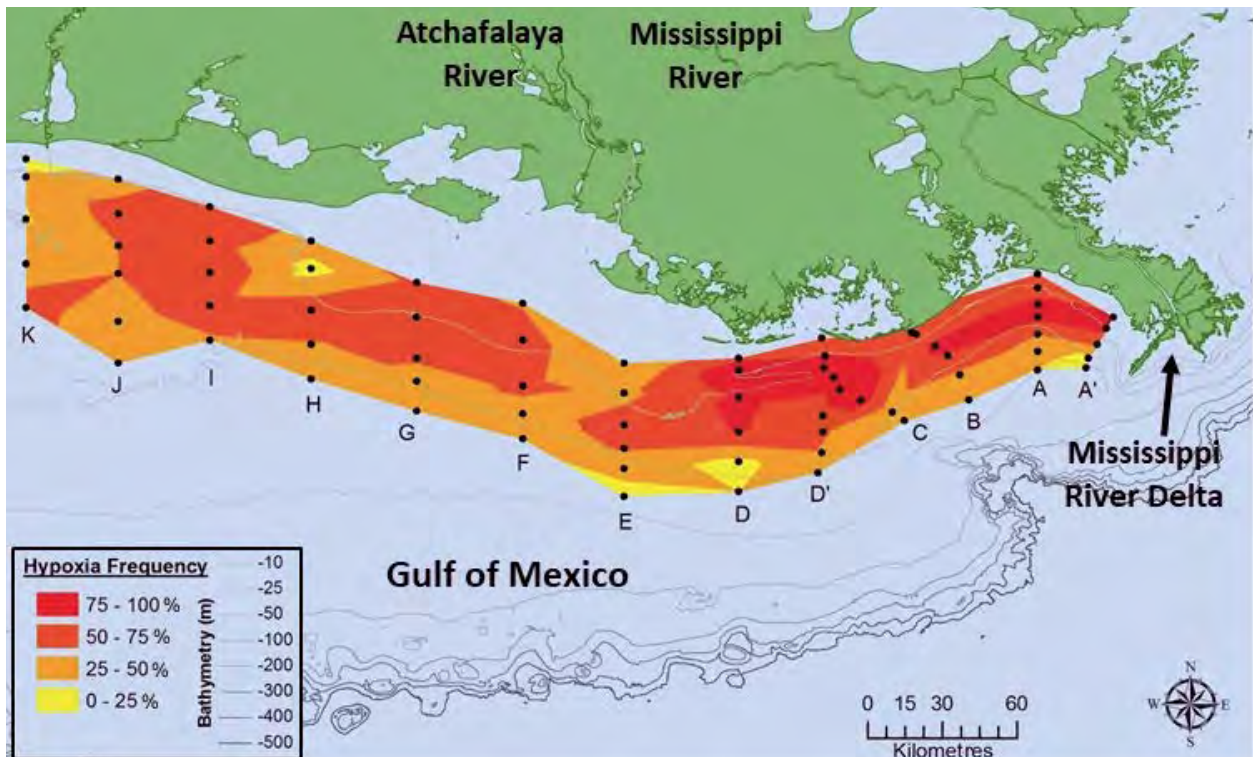


Figure 8.7.7 The frequency of bottom-water hypoxia occurrence from shelf wide hypoxia mapping from 1985 through 2014 (Rabalais et al., 2018) is shown in shades of yellow to red; frequency is determined from stations for which there are data for at least half of all cruises. Hypoxia frequency: Dark red >75%; Dark orange 50 – 75%; Orange 25 – 50%; Yellow <25%. Source: N.N. Rabalais.

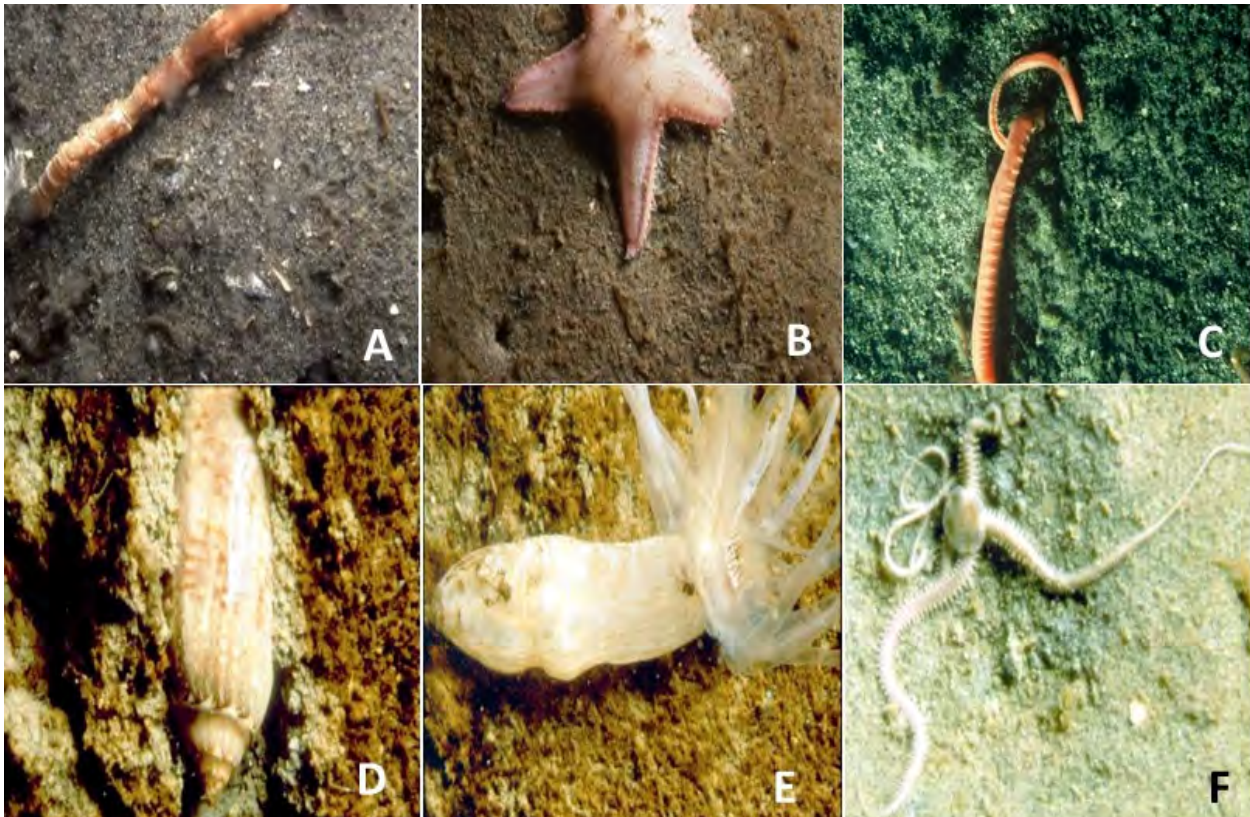


Figure 8.7.8 Living but stressed benthic infauna at the surface of the sediments. (A) polychaete *Owenia fusiformis*; (B) *Astropecten* starfish; (C) Terebellid polychaete; (D) gastropod *Oliva sayana*; (E) Cerianthid anemone; (F) brittlestar. © F. Viola & D.E. Harper, Jr.

macroinfauna (Rabalais et al., 2001b). Dead and decaying polychaetes and crustaceans were observed on the sediment surface at oxygen concentrations of less than 0.25 mg L^{-1} (Figure 8.7.9). Despite the anoxic appearance of sediments and detection of hydrogen sulphide in overlying waters, there usually remained some surviving fauna, typically polychaetes of the genera *Magelona*, *Paraprionospio* and *Sigambra* or sipunculans (Rabalais et al., 2001b) so that the sediments were not completely azoic. At oxygen values below 0.2 mg L^{-1} but above anoxia (0 mg L^{-1}) various-sized patches of “cottony” bacterial mats, *Beggiatoa* sp. covered the sediment surface (Figure 8.7.10).

Benthic communities in seasonally severe hypoxic conditions on the Louisiana continental shelf are characterized by loss of longer-lived deeper burrowing infauna to shallow sediment dwellers, and decreases in species richness, abundance and biomass of organisms relative to similar habitats not suffering low oxygen levels (Rabalais et al., 2001b). These changes occur when the dissolved oxygen concentrations are well below 2 mg L^{-1} , close to anoxia, for an extended period of time. A spring through autumn continuous bottom-water dissolved oxygen record from a meter in

20 m depth about 100 km west of the Mississippi River delta illustrates these patterns. Water-column oxygen levels rose during mixing from cold fronts in spring and tropical storms in summer followed by respiration below the stratification that led to low bottom-water dissolved oxygen from the beginning of July through early October, when cold fronts began to occur more frequently (Figure 8.7.11). Bottom-water dissolved oxygen values of less than 2 mg L^{-1} occurred for 80% of the record and below 1 mg L^{-1} for 71% of the total record and were anoxic for more than 60% of the record (Rabalais et al., 1994).

Polychaetes comprised most of the species in the hypoxic area at 20 m depth 100 km west of the Mississippi River delta. Composition by other major taxonomic groups was high in the spring, and then reduced to four to six major taxa in July-October (Figure 8.7.12) (Table 8.7.1). The polychaetes *Ampharete* sp., *Paraprionospio pinnata* and *Mediomastus ambiseta* were common in spring and early summer of 1990, but as hypoxia worsened, the community was reduced to the small, surface feeding polychaetes *Ampharete* sp. and *Magelona* sp., and the sipunculan *Aspidosiphon* sp. Only *Magelona* sp. and *Aspidosiphon* sp. maintained any significant population levels in August 1990. There was evidence from

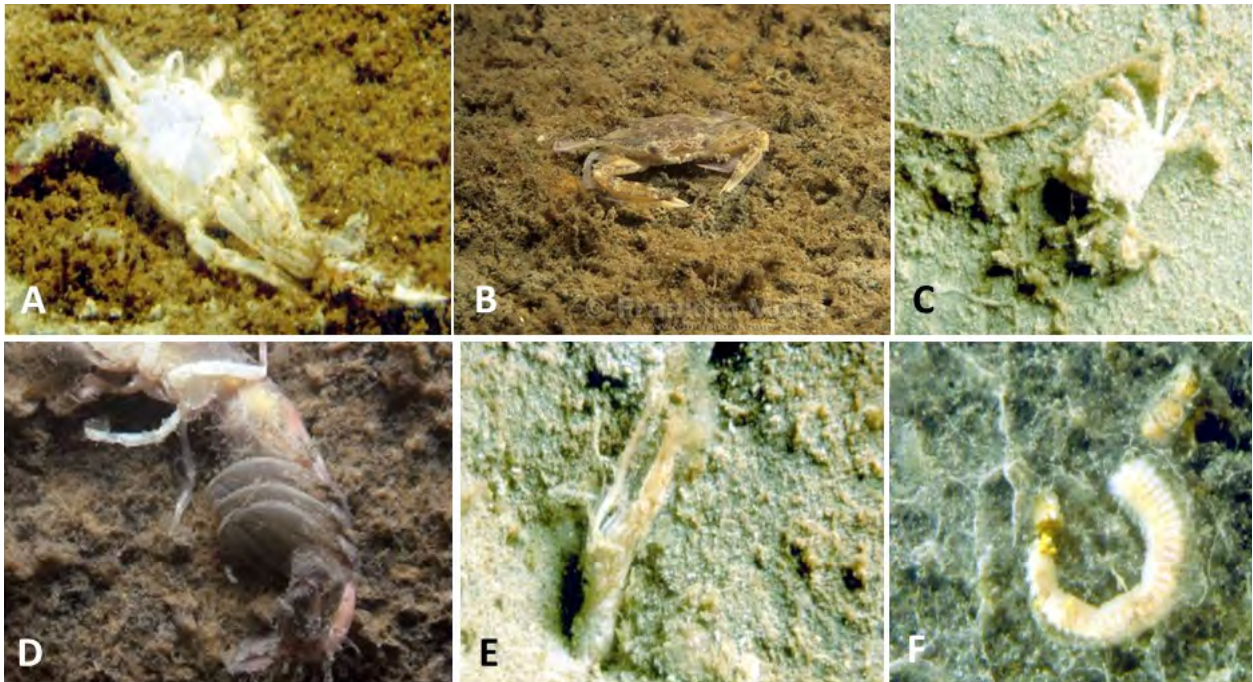


Figure 8.7.9 Dead and decomposing benthic infauna. (A) Portunid crab; (B) Portunid crab; (C) Goneplacid crab; (D) Thalassinid shrimp; (E) Alpheid shrimp; (F) Spionid polychaete. © F. Viola & D.E. Harper, Jr.

settlement traps deployed in the area of hypoxia that the polychaete *Paraprionospio pinnata* delayed settlement and remained in the water column until oxygen values returned to a level above 2.0 mg L^{-1} (Powers et al., 2001).

During September and October 1990, the overall increase in number of individuals was due primarily to the recruitment of *Paraprionospio pinnata* and *Armandia maculata* and sustained levels of *Magelona* sp. and *Aspidosiphon* sp. Species richness again increased during the spring of 1991, but polychaetes remained the dominant taxa (Figure 8.7.12). *Owenia fusiformis*, which had been a dominant member of the community in 1990,

was replaced by a population of *Sigambra tentaculata* in spring 1991.

The number of individuals and biomass of infaunal benthos decreased substantially from periods of normoxia to severely hypoxic conditions (Table 8.7.1). Abundance of individuals was high in April and June 1990 but dropped dramatically in July through September 1990. There was a slight recruitment of individuals in October 1990. Abundance increased somewhat in February–April 1991, then increased substantially in May 1991. A seasonal decrease began in June 1991 with a significant reduction in abundance in July and August. Abundance increased in September and October 1991 to about the same level

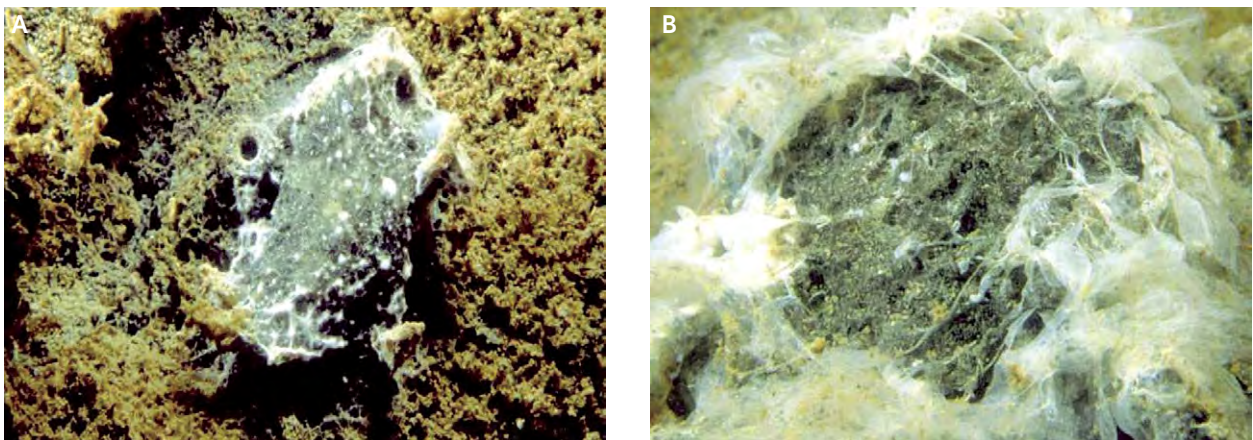


Figure 8.7.10 Sulphide oxidizing bacteria. (A) sulphide oxidizing bacteria on anoxic sediments; note tube opening is for the polychaete *Diopatra cuprea*, also the thick blanket of organic detritus on the sediment surface. (B) thicker mats of sulphide oxidizing bacteria on anoxic sediments. © F. Viola & D.E. Harper, Jr.

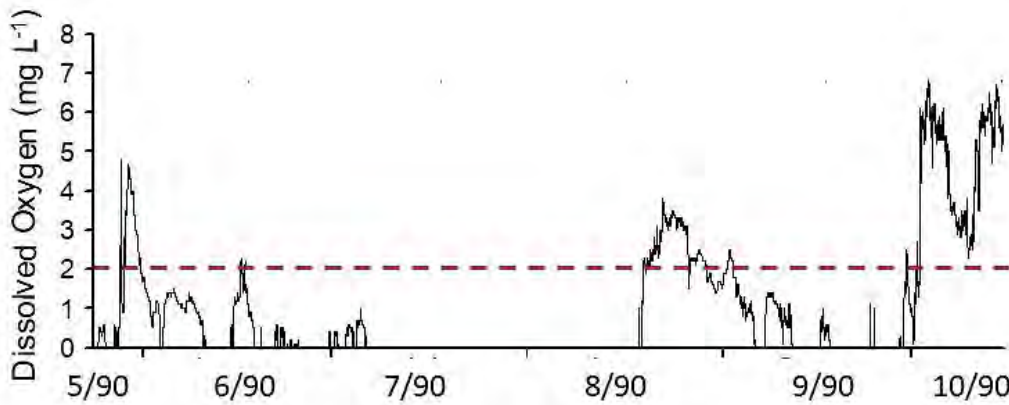


Figure 8.7.11 Time series plot of near-bottom dissolved oxygen concentration at a 20 m station 100 km west of the Mississippi River delta in 1990 (modified from Rabalais et al., 1994, 2001b). The horizontal dashed line defines hypoxia (from Rabalais et al., 2007).

as early spring 1991. Biomass generally followed the same pattern as number of individuals.

A similar cycle of more taxa and individuals in spring with a dramatic decline during deoxygenation in summer was described by Baustian and Rabalais (2009) for the same study area in May 2003 – October 2004. Similar organisms, primarily the polychaetes *Paraprionospio pinnata*, *Armandia maculata*, and *Magelona* sp., and nemertean remained as part of the benthic infaunal community during periods of low oxygen.

Murrell and Fleeger (1989) surveyed the meiofaunal assemblages at three stations (8 – 13 m) over an annual cycle of decreasing dissolved oxygen in the same area of severe and persistent low oxygen in the northern Gulf of Mexico. Total meiofaunal abundances were high in spring ranging from 800 to 3800 individuals 10 cm^{-2} before a hypoxic event. During severely low dissolved oxygen concentrations there were pronounced declines in abundance and diversity of major meiofauna taxa (Murrell & Fleeger, 1989). Harpacticoid copepods were least tolerant to low oxygen, while nematodes and kinorhynchans were less affected. Copepods declined from

high values of 100 – 410 to 0 individuals 10 cm^{-2} when hypoxia developed. Nematode abundance ranged from 600 to 3100 individuals 10 cm^{-2} before hypoxia and from 500 to 1100 individuals 10 cm^{-2} after hypoxia. There was evidence from settlement traps deployed in the area that nematodes migrated into the water column away from hypoxic sediments and resettled on the sediments with the return of normoxic conditions (Wetzel et al., 2001).

8.7.3.3.2 Chesapeake Bay and tributaries

Moderate hypoxia (dissolved oxygen of 2 mg L^{-1}) to anoxia (no oxygen) affects much to all of the sub-pycnocline waters in the central one-third of Chesapeake Bay for most or all of the summer (Hagy et al., 2004). Chesapeake Bay is a large estuary on the east coast of the United State (Figure 8.7.13) stretching 320 km from the Susquehanna River in the north to where it connects with the Atlantic Ocean at its seaward end. Deoxygenation has been a feature of the Chesapeake Bay since at least 1600 and seasonally since 1900 (Zimmerman & Canuel, 2002). Seasonal hypoxia has increased in extent, duration and intensity since the 1950s (Brush, 2009; Hagy et al., 2004).

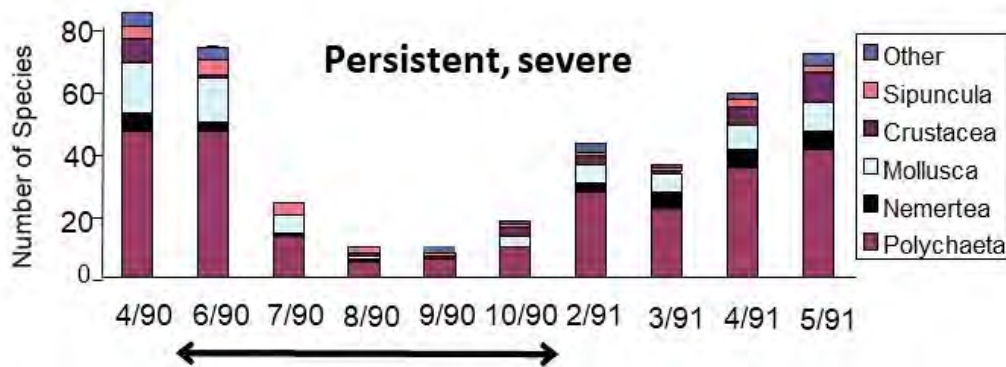


Figure 8.7.12 Number of species within taxonomic groups (total for $n = 10 \times 0.02\text{ m}^2$ cores) at a 'persistent, severe' site for months indicated in 1990 and 1991 (from Rabalais et al., 2001b). The arrow corresponds to the duration of the bottom-water dissolved oxygen levels illustrated in Figure 8.7.11.

Table 8.7.1 Comparisons of benthic community parameters in areas with seasonally persistent and severe hypoxia and seasonal but intermittent hypoxia. Data for the northern Gulf of Mexico are from Rabalais et al. (2001b) and for the Chesapeake Bay are from Dauer et al. (1992). There were also sedimentary and salinity differences among the sites that explained some differences in fauna.

	<i>Periodicity</i>	<i>Oxygen Level</i>	<i>Density (no. m⁻²)</i>	<i>Species Richness (no. 0.02-m⁻²)</i>	<i>Biomass (g AFDW m⁻²)</i>
Northern Gulf of Mexico					
Silty mud, Apr 1990, <i>n</i> = 10	Intermittent	Normoxic	8,637	22	2.59
Silty mud, Sep 1990, <i>n</i> = 10	Intermittent	Hypoxic	1,431	12	0.45
Sandy mud Apr 1990, <i>n</i> = 10	Persistent	Normoxic	18,437	51	2.92
Sandy mud Sep 1990, <i>n</i> = 10	Persistent	Hypoxic	730	4	0.23
Sandy mud, Feb-May, <i>n</i> = 10	Persistent	Normoxic	6,486	22	1.55
Sandy mud, Jul-Aug, <i>n</i> = 10	Persistent	Hypoxic	1,346	8	0.46
Chesapeake Bay					
Mainstem, polyhaline mud, spring, <i>n</i> = 4	Persistent	Normoxic	1,978	10	9.9
Mainstem, polyhaline mud, summer, <i>n</i> = 4	Persistent	Hypoxic	1,723	6	1.7
Tributaries, mesohaline mud, spring, <i>n</i> = 4	Persistent	Normoxic	3,065	9	2.5
Tributaries, mesohaline mud, summer, <i>n</i> = 4	Persistent	Hypoxic	902	4	1.1
Intermittent, varying levels of dissolved oxygen over the annual cycle, even in summer					
Persistent, seasonal cycle with severely low dissolved oxygen for extended periods in summer					

There is compression of suitable habitat for fishes and mobile crustaceans, such as blue crabs *Callinectes sapidus*, and potentially reduced access to food or overall food availability (Officer et al., 1984). However, demersal fishes may feed on moribund benthos at the sediment-water interface during hypoxia in the York River tributary to Chesapeake Bay (Pihl et al., 1992). The demise of benthic species and assemblages has been well documented in Chesapeake Bay and its tributaries with reduced species diversity (50% lower), lower biomass (70% lower), loss of deep-dwelling, long-lived species and dominance of shallow-dwelling, short-lived opportunistic species (Dauer et al., 1992), similar to persistent deoxygenation on the northern Gulf of Mexico (Table 8.7.1).

8.7.3.4 Intermittent hypoxia

8.7.3.4.1 Northern Gulf of Mexico continental shelf west of the Mississippi River delta

Intermittent exposure to low oxygen conditions occurs at depths on the periphery of more severely hypoxic waters. In the case of a 20 m depth site 50 km west of the Mississippi River delta on the Louisiana continental shelf, the cycle of mixing with reoxygenation and decrease in oxygen concentrations from respiration are similar to Figure 8.7.11, with the exception of a strong tidal advection component (Rabalais et al., 1994) (Figure 8.7.14). Bottom-water dissolved oxygen values less than 2 mg L⁻¹ occurred for 50% of the record from (June 15

– October 16) with many incursions below and above 2 mg L⁻¹.

Species richness at the intermittently hypoxic station was 2-fold lower in summer hypoxia than either spring period compared to a 13-fold decrease in species richness at the ‘persistent, severe’ station from spring through summer (Table 8.7.1). Polychaete species comprised about half of all benthic species at the ‘intermittent’ site but increased in relative proportion during the summer (Figure 8.7.15) as less tolerant infauna taxa decreased. The benthic community at the ‘intermittent’ station was diverse, with a complement of pericaridean crustaceans, bivalves, gastropods and other taxa, but the dominant species were small, surface-feeding polychaetes.

Dominant species for most months were *Paraprionospio pinnata* and *Mediomastus ambiseta* (Rabalais et al., 2001b). The abundance of *Armandia maculata* increased in August 1990. Changes in several dominant species through 1990 were evident, with *Prionospio cristata*, *Nephtys incisa*, *Magelona* spp., *Ampharete* sp., and *Owenia fusiformis*. *Armandia maculata*, *Ampharete* sp., and *Magelona* sp., replaced in spring 1991 by *Sigambra tentaculata* and *Cossura soyeri*.

8.7.3.4.2 Chesapeake Bay and tributaries

The washing of water from the main Chesapeake Bay onto the adjacent shores via a combination of winds and tides generates similar intermittent episodes of

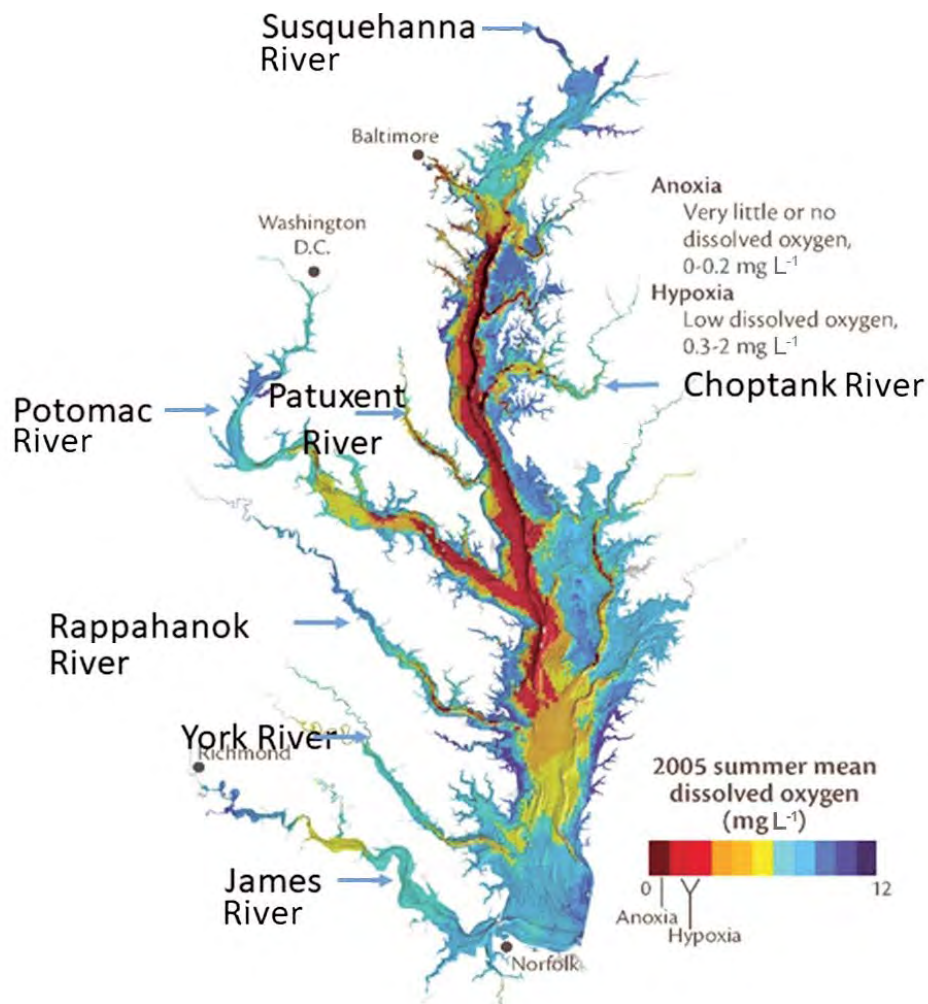


Figure 8.7.13 Map of bottom-water dissolved oxygen concentrations in Chesapeake Bay and its tributaries in the summer of 2005 that are detrimental to benthic and demersal assemblages (from Chesapeake Bay Program, http://www.eco-check.org/pdfs/do_letter.pdf, accessed 1-8-18).

severe hypoxia in summer (Breitburg, 1990). Collection of continuous bottom-water oxygen concentrations at a 4 m deep station on the western shore of Chesapeake Bay recorded about 40% of the days during the instrument deployment that fell below 2 mg L^{-1} , similar to the 50% of time on the Louisiana shelf (Rabalais et al., 1994). Oxygen fell below 1 mg L^{-1} 10% of the time during the same Chesapeake Bay deployment. Yet, the temporary nature of the intrusions allowed water of sufficient dissolved oxygen to support most estuarine organisms during part of the day.

The Patuxent River, a tributary of Chesapeake Bay (Figure 8.7.13), has deoxygenated waters in its lower reaches that are well below 2 mg L^{-1} and often anoxic. Benthic invertebrates that recruit to these deeper waters likely suffer extensive mortality during the summer as oxygen levels approach 0.5 to 0.1 mg L^{-1} . Samples of the benthic community in 3 to 16 m water depth show declining biomass, and below 8 m is essentially zero.

The assumption drawn by Breitburg et al. (2003) was that extremely low oxygen values were the probable cause for the decline of benthic invertebrates.

8.7.3.4.3 Baltic Sea coastal

The Baltic Sea is a brackish, permanently stratified, semi-enclosed sea with a geologic history of deoxygenation through the Holocene (Zillén et al., 2008). Severely low oxygen, often anoxia, occurs below the halocline at 80 - 100 m over as much as $60,000 \text{ km}^2$. In addition to salinity stratification and physical processes, human-caused nutrient-driven eutrophication has led to a 10-fold increase in deoxygenation in the Baltic Sea since 1900 (Carstensen et al., 2014). Deeper anoxic seas such as the Baltic Sea and Black Sea are not part of this review, but the Baltic Sea coastal areas are increasingly experiencing low levels of dissolved oxygen (Conley et al., 2011) (Figure 8.7.16). Most of these areas experience intermittent low oxygen.

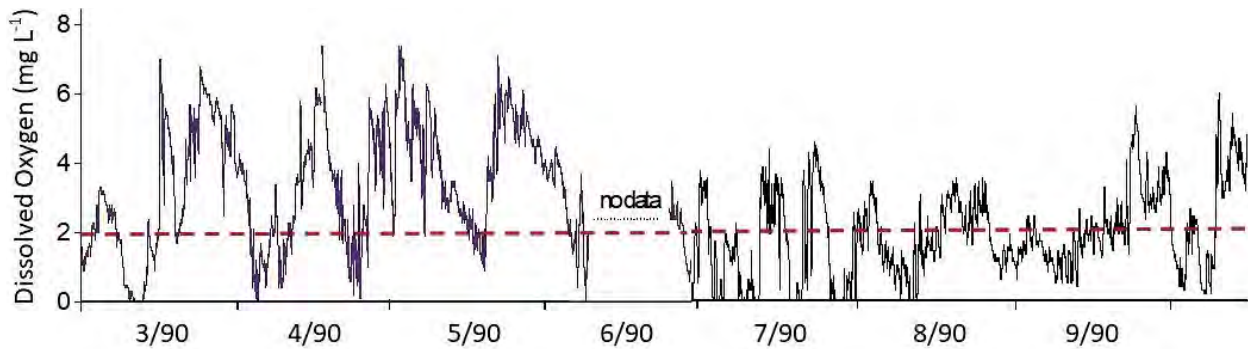


Figure 8.7.14 Continuous bottom-water dissolved oxygen in 20 m depth on the continental shelf (50 km west of the Mississippi River) (March – October 1990) (modified from Rabalais et al., 1994, 2001b). The horizontal dashed line defines hypoxia (from Rabalais et al., 2007).

Many studies of benthic communities have been conducted in the Baltic Sea in a continuum of depths of a few metres to 400 m and along a longitudinal salinity gradient, but this section focuses on depths less than 60 to 100 m. The brackish Baltic Sea typically supports low species richness because of salinity inhibitions (Villnäs & Norkko, 2011). Above the halocline, benthic macrofauna abundances increased with eutrophication (Elmgren, 1989; Karlson et al., 2002) with more recent declines in benthic macrofauna related to declines in oxygen concentration. Where species diversity is low, such as in the Baltic Sea and where diversity further decreases under deoxygenation, the relative abundance of a few species, may be more important in modifying ecosystem function than higher diversity, multi-functional group assemblages in the Baltic Sea (Törnroos & Bonsdorff, 2012).

A study by Josefson et al. (2012) on bioturbation and burial of phytoplankton debris provided the opportunity to examine abundance of benthos in a gradient of dissolved oxygen concentrations in depths of 45 to 290 m from north to south in the Baltic Sea coastal

areas. Most continental shelf studies of deoxygenation are restricted to 70 m and less. Thus, relationships of dissolved oxygen concentrations, abundance of individuals of a few species, and bioturbation potential (BPI) were examined for depths of ≤ 70 m from a gradient to 290 m coastal areas of the Baltic – Gulf of Finland, Eastern Gotland Basin, and Southern Baltic. The relationships were strong – the number of organisms increased with increasing oxygen levels and the bioturbation potential increased with the number of organisms.

8.7.3.5 Diel exposure

Changes in dissolved oxygen levels on a diel (day/night) or tidal cycle (Perez-Dominguez et al., 2006) are natural, but human activities that constrict or eliminate flow into and out of a tidal lagoon (Kauffman et al., 2018; Tweedley et al., 2016; Vignes et al., 2009) or enhanced primary production can aggravate or worsen low oxygen conditions (Beck et al., 2001; Beck & Bruland, 2000; Ringwood & Keppler, 2002). The oxygen dynamics are most pronounced in summer warming as

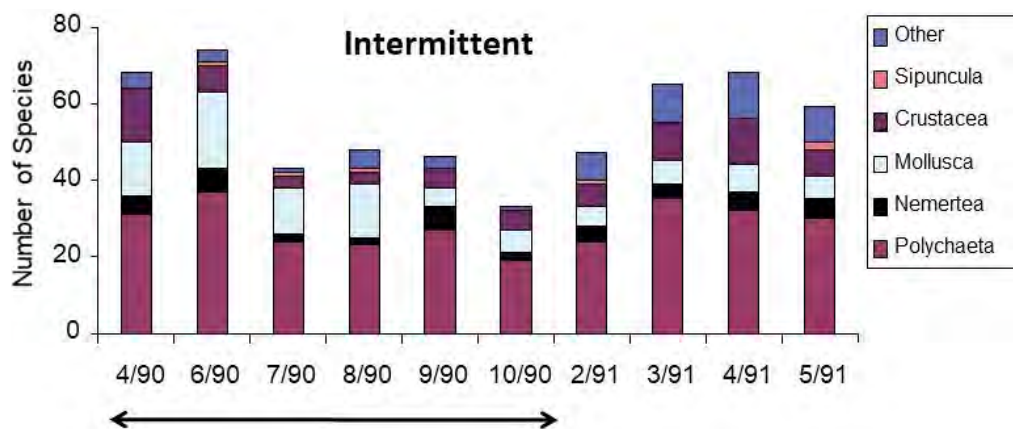


Figure 8.7.15 Number of species within taxonomic groups (total for $n = 10 \times 0.02 \text{ m}^2$ cores) at intermittently hypoxic sites for months indicated in 1990 and 1991. The arrow corresponds to the duration of the bottom-water continuous dissolved oxygen levels in Figure 8.7.11. Source: Rabalais et al. (2001b).

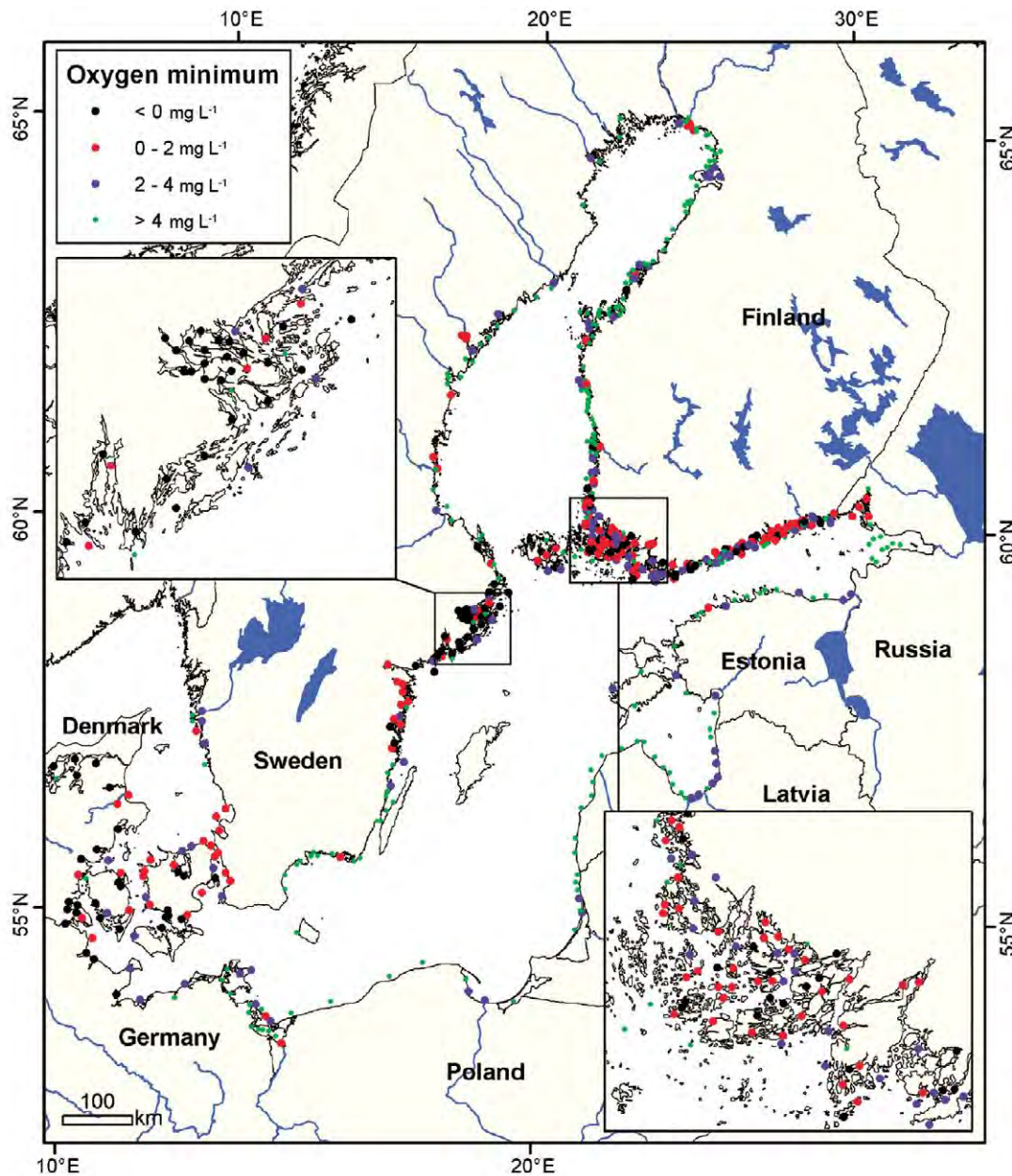


Figure 8.7.16 Lowest recorded oxygen concentration at all monitoring locations through the period (1955-2009) in the coastal areas of the Baltic Sea with insets for the Stockholm Archipelago (upper left) and the Finnish Archipelago Sea (lower right) (from Conley et al., 2011). Oxygen concentrations in bottom waters are (< 0 mg L⁻¹, anoxic; 0-2 mg L⁻¹, hypoxic; 2-4 mg L⁻¹, oxygen stressed; > 4 mg L⁻¹, adequate oxygen).

higher temperatures reduce dissolved oxygen solubility and increase rates of oxygen consumption by aerobic bacterial decomposition.

Mortality is usually minimal if the exposure to lower oxygen levels is over a short period but sublethal effects on juvenile clam growth were identified by Ringwood and Keppler (2002). Juvenile clams, *Mercenaria mercenaria*, were deployed with co-occurring oxygen meters for 7 day periods in tidal creeks near Charleston, South Carolina, USA. The primary effect related to lower

growth rate was the pH, intermediate was the dissolved oxygen, and minimal was salinity.

The invasive Eurasian milfoil *Myriophyllum spicatum* is now the dominant aquatic vegetation in the Mobile-Tensaw Delta, Alabama, USA, in protected waters north of a human-made obstruction to flow in the form of a causeway that significantly reduced wave action. The more quiescent waters north of the causeway resulted in lower dissolved oxygen values, and associated nektonic and benthic fauna were less abundant (a five-fold reduction in faunal abundance) during night

compared to the fauna collected during the day in the *Vallisneria americana* beds, the dominant native vegetation, to the south of the causeway. This nocturnal decrease in dissolved oxygen was accompanied by reductions in invertebrates such as *Gammarus* amphipods, *Neritina* snails, and blue crabs *Callinectes sapidus*, leaving behind mostly *Gammarus* amphipods and insects at much lower abundance. In contrast, faunal communities in *V. americana*, although distinct from *M. spicatum*, exhibited little spatial or temporal (diel) difference.

8.7.4 Ecosystem consequences

The community structure of benthos exposed to deoxygenation, because they are relatively immobile, varies by the severity of oxygen deficiency, the duration of exposure to low levels of dissolved oxygen concentrations, their susceptibility to low oxygen, and their functional group (Solan et al., 2004). Typical responses of benthic communities to oxygen stress are a loss of diversity and a change in faunal composition. Abundance of organisms decreases along with a reduction in overall biomass. Large longer-lived, deep burrowing species are replaced by small opportunistic species that live within the upper few cm of sediments. The loss of deeper burrowing species reduces the bio-irrigation and bioturbation of the sediments (Solan et al., 2004), resulting in a shift of the redox potential discontinuity layer towards the sediment-water interface and a compression of suitable benthic habitat. On the other hand, some deep burrowing species are responsible for transporting organic matter deeper into the sediments and increasing the biological oxygen demand and eventually deoxygenation (e.g. the invasive polychaete *Marenzelleria* spp. in the Baltic Sea (Josefson et al., 2012).

The types of benthos and their shifts with deoxygenation influence nutrient cycling of both nitrogen and phosphorus in the sediments and overlying water. Bottom water hypoxia typically leads to enhanced regeneration of phosphate and ammonium from deoxygenated sediments (Gammal et al., 2017) with a positive feedback in enhanced productivity in the surface waters and a negative feedback of an increased flux of organic matter to the sediments and continued deoxygenation (Conley et al., 2002). Elevated levels of ammonium and ortho-phosphate are typical in severely deoxygenated waters overlying reduced

sediments (Rabalais et al., 2014). Phosphorus returns to the sediments during oxic conditions. Savchuk (2005) estimated the net sediment burial of P for 1991-1999 to be ca. 20 kt P y⁻¹, far exceeding the P received from external sources. The nitrogen cycle is highly dependent on oxygen concentrations. Nitrogen removal through nitrification/denitrification is dependent on oxic conditions. Nitrification/denitrification rates decrease as dissolved oxygen concentrations decrease but can recover as oxic conditions return; recovery is curtailed following long periods of highly reduced sediments (Karlson et al., 2005).

8.7.5 Societal consequences

Benthic organisms and their productivity in areas of nutrient-enhanced eutrophication support high yield demersal fisheries, such as the commercially important shrimping industry in the northern Gulf of Mexico (Figure 8.7.17). Loss of secondary production where deoxygenation is widespread is assumed to curtail fisheries yields, but this is not always the case (Chesney et al., 2000; Rose et al., 2018). Sturdivant et al. (2013) estimated benthic community production in the lower Rappahannock River, a tributary of the Chesapeake Bay, over four months coupled with continuous dissolved oxygen concentrations at selected sites for discrete periods. They estimated that hypoxic sites had as much as 85% lower macrobenthic production compared to normoxic sites. Diaz and Rosenberg (2008) projected lost secondary production in terms of carbon biomass and loss of energy transfer to higher trophic levels. Area estimates of missing biomass for about a third of the world's oxygen-depleted coastal areas indicated that as much as 343,000 to 734,000 metric tons of carbon are displaced over a total area of 245,000 km² as a result of deoxygenation.

Relating an economic model with secondary production loss of a fishery exposed to low oxygen conditions has been elusive (Diaz & Solow, 1999). Huang et al. (2010) estimated that hypoxia might have resulted in a 12.9% annual decrease in the North Carolina brown shrimp harvest during the period 1999–2005, and a monetary value of US\$8,645,167 for Pamlico Sound. Smith et al. (2017) tackled the economic side of the Louisiana brown shrimp fishery on market prices for small and large shrimp based on the disruptive expanse of a severely depleted dissolved oxygen area across the Louisiana inner shelf in summer. The presence of areas



Figure 8.7.17 Shrimp boat on the Gulf of Mexico coast © Ruth Burke / Alamy stock photo.

of dissolved oxygen below 2 mg L^{-1} cause migration of shrimp to the nearshore coastal zone or farther offshore of the low oxygen water mass in deeper waters with no trawlable shrimp populations in between (Craig & Crowder, 2005; Zimmerman & Nance, 2001). This results in reduced suitable habitat, impaired growth of individuals exposed to low oxygen, 'herding' of smaller individuals closer to shore where they are easily captured in high abundance, inability of smaller shrimp to migrate offshore as part of their natural annual cycle to increase in size and thus attract better market prices, and decisions of trawlers to not target the farther offshore population because of increased distance and fuel costs. What Smith et al. (2017) were able to show was that hypoxia decreased the quantity of large shrimp relative to small shrimp and increased the price of large shrimp relative to small shrimp. Smaller shrimp were a larger proportion of the inshore population and the higher abundance of small shrimp drove down their market price. Fewer, larger shrimp further offshore drove up their market price. Imports of larger non-native shrimp were cheaper than the native shrimp to the detriment of local trawler incomes. These economic data were the first to demonstrate negative economic impacts on a valuable commercial fishery of the Louisiana shelf.

8.7.6 Conclusions / Recommendations

Increasing deoxygenation is occurring more and more in estuaries and coasts. In these productive systems, members of the benthic communities are critical as food resources for higher trophic levels and for the healthy functioning of a coastal ecosystem. When these assemblages are exposed to low oxygen conditions, there is a standard response of mobile species evacuation from the area, loss of deeper burrowing community members, and reduced diversity, abundance, and replacement by individuals that are mostly opportunistic species with limited burrowing ability. Living resources are disrupted and even lost, including commercially important demersal species. In the case of limited examples of economic costs of deoxygenation on benthic communities and commercial resources, results point to loss of secondary production and less desirable market prices and monetary losses. Economic considerations of coastal resources should be coupled into models of economic costs and benefits of nutrient mitigation to reduce deoxygenation in coastal waters and their watersheds. There are additional disruptive effects on coastal ecosystems, such as habitat alteration, chemical pollutants, altered hydrology,

overfishing and sea-level rise, which may mask or compound the effects due to deoxygenation.

Recovery pathways for eutrophied and deoxygenated benthic communities are not the same among the limited examples where steps have been taken to reduce nutrient inputs to estuarine and coastal waters (Carstensen et al., 2014; Kemp et al., 2009; Riemann et al., 2016). Long-lived species, especially deep-burrowing ones require longer periods for recovery to the extent that they can affect positive feedbacks (Norkko et al., 2010, 2013). Recovery of benthic assemblages may take years to decades following long-term exposure to long-lasting deoxygenation. Furthermore, return to normoxic conditions is not immediate or even after a few years (Riemann et al., 2016). An integrated coastal ecosystem understanding of recovery (e.g. phytoplankton, rooted or attached vegetation, food webs, invasive species, species interactions, and shifts in biogeochemical processes) is the larger context into which oxygen condition recovery and improved benthic communities should be placed. This is not to deter nutrient mitigation, but to place it within the larger context of ecosystem recovery so that nutrient mitigation efforts are not abandoned but continue.

8.7.7 References

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8.8 The significance of ocean deoxygenation for tropical ecosystems – corals, seagrasses and mangroves

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Summary

- Deoxygenation affects tropical coastal ecosystems but is relatively understudied and poorly understood.
- The number of hypoxic ecosystems may be underestimated by an order of magnitude in the tropics due to lack of research capacity.
- Corals, seagrasses and mangroves themselves are vulnerable to hypoxia, and also have the ability to influence oxygen concentrations in the surrounding water, leading to feedbacks that can influence deoxygenation rates.
- Corals, seagrasses, and mangroves provide habitat to diverse communities of organisms that are vulnerable to low concentrations of oxygen.
- The warmer temperatures typical of tropical ecosystems, combined with the dependence of coral reefs on calcification, suggests that a multiple-stressor perspective is needed for predicting the effects of deoxygenation in this region.

Ocean hypoxia effect	Potential consequences
Hypoxia establishes along gradients of connectivity between terrestrial inputs and oceanic flushing.	<ul style="list-style-type: none"> Species may segregate or become restricted to a portion of their former range. Fisheries catches may decline or be displaced.
Low oxygen can trigger biogeochemical changes that exacerbate hypoxia in feedback loops.	<ul style="list-style-type: none"> Low oxygen can foster production of toxic sulphides, leading to further death of benthic plants and algae.
Differential tolerances and abilities to acclimate in foundation species of corals, seagrasses, and mangroves.	<ul style="list-style-type: none"> Overall diversity of foundation species may decrease, as seen in reef building corals. Communities may shift to dominance by stress tolerant species that have lower habitat complexity.
Hypoxia mediates species interactions because of different stress tolerances of interactors.	<ul style="list-style-type: none"> Pathogens may gain an advantage over stressed hosts, as in black band disease on corals. Increased stress may increase dependence on mutualisms, as in sleep-swimming fish that flush hypoxic coral crevices with oxygenated water. Algae may increase on reefs because they are more tolerant than corals to extremely low oxygen conditions.
Low-oxygen events can cause mass mortality of habitat-forming seagrass and corals.	<ul style="list-style-type: none"> Ecosystem services including nursery function are lost. Structural complexity of habitats simplify with loss of structures such as coral reefs and seagrass beds that are built and maintained by aerobic organisms.
Hypoxia in tropical ecosystems may interact with other global change stressors including ocean acidification and warming.	<ul style="list-style-type: none"> The health and survivorship of corals and seagrasses may respond non-linearly to changes in dissolved oxygen concentrations. Photosynthetic consumption of CO₂ and production of O₂ by corals and seagrasses may alleviate stresses associated with ocean deoxygenation and acidification; on the other hand, increased respiration by photosynthetic organisms, particularly with warming, can have the opposite effect.

8.8.1 Introduction

Oxygen depletion is a worldwide phenomenon. However, deoxygenation in coastal marine ecosystems, which is accelerating due to anthropogenic impacts including eutrophication and climate change, is most widely recognized and studied in temperate ecosystems (Breitburg et al., 2018; Diaz et al., 2011; Diaz & Rosenberg, 2008; Rabalais et al., 2010). Hypoxia (oxygen concentrations < 2.8 mg L⁻¹, Diaz & Rosenberg, 1995) has been documented in tropical coastal marine ecosystems, but to a lesser degree than in temperate counterparts (Figures 8.8.1 and 8.8.2). After correcting for differences in length of shoreline (a basic approximation of potentially hypoxic coastal habitat), the number of documented dead zones in temperate regions outnumbers those in the tropics by an order

of magnitude (Altieri et al., 2017). Analysis suggests this disparity is at least partially due to underreporting and a lack of targeted research capacity in the tropics (Figure 8.8.2). In many cases, signs of hypoxic stress and mortality are evident in tropical habitats such as coral reefs, even where the quantitative data to verify the severity of low oxygen stress is unavailable (Altieri et al., 2017; Nelson & Altieri, 2019). In this section, we argue that: (1) it is likely that ocean deoxygenation is more widespread in the tropics than currently recognized, (2) hypoxia has a variety of negative effects on the dominant structure-forming species in coral, seagrass, and mangrove ecosystems, as well as the diverse communities of organisms which they support, and (3) there are a variety of natural and social impacts of hypoxia already documented in the coastal tropics, and more are likely to be identified as the intensity of

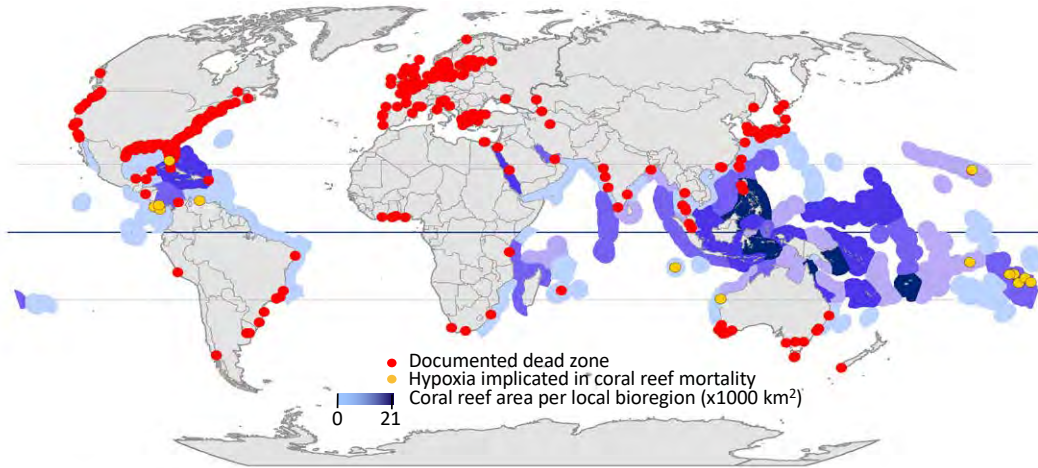


Figure 8.8.1 Map of hypoxic ecosystems worldwide. Red dots are documented hypoxic ecosystems and gold dots are additional tropical sites where hypoxia was inferred from mass mortality events or other signs of stress. Purple represents the relative abundance of coral in various bioregions. From Altieri et al. (2017).

hypoxia research in the coastal tropics approaches that of temperate areas.

Despite the relative lack of attention that deoxygenation in the coastal tropics has received, sufficient studies have accumulated to develop an understanding of its impacts on living systems. In many cases our understanding comes from ecosystems where hypoxia appears to occur naturally, such as the isolation of reef flats by tides (Kinsey & Kinsey, 1967) or accumulation of detritus in seagrass beds (van der Heide et al., 2012). In general terms, the mechanisms that drive the formation of hypoxia in

tropical ecosystems, and the biological responses to that stress, are not so different from in temperate ecosystems. However, there are several key features of tropical systems that may make hypoxia of greater concern than in temperate ecosystems. First, tropical ecosystems are typically exposed to warm temperatures year-round. This is important given that higher temperatures decrease water's saturation capacity for dissolved oxygen, increase biological oxygen demand of both the microbes that can generate hypoxic conditions and the metazoans that depend on oxygen, and can stimulate primary productivity that fuels microbial activity (Altieri & Gedan,

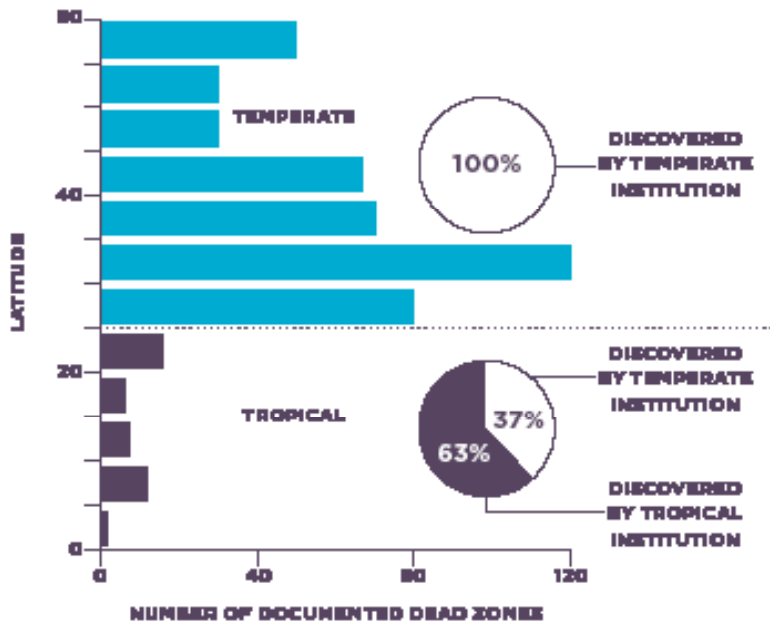


Figure 8.8.2 Distribution of hypoxic ecosystems by latitude. There is approximately an order of magnitude fewer documented dead zones in the tropics than there are in temperate regions. The disparity in research effort, evident by the number of tropical dead zones first identified by a temperate investigator, suggests that the number of tropical dead zones has been underestimated due to a deficit in research capacity. From Altieri et al. (2017).

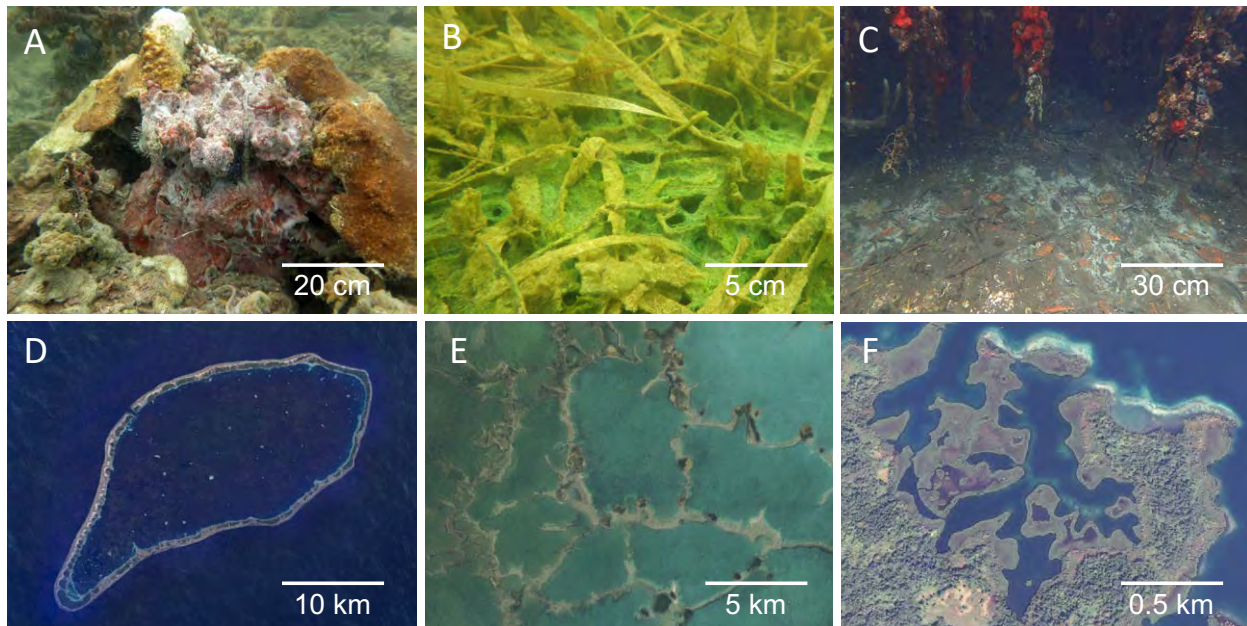


Figure 8.8.3 Photographic evidence of hypoxia in three of the main tropical, coastal ecosystem types: (A) coral reefs: dead urchins and brittlestars strewn atop a dying coral head on the Caribbean coast of Panama, (B) seagrass meadow: dead seagrass coated with microbial mats accumulated during a die-off event associated with concentrations of low oxygen and high hydrogen sulphide in Florida Bay, USA, and (C) mangroves: mats of *Beggiatoa* bacteria below the roots indicating activity of aerobic sulphur reducing bacteria in Bocas del Toro, Panama. Deoxygenation is a common occurrence in each ecosystem with similar indicators including mortality of macro-biota and proliferation of microbial mats. Coral bleaching (A), which is typically associated with thermal stress, can also be triggered by hypoxia. Coral, seagrass, and mangroves can contribute to the creation of hypoxia by forming ponds, channels, and other semi-enclosed basins as seen in (D) coral reef atoll, Manihi Atoll, French Polynesia, (E) basins within a seagrass bed in Florida Bay, USA, and (F) mangrove ponds in Bocas del Toro Panama. (A) © Maggie Johnson, (B) © Brad Furman, (C) © Andrew Altieri, (D-E) © Google, Landsat, (F) © Google, CNES.

2015). Second, many tropical ecosystems are regularly affected by large tropical storms, such as typhoons and hurricanes, that can affect the nutrient and stratification characteristics that generate hypoxic conditions (Herbeck et al., 2011). Third, many coastal, tropical countries are developing nations, where hypoxia drivers and social vulnerabilities are both elevated. In developing nations, fertilizer inputs are increasing at a more rapid rate than in temperate ecosystems, and human population growth and agricultural practices have outpaced growth in their capacity to manage sewage and run-off (Lu & Tian, 2017; MEA, 2005a). Moreover, in many tropical countries, human populations are more reliant on local marine habitats for vital ecosystem services including food, tourism-related income, and shoreline protection. In such places, the negative effects of deoxygenation on coastal ecosystem function will directly affect human well-being (Barbier et al., 2011).

Tropical shorelines are characterized by three key biogenic habitats that define their ecological organization: coral reefs, seagrass meadows, and mangrove forests. Deoxygenation and its effects are observed in all three coastal ecosystems (Figure 8.8.3). Much of our understanding about the structure and function of coastal tropical ecosystems has been developed in the

study of these habitats (Bertness et al., 2001). We posit that the study of coral reefs, mangrove forests, and seagrass beds, which has contributed unique insights to general ecological theory, also has the potential to enrich our understanding of ocean deoxygenation. For comparison, the study of hypoxia in temperate ecosystems has been dominated by the study of soft sediment communities (Diaz & Rosenberg, 1995; Levin et al., 2009; Middelburg & Levin, 2009) (but see examples of interactions between oxygen conditions and temperate bivalve reefs: e.g. Altieri & Witman, 2006; Lenihan, 1999). By adopting a perspective focused on habitat-forming species of corals, seagrasses, and mangroves, we offer a globally relevant perspective on deoxygenation in tropical ecosystems that considers the effects of: 1) these species on oxygen conditions, 2) deoxygenation on these species, and 3) hypoxia on the community of species that reside in each habitat.

8.8.2 Definition of species group

Many ecosystems are defined by biomass dominants that create habitat and modify environmental conditions (Altieri & Van De Koppel, 2013). These species are commonly referred to as foundation species (*sensu* Dayton, 1972) because their establishment is the basis



Figure 8.8.4 (A) Coral reef, (B) Seagrass bed, (C) Mangroves. (A) © blue-sea.cz, (B) © Ethan Daniels / Shutterstock.com, (C) © happystock / Shutterstock.com.

for diverse communities and numerous secondary ecological interactions (Bruno & Bertness, 2001). For example, coral reefs, which cover less than 1% of the sea floor, host over 25% of known marine species (Reaka-Kudla, 1997). Studying ocean deoxygenation in tropical ecosystems from the perspective of these habitats, and in the context of the foundation species, is particularly insightful because effects on each of these habitats cascade to associated organisms, which, overall, represent a large portion of the earth's marine biodiversity. Moreover, corals, seagrasses, and mangroves are themselves organisms that have their own dependence on oxygen and potential vulnerability to hypoxic conditions.

Corals, seagrasses, and mangroves (Figure 8.8.4) form large aggregated living structures that can influence concentrations of dissolved oxygen through their

metabolic activities (Figure 8.8.5). Seagrasses and most corals (along with their zooxanthellae) are submerged autotrophic organisms that exchange gases with the surrounding water column. During the night and other light limiting conditions they are net consumers of oxygen (and producers of CO_2) which can contribute to low oxygen conditions (Shashar et al., 1993). Mangroves differ in that their primary gas exchange structures are in an emergent canopy. Similar to seagrasses, however, they transport oxygen to their roots (to overcome naturally oxygen depleted sediment conditions) which release oxygen into the surrounding sediments (McKee, 1993). Mangroves and seagrasses are highly productive and form large swaths at the land-sea interface capable of intercepting terrigenous nutrients in rivers and other sources of run-off, and thereby reducing eutrophication of neighbouring marine environments and the likelihood of hypoxic conditions that can result (Boto & Wellington,

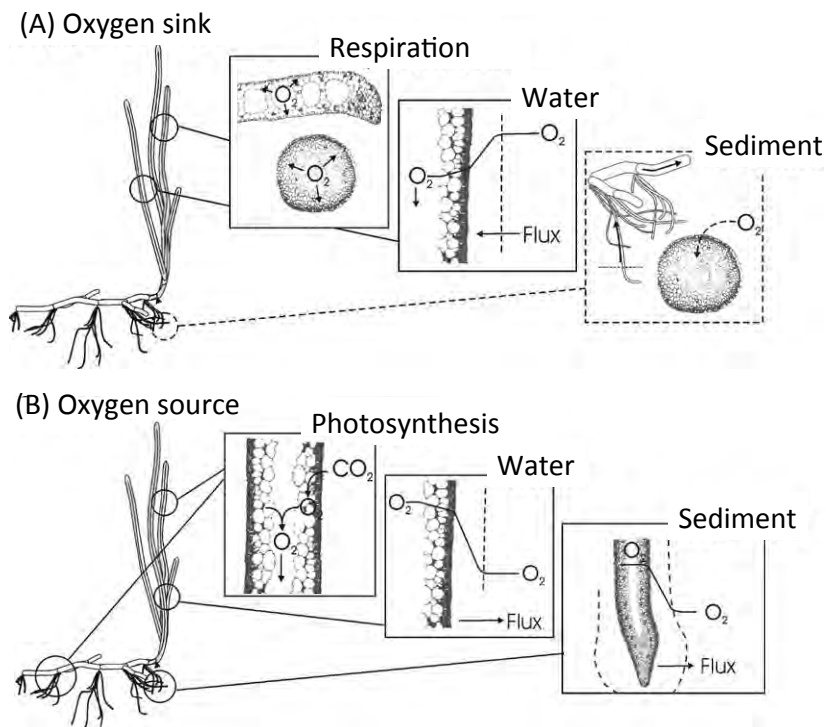


Figure 8.8.5 Diagram of oxygen production, consumption, and exchange in seagrass both in the water column and below ground. Corals and mangroves similarly exchange oxygen with the water column, and mangroves with the sediments. From Borum et al. (2006).

1988; Vonk et al., 2008). However, the detritus and other organic matter trapped by seagrasses, mangroves, and corals (including from their own production) can fuel local oxygen depletion (Bjork et al., 2008).

The physical structure of coral reefs, seagrass beds, and mangrove forests can also influence oxygen dynamics by modifying the movement of water and other materials. They act as barriers that limit water movement and exchange and thereby prevent re-oxygenation of hypoxic waters from open-ocean and surface waters (Figure 8.8.3 D-F). Coral atolls, barrier reefs, and reef flats can create lagoons susceptible to oxygen depletion (Andrefouet et al., 2015; Kinsey & Kinsey, 1967). Likewise, mangroves can form creeks and ponds with limited exchange and vulnerability to oxygen depletion (Mattone & Sheaves, 2017). In some settings, seagrass shoals enclose basins that become hypoxic (Robblee et al., 1991), and more commonly their effect on water chemistry is noticeable within the canopy where water can stagnate and be influenced by gas exchange of the blades and sediments below.

8.8.3 Trends and impacts

8.8.3.1 Coral reefs

Over the last several decades, coral reef ecosystems (Figure 8.8.6) have suffered significant declines in the abundance and diversity of reef-building corals (Bellwood et al., 2004; Bruno et al., 2007; Gardner et al., 2003). While much of this degradation has been attributed to increased temperatures due to climate change (Hoegh-Guldberg et al., 2007; Hughes et al., 2003; Munday et al., 2008), an increase in mass mortality events (i.e. “dead zones”) associated with low oxygen within the last 20 years suggests that hypoxia is another important, but largely overlooked, stressor on reefs (Altieri et al., 2017). Not only are coral tissues and surrounding boundary layers routinely hypoxic in some locations at night (Kinsey & Kinsey, 1967; Niggel et al., 2010; Ohde & van Woesik, 1999; Orr & Moorhouse, 1933), due to the depletion of oxygen by polyp and zooxanthellae respiration (Gardella & Edmunds, 1999; Kuhl et al., 1995; Shashar et al., 1993) (Figure 8.8.7), but entire



Figure 8.8.6 Healthy coral reef. © Vlad61.

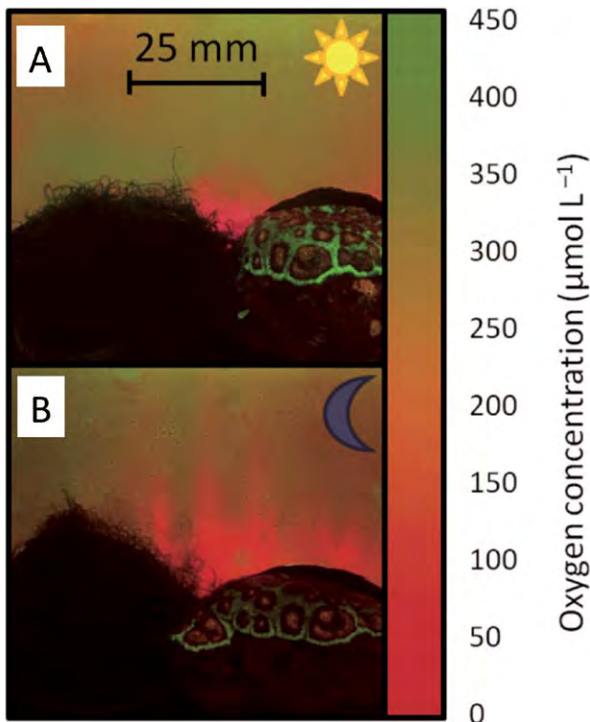


Figure 8.8.7 False colour image of oxygen depletion at the interface of algae (filamentous mat) and coral (polygons with green trim) during both day (A) and night (B). The oxygen depletion contributes to the competitive dominance of algae over coral. From Haas et al. (2013).

reefs can undergo prolonged periods of hypoxia due to natural oceanographic and meteorological processes or the anthropogenic formation of dead zones (Altieri et al., 2017) (Figure 8.8.8). Hypoxia has been implicated in the mass mortality of coral reef organisms in over 20 events around the world (Nelson & Altieri, 2019) (Figure 8.8.1), with the majority of these events occurring within the last two decades (Altieri et al., 2017).

Like other ecosystems, coral reef dead zones occur when processes that increase oxygen demand occur in tandem with processes that prevent the restoration of oxygen in the system (i.e. reoxygenation). Increases in oxygen demand and deoxygenation in reef environments have been attributed to coral spawn slicks (Hobbs & Macrae, 2012; Simpson et al., 1993) (Figure 8.8.9), algal blooms (Dupont et al., 2010; Genin et al., 1995; Guzman et al., 1990; Smith, 1975), higher seawater temperatures due to the seasonal conditions (Andrefouet et al., 2015) or climate change (Altieri & Gedan, 2015), and excess organic matter due to sewage pollution (Jokiel et al., 1993; Pastorok & Bilyard, 1985; Smith et al., 1981), mariculture effluent (Loya, 2004; Villanueva et al., 2005), or the presence of benthic algae (Brown & Carpenter, 2013; Gregg et al., 2013; Haas et al., 2010, 2011). In contrast to the mostly

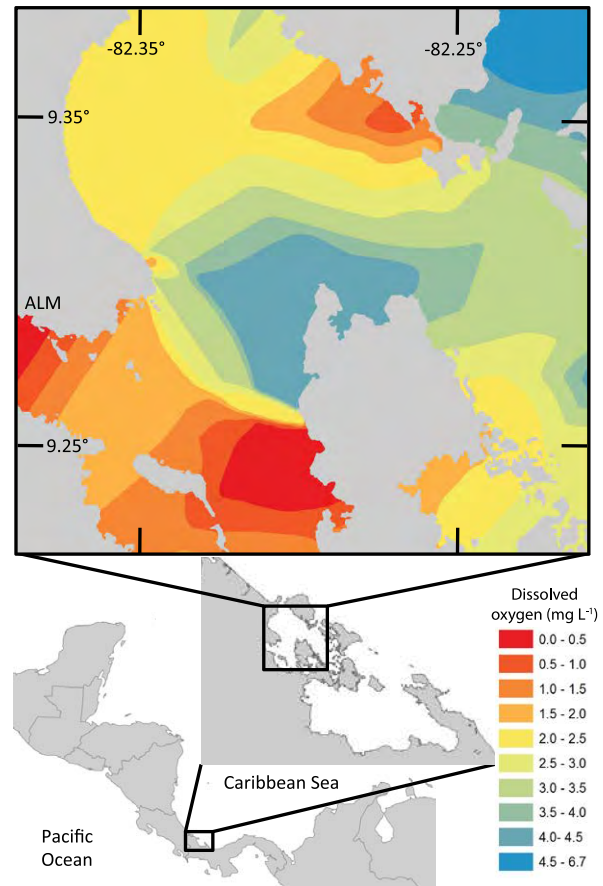


Figure 8.8.8 Map of hypoxia within Bahía Almirante on the Caribbean coast of Panama. Hypoxia (orange and red false colour) developed near human settlements, and led to declines in coral cover and diversity. From Altieri et al. (2017).

biological processes that increase oxygen demand on reefs, the factors that prevent reoxygenation on reefs are predominately physical. Coral reef dead zones occur more frequently in semi-enclosed or closed basins that exhibit water-column stratification and poor flushing (e.g. Altieri et al., 2017; Andrefouet et al., 2015) and during periods of calm seas with unusually light winds and low swell (e.g. Andrefouet et al., 2015; Hobbs & McDonald, 2010; Hobbs & Macrae, 2012).

In general, the response of organisms to hypoxia is dependent on both the magnitude and duration of deoxygenation (Best et al., 2007). The effects of hypoxia on corals range from reduced photosynthesis (Gardella & Edmunds, 1999) and calcification (Al-Horani et al., 2007; Colombo-Pallotta et al., 2010; Wijgerde et al., 2012, 2014), to bleaching (Altieri et al., 2017; Yonge et al., 1932), and in extreme cases, mortality (Altieri et al., 2017; Yonge et al., 1932). The ability of corals to withstand hypoxia varies among species; corals have been shown to survive severe hypoxic conditions



Figure 8.8.9 Coral spawn slick on surface of water. © Suzanne Long / Alamy stock photo.

(< 5% air saturation) in the laboratory for periods ranging from several hours to at least a week, depending on the species (Altieri et al., 2017; Dodds et al., 2007; Haas et al., 2014; Mayer, 1917; Sassaman & Mangum, 1973; Weber et al., 2012; Yonge et al., 1932). Generally, branching and solitary species typically suffer the highest mortality during severe hypoxic events (Figure 8.8.10), whereas massive, submassive, and encrusting corals are usually less affected (Adjeroud et al., 2001; Genin et al., 1995; Guzman et al., 1990; Laboy-Nieves et al., 2001; Simpson et al., 1993). The response of organisms to hypoxia also depends on the presence of other stressors. There is evidence that some coral communities might be relatively robust to the combination of low pH and deoxygenated waters (Camp et al., 2017), and that the endosymbiotic dinoflagellates belonging to the genus *Symbiodinium* may mitigate some of the impacts of hypoxia and concurrent respiration-driven acidification in cnidarians (Klein et al., 2017). However, additional research is needed to better understand the physiological responses of coral to hypoxia (and co-occurring stressors including acidification and excess nutrients) and to develop a mechanistic explanation

of this variation in tolerance among species. Such findings would allow for predicting shifts in community composition with increasing hypoxia and establish the scope for adaptation within species.

8.8.3.2 Seagrass beds

Seagrasses (Figure 8.8.11) are declining globally at an accelerating rate (current loss at 1.5% per year) comparable to loss rates for mangroves, coral reefs, and tropical rainforests (Orth et al., 2006; Waycott et al., 2009). In the tropical Atlantic and Indo-Pacific regions, conservative estimates are that 21% of the 72 known seagrass species exhibit decreasing population trends and 11% of species have been designated as threatened on the IUCN Red List (Short et al., 2011). Several tropical seagrass mass mortality events have been reported in recent decades (Carlson et al., 1994; Hall et al., 1999; Plus et al., 2003; Robblee et al., 1991; Seddon et al., 2000; Zieman et al., 1999). Although causality is rarely established in these events (Ralph et al., 2007), correlative evidence and work from experimental studies suggests that hypoxia is one of the main factors underlying these die-offs (Borum et al., 2005; Carlson et al., 1994; Durako & Kuss, 1994).

One of the primary drivers of repeated, sustained hypoxia in seagrass ecosystems is eutrophication (Burkholder et al., 2007). While some level of nutrient enrichment can result in increased seagrass productivity (Ferdie & Fourqurean, 2004; Short et al., 1985; Short & Wyllie-Echeverria, 1996; Terrados et al., 1999), chronic nutrient enrichment in seagrass meadows causes excessive growth of macroalgae, epiphytes, and phytoplankton, resulting in the development of hypoxic conditions (Bjork et al., 2008). Nutrients and organic matter from both terrestrial watershed inputs and coastal development (e.g. sewage) contribute to chronic nutrient enrichment in seagrass ecosystems (Burkholder et al., 2007). Eutrophication-induced hypoxia in seagrass meadows occurs most often during the warm summer months, especially in calm, poorly flushed bodies of water where nutrient loads are concentrated and frequent (Burkholder et al., 2007; Lapointe & Clark, 1992).

Seagrasses are both a source and sink for oxygen in the surrounding water column and sediments (Figure 8.8.5). During the day, when seagrass is photosynthesizing, oxygen partial pressures within seagrass are primarily dependent on changes in surface irradiance (Borum et al., 2005, 2007; Greve et al., 2003). In contrast, at night,



Figure 8.8.10 A thicket of the endangered staghorn coral *Acropora cervicornis* that succumbed to an acute hypoxia event in Bocas del Toro, Panamá. The coral was one of the few remaining stands of live *A.cervicornis* inside the Bay of Almirante prior to the 2017 hypoxia event. © Dr Maggie D. Johnson.

internal seagrass oxygen partial pressures are linearly related to the oxygen concentration in the water column, so low water column oxygen concentrations often results in hypoxic seagrass tissues (Borum et al., 2005, 2007; Greve et al., 2003). At the same time as tissue and water column concentrations of CO_2 are elevated by night-time respiration. Seagrasses face hypoxic conditions not only in the water column, but also in their sediments (Borum et al., 2007; Pedersen et al., 1998).



Figure 8.8.11 Seagrass bed © Rich Carey / Shutterstock.com.

In general, coastal marine sediments are mostly anoxic and highly reduced below their surface layer because of the slow oxygen diffusion from the water column and degradation of organic matter within the sediment (Borum et al., 2007). Consequently, seagrass sediments represents a large oxygen sink and seagrasses must supply oxygen to their below-ground tissues through either photosynthesis or by diffusing oxygen from the water column through leaves to rhizomes and roots (Pedersen et al., 1998). Environmental factors that disrupt seagrass oxygen balances, for example by increasing seagrass respiration or increasing the oxygen demand within the sediment, can result in hypoxic seagrass tissues (Borum et al., 2005). Environmental factors that disturb seagrass oxygen balances include hypersalinity, higher water temperatures, and infections by pathogens (Durako & Kuss, 1994; Koch & Erskine, 2001; Zieman et al., 1999).

The tolerance of seagrass to hypoxia differs among species (Koch et al., 2007a; Pedersen et al., 2016), but hypoxia generally has negative effects on seagrass



Figure 8.8.12 (A) Red mangrove *Rhizophora mangle* seedlings, (B) black mangrove *Avicennia germinans* seedlings. (A) © Mark Conlin / Alamy stock photo, (B) © FLPA / Alamy stock photo.

growth, metabolism, and survival (Holmer & Bondgaard, 2001; Pedersen et al., 2016). Seagrasses exposed to hypoxic water column conditions show increased respiration, reduced rates of photosynthesis, smaller leaves, and reduced number of leaves per shoot (Holmer & Bondgaard, 2001). When the supply of oxygen to belowground tissues is insufficient for aerobic respiration, seagrasses must rely on less-efficient anaerobic respiration (Borum et al., 2005, 2007; Pregnall et al., 1984). Poor energy availability and the accumulation of toxic plant metabolites during anaerobiosis can eventually result in seagrass mortality (Perez et al., 2008). Seagrass die-offs create a positive feedback cycle where mortality begets further mortality as higher ecosystem oxygen demands are created when dead plant material is decomposed (Bjork et al., 2008).

Aside from the direct effects of hypoxia on seagrass tissues, hypoxia also negatively affects seagrass by indirectly mediating the invasion of sulphides in seagrass tissues. Sulphide is a potent phytotoxin, which negatively affects seagrass photosynthesis, metabolism, and growth (Holmer & Bondgaard, 2001). Tropical marine seagrass beds have especially high sulphide concentrations because high temperatures stimulate microbial sulphate reduction rates within sediments and the low availability of iron in the carbonate sediments of tropical seagrass beds reduces their sulphide binding capacity (Chambers et al., 2001; Koch et al., 2007a). Seagrasses are able to prevent sulphide from invading their tissues by supplying sufficient oxygen to below-ground tissues to maintain an oxic microsphere around their roots and rhizomes (Koch et al., 2007b; Pedersen et al., 1998, 2004). When seagrasses are unable to maintain this supply of oxygen to below-ground tissues, sulphides are able to enter and accumulate within the plant tissues, frequently resulting



in plant mortality (Borum et al., 2005; Carlson et al., 1994). This process has been implicated as the most likely mechanism responsible for mass die-offs of the tropical seagrass *Thalassia testudinum* in the Florida Bay (Borum et al., 2005) (Figure 8.8.3B).

8.8.3.3 Mangrove forests

Compared to coral reefs and seagrass beds, hypoxia is naturally a more common occurrence in mangrove ecosystems (Figure 8.8.3C), though it is also being exacerbated by anthropogenic nutrient inputs and land use modification. Mangroves themselves are generally tolerant of hypoxic conditions because most of their structure is exposed to the atmosphere, and the roots that encounter hypoxic conditions in the water and sediments are supplied with oxygen from above (McKee, 1993). Like seagrasses, mangrove trees are able to transport oxygen to roots and rhizomes, a process that can locally oxygenate the rhizosphere, reduce sulphide concentrations, and alter microbial communities at the scale of centimetres (McKee, 1993; McKee et al., 1988). However, oxygen can be limiting for mangrove performance, and the effects of hypoxia on mangrove trees varies by species. For example, young

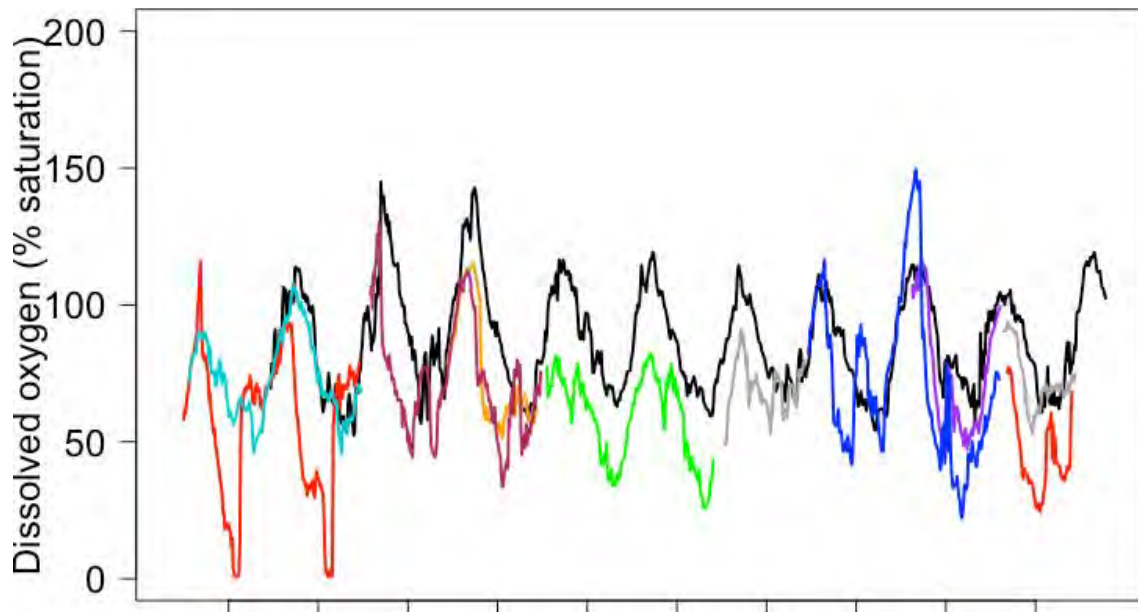


Figure 8.8.13 Diel cycling of oxygen in ponds that are isolated by mangroves. Diel cycling is evidence of biological oxygen demand where a system turns from a net producer of oxygen to a net consumer of oxygen under light limiting conditions. Coloured lines represent a sequence of monitoring periods in several mangrove ponds, and the black line represents conditions in a nearby seagrass bed. From Gedan et al. (2017).

seedlings of the red mangrove *Rhizophora mangle* (Figure 8.8.12A), which lives at frequently inundated depths, can tolerate hypoxia, but seedlings of the black mangrove *Avicennia germinans* (Figure 8.8.12B) and white mangrove *Laguncularia racemosa*, which tend to predominate at higher elevation and more inland areas of neotropical mangrove forests, are less tolerant of hypoxic stress (McKee, 1993, 1996).

Short-duration hypoxia or anoxia naturally occurs in many mangrove subhabitats, as demonstrated by studies of dissolved oxygen patterns in mangrove forests in remote locations and undisturbed watersheds. Diel-cycling hypoxia is common in shallow, aquatic mangrove ponds (Figure 8.8.13) (Gedan et al., 2017) and pools in the mangrove forest interior (Mattone & Sheaves, 2017). The diel-cycling pattern in dissolved oxygen is a reflection of daytime photosynthesis and nighttime respiration that depletes dissolved oxygen concentrations (Baumann et al., 2015; Nixon & Oviatt, 1973). Short duration hypoxia also occurs in high intertidal areas that are submerged for only a portion of the day on flood tides. Tide pools form in these basin interior areas during ebb tides, when most of the dissolved oxygen delivered with the tide is consumed by microbial and benthic communities (Knight et al., 2013; Mattone & Sheaves, 2017).

On monthly time scales, spring flood tides bring more oxygenated water to the hypoxic areas of the mangrove interior than neap tides (Mattone & Sheaves, 2017),

although the opposite pattern has also been observed in a Malaysian mangrove estuary, when spring tides were high enough to liberate hypoxic water trapped in tidal creeks and resuspend sulphide-laden sediments that consume dissolved oxygen (Figure 8.8.14) (Okamura et al., 2010). In either case, dissolved oxygen is most readily consumed in the interior of the mangrove forest and hypoxic water is exported towards the mouth of the estuary where it mixes with more oxygenated water. This phenomenon creates a down-estuary dissolved oxygen gradient in many mangrove forests (Figure 8.8.14) (Mattone & Sheaves, 2017; Okamura et al., 2010). As with many coastal and estuarine environments, inundation, connectivity, and tidal flushing alleviate hypoxic conditions towards the edge of mangrove stands, whereas isolation in pools and reduced tidal influence exacerbate hypoxic conditions in the interior of mangrove forests (Figure 8.8.14) (Knight et al., 2013; Mattone & Sheaves, 2017).

This spatial pattern sets up a gradient of environmental stress and can structure the distribution of species living in mangrove ecosystems at various scales. Many more aquatic species can tolerate the dissolved oxygen conditions at the mangrove fringe and mouth of tidal creeks than conditions in the basin interior or heads of tidal creeks, thus establishing gradients in the diversity of macrofauna at the scale of metres or kilometres (Knight et al., 2013; Okamura et al., 2010). The aquatic species that live in the mangrove interior must be extremely

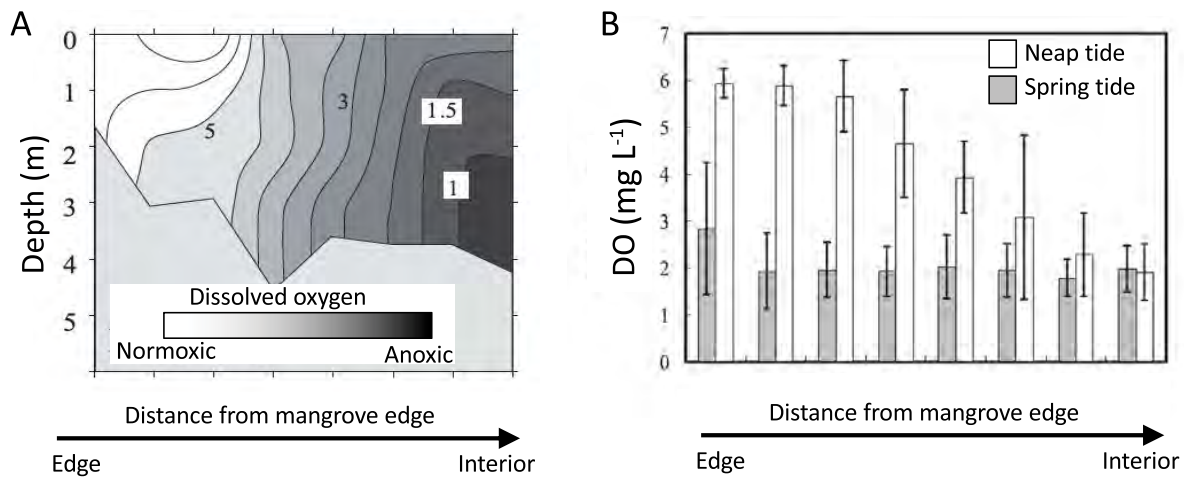


Figure 8.8.14 (A) Spatial gradient of hypoxia in a mangrove forest. Isolation of water in the interior of a mangrove stand inhibits flushing and reoxygenation by surrounding waters. (B) The role of limited water exchange in contributing to hypoxic conditions is evident from the establishment of hypoxic conditions at only at the most interior sites during the neap tides (when the tidal volume is relatively low). During spring tides, hypoxic water was liberated from isolated creek sheds to result in widespread hypoxia in this system. From Okamura et al. (2010).

tolerant of hypoxic conditions. Notable examples include the well-studied amphibious mangrove killifish, *Kryptolebias marmoratus*, which leaves the water to escape episodic hypoxia (Figure 8.8.15), and fish that surface-breathe which are common in mangrove forests (Dunson & Dunson, 1999). Some common mangrove fishes, such as the sailfin molly and sheepshead minnow, can tolerate more than a day at low oxygen saturation (Peterson, 1990). There has been little research into the movement of species in response to hypoxia in mangrove ecosystems, but mobile species likely migrate between various subhabitats to reduce hypoxia exposure as in other ecosystems (Breitburg et al., 2009).

Overlain on these natural dynamics and spatial patterns in mangrove ecosystems, anthropogenic eutrophication and shoreline development can exacerbate hypoxia



Figure 8.8.15 The mangrove killifish, *Kryptolebias marmoratus*, leaves water to escape hypoxic conditions that frequently occur in mangrove habitats. Image reprinted with permission from Turko & Wright (2015).

in mangrove ecosystems. Anthropogenic inputs may exceed the limits of macrofaunal survival in many mangrove microhabitats. For example, sewage effluent in a formerly oligotrophic tidal creek in Darwin, Australia amplified the diel-cycle of hypoxia and reduced dissolved oxygen saturation to half that of a reference creek (Smith et al., 2012). Similarly, Krebs et al. (2014) found a higher frequency of hypoxia in urban mangrove tidal creeks than in non-urban watersheds in Tampa Bay, Florida, USA. Untreated sewage disposal in Brazilian mangrove streams elevated nutrient levels and caused severe hypoxia and regular anoxia with mean DO concentrations below 1 mg L⁻¹ (Aguir et al., 2011).

Shrimp ponds (Figure 8.8.16) constructed in mangrove forest are viewed as the greatest anthropogenic threat to mangrove ecosystems (Alongi, 2002; McLeod & Salm, 2006). The tremendous expansion of shrimp aquaculture in the 1980s and 1990s converted an estimated 50% of the mangroves in Thailand and China (Spalding et al., 2010) and 17% in Peru (Mialhe et al., 2013) to ponds. Shrimp ponds reduce estuarine circulation and water quality, and thereby also promote diel-cycling hypoxia within mangroves (Johnston et al., 2002; Stram et al., 2005). The vast majority of these ponds are quickly abandoned when water quality degrades (Ewel et al., 1998; McLeod & Salm, 2006). Moreover, the effluent from shrimp farming, estimated to be 43 billion tons of wastewater in China alone (Biao & Kaijin, 2007), represents a major source of pollution that can promote hypoxia in adjacent habitats (Dierberg & Kiattisimkul, 1996; Paul & Vogl, 2011).



Figure 8.8.16 Shrimp farms in Phang Nga bay, Thailand. © Stephane Bidouze.

8.8.4 Ecosystem consequences

8.8.4.1 Coral reefs

Aside from the direct impacts of hypoxia on coral reef organisms, hypoxia also has indirect effects, such as through the abundance of algae and spread of coral diseases in coral reef ecosystems. While corals in some locations, especially at low flows, routinely experience hypoxia at night (Gardella & Edmunds, 1999; Goldshmid et al., 2004; Kuhl et al., 1995; Nilsson et al., 2004; Ohde & van Woerik, 1999; Shashar et al., 1993; Wild et al., 2008), hypoxic conditions are also present in the interaction zone between corals and algae during the day (Barott et al., 2009; Haas et al., 2013; Smith et al., 2006) (Figure 8.8.7). The hypoxia that develops in coral-algal interfaces can have severe negative consequences for corals, including bleaching (Barott et al., 2009) and death (Smith et al., 2006). Algae, in contrast, are significantly more tolerant to extremely low oxygen conditions (Haas et al., 2014). Therefore, natural or anthropogenic stressors that increase algal biomass or productivity could result in feedbacks that promote further coral mortality and the spread of algae.

This feedback is reinforced by coral diseases, such as black band disease (BBD) (Figure 8.8.17), which kills underlying coral tissue through the high concentrations

of sulphide and hypoxic conditions produced by the BBD mat (Carlton & Richardson, 1995; Glas et al., 2012). The rate at which BBD mats spread is correlated with oxygen depletion (Glas et al., 2012). Not only does BBD create localized zones of hypoxia that kill corals, but also BBD is more common at reefs repeatedly stressed by larger-scale hypoxic events (Onton et al., 2011). Thus, reefs that undergo frequent hypoxic events are more likely to have a higher incidence of disease.

Interactions between coral, algae, and disease are integrated within the Dissolved Organic Carbon (DOC), Disease, Algae and Microbes (DDAM) model, which explains how hypoxia, algae, and disease are linked in a positive feedback loop that results in coral degradation (Barott & Rohwer, 2012; Dinsdale & Rohwer, 2011; Gregg et al., 2013). Algae release DOC, which stimulates rapid microbial growth, creating localized hypoxic zones, which results in increased coral disease and mortality, leading to bare space for the recruitment of even more algae, thus perpetuating the loop (Barott & Rohwer, 2012; Dinsdale & Rohwer, 2011; Gregg et al., 2013) (Figures 8.8.7 and 8.8.18).

The fish and invertebrates that inhabit coral reefs exhibit a wide variety of behavioural and physiological responses to hypoxia. Mobile reef organisms often respond to hypoxia by moving upward to find more oxygenated water. For example, moray eels and other bottom-dwelling reef



Figure 8.8.17 Progression of black band disease (BBD) sweeping over a coral colony. BBD depletes oxygen at its leading edge which contributes to coral death. BBD is also more prevalent in areas that experience reef-scale hypoxia. Image reprinted with permission from Rogers et al. (2008).

fishes have been observed swimming at the surface of the water during a hypoxic event (Simpson et al., 1993). In response to severe hypoxia, some reef fish enter a phase of metabolic and ventilatory depression (Routley et al., 2002). Mobile reef invertebrates have been observed migrating out of crevices and burrows to the surface of the substratum (Figure 8.8.19) (Altieri et al., 2017; Laboy-Nieves et al., 2001; Simpson et al., 1993) or moving to the tips of arborescent coral colonies (Johnson et al., 2018; Simpson et al., 1993) in severely hypoxic conditions. Relatively little is known about the metabolic adaptations of reef invertebrates to hypoxia, but generally invertebrates demonstrate depression of activity (Diehl et al., 1979), reduced feeding (Bell et al., 2003; Llanso & Diaz, 1994; Tamai, 1993), metabolic depression (Rutherford & Thuesen, 2005), and/or altered heart rates (Harper & Reiber, 1999) in response to low oxygen levels.

Reef fishes that form obligatory associations with living corals and inhabit the nocturnally hypoxic spaces within branching coral colonies (e.g. *Gobiodon histrio*) (Figure

8.8.20) and generally exhibit a greater hypoxia tolerance than other reef fish (Nilsson et al., 2004, 2007). Among coral reef invertebrates, there are limited data on the differences in hypoxic tolerances among species, but there is considerable variation in susceptibility, with some species undergoing mass mortalities during severe hypoxic events while others appeared unaffected (e.g. Adjeroud et al., 2001; Laboy-Nieves et al., 2001). In general, predicting the response of coral reef organisms to hypoxia is challenging given the large variability of lethal and sublethal thresholds among benthic taxa (Vaquer-Sunyer & Duarte, 2008). Under-reporting of hypoxic events in the tropics (Altieri et al., 2017) and the difficulty of sampling reef diversity (Plaisance et al., 2011), suggests the impacts of hypoxia on most coral reefs organisms remains largely undetected or poorly understood.

8.8.4.2 Seagrass beds

Deoxygenation both directly and indirectly affects the biodiversity of seagrass ecosystems. Directly,

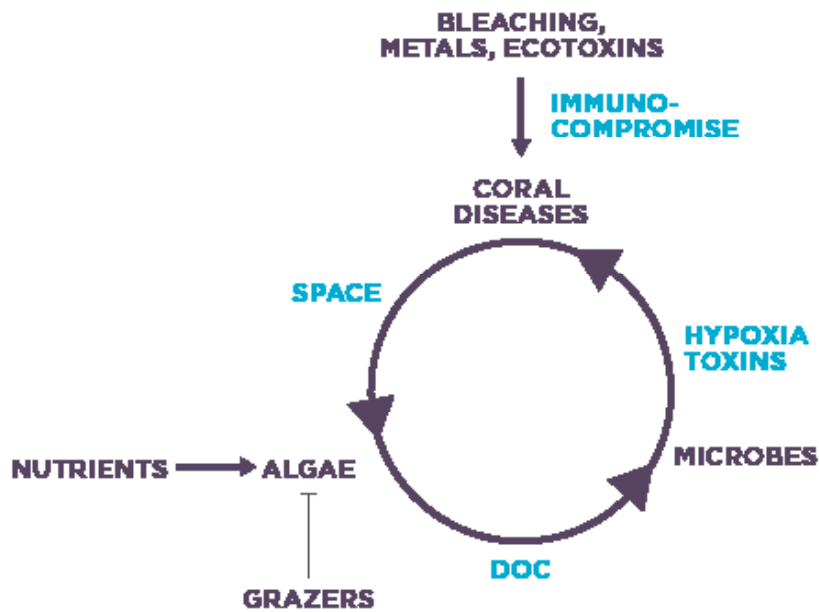


Figure 8.8.18 The 'DDAM loop', in which oxygen depletion plays a critical link in a feedback loop that includes anthropogenic factors such as climate change, overfishing, and eutrophication that leads to coral mortality through algal overgrowth through microbial proliferation. From Dinsdale and Rower (2010).

deoxygenation can reduce the diversity of organisms inhabiting seagrass beds by eliminating species that cannot tolerate low oxygen conditions. For example, experimental anoxia in a *Posidonia oceanica* meadow in north-west Spain resulted in an immediate reduction of metazoan meiofauna richness (Gambi et al., 2009). Indirectly, the loss and degradation of seagrass due to deoxygenation threatens the numerous species that rely on seagrass habitat for shelter or food. Overall, about one third of seagrass-associated species are listed as threatened on the IUCN Red List, in many cases related to a decline in seagrass habitat (Short et al., 2011).

The loss of seagrass affects not only the biological communities that inhabit seagrass ecosystems, but also the physical characteristics and resilience of seagrass ecosystems. For example, die-offs of the dominant seagrass *T. testudinum* in Florida Bay has resulted in elevated nutrient levels and increased turbidity due to available nutrients and suspended sediment that were previously taken up or trapped by seagrass beds (Durako, 1994). Increased turbidity decreases the light available for seagrass photosynthesis (Hemminga & Duarte, 2000), which affects the ability of seagrass to recolonize areas where mass mortality events have occurred.

8.8.4.3 Mangroves forests

Some studies have attributed a low density of aquatic organisms in mangrove forests to hypoxia, and

recognized the harsh hypoxic conditions as a barrier to fish moving upstream (Mattone & Sheaves, 2017; Okamura et al., 2010). By comparing mangrove ponds on the Caribbean coast of Panama that varied in magnitude of diel-cycling hypoxia, Gedan et al. (2017) found reduced fish diversity in ponds with higher magnitude diel swings, and noted that echinoderms were largely absent from all ponds. However, they observed a rich community of benthic invertebrates and macroalgae that apparently tolerate regular exposure to short-duration hypoxia (Gedan et al., 2017).

Spatial gradients in hypoxia in mangroves (Figure 8.8.14) shape the landscape of secondary production. Due to the frequent hypoxic conditions, the mangrove forest interior does not provide the fish habitat or fishery benefits of fringe or riverine mangroves (Ewel et al., 1998). When the ecosystem is perturbed to more extreme hypoxia, ecosystem function can collapse. In Australia, eutrophication and hypoxia were associated with higher phytoplankton productivity, accumulation of a dense algal mat, and fish kills (Smith et al., 2012).

Despite the established links between eutrophication and hypoxia, it can be difficult to assess the overall effects of these processes on the fauna associated with mangroves, in part due to the contradictory effects of nutrient enrichment and hypoxia (Breitburg et al., 2009). For example, in the mangrove tidal creeks of Tampa Bay, the body condition and abundance of grass shrimp were higher in developed, relative to undeveloped,



Figure 8.8.19 Brittlestars and gastropods, normally hidden in cryptic spaces on a coral reef, attempting to flee low-oxygen conditions during a hypoxia event that affected coral reefs on the Caribbean coast of Panama in 2017. Hypoxia resulted in the mass mortality of brittlestars, gastropods, and other motile invertebrates. © Dr Maggie D. Johnson.

watersheds, whereas killifish and sheepshead minnows showed the opposite pattern (Krebs et al., 2014).

Overall, mangrove fauna is much more tolerant of environmental stresses including hypoxia than coral reef- and seagrass-associated fauna. In an illustrative example, a stressful upwelling event in a Venezuelan estuary that reduced DO, water temperatures, and salinity annihilated up to 98% of the corals at locations within the estuary, but mangrove prop root communities were unaffected (Laboy-Nieves et al., 2001). This may be a result of the foundation species in mangrove forests, the mangroves themselves, being more resistant to aquatic hypoxic conditions because they are partially exposed to air.

8.8.5 Societal consequences

8.8.5.1 Coral reefs

Around six million people, the majority of whom live in developing countries, depend on coral reef fisheries which can account for 51–94% of the total animal protein consumed (Bell et al., 2009; Teh et al., 2013). Mass die-offs due to extreme hypoxic events can have severe impacts on reef fish populations. For example,

a hypoxic event on Ningaloo Reef (western Australia) in 1989 resulted in over one million dead fish washed ashore (Simpson et al., 1993), and over 200,000 dead fish within a couple days in 2012 in the hypoxic lagoon surrounded by the South Keeling Islands (Hobbs & Macrae, 2012). These massive hypoxic fish kills can result in local extirpation of some fishes, as observed on the west Florida shelf where five species of demersal fish failed to recolonize artificial reefs within the two years following a red tide that resulted in massive fish kills (Dupont et al., 2010). In remote settings, such as islands in the Pacific where there is a limited range of crops and animal protein available locally or through import (Bell et al., 2009), the loss of fish due to hypoxic dead zones events presents a serious threat to food security and nutrition.

Aside from providing seafood products, coral reef ecosystems provide a variety of essential ecosystem services, including shoreline protection, nitrogen fixation, waste assimilation, and tourism opportunities (Moberg & Folke, 1999). Given the dependence of such ecosystem goods and services on biodiversity and biomass, the mortality and loss of coral diversity due to hypoxia will likely have a variety of cascading social consequences.

8.8.5.2 Seagrass beds

Seagrasses also provide nursery grounds and habitat for many harvested commercial, recreational, and subsistence fish and shellfish (Beck et al., 2001; de la Torre-Castro & Ronnback, 2004; Heck et al., 2003; Unsworth & Cullen, 2010; Watson et al., 1993). In many tropical regions, such as East Africa and the Indo-Pacific, local people are dependent on seagrass-associated fisheries for their livelihoods and as a source of animal protein (de la Torre-Castro & Ronnback, 2004; Samonte-Tan et al., 2007; Unsworth & Cullen, 2010). The loss and deterioration of seagrass meadows due to stressors, such as hypoxia, could threaten the food security and income of these communities (Unsworth & Cullen, 2010).

In addition to furnishing food, habitat, and nursery grounds for many seagrass-associated species valued by humans, seagrass meadows provide a plethora of ecosystem services including water purification, coastal protection and erosion control via sediment stabilization, nutrient and carbon sequestration, and delivery of trophic subsidies to adjacent marine and terrestrial habitats (Barbier et al., 2011; Heck et al., 2008; Orth et al., 2006). The decline of seagrass habitats due to hypoxia threatens the ability of these ecosystems to provide essential goods and services.

8.8.5.3 Mangrove forests

Given that mangroves themselves are tolerant of low oxygen conditions, ocean deoxygenation will have minimal direct societal impacts through changes in mangrove distributions and abundances. However, hypoxia is likely to affect the organisms that inhabit mangroves, including fish, which can be an important



Figure 8.8.20 *Gobiodon histrio* a species that exhibits greater hypoxia tolerance than other reef fish © Roberto Nistri / Alamy stock photo.

source of food and livelihood for local human populations (Ronnback, 1999). Since mangrove nurseries can supply half or more of the fish on nearby coral reefs (Mumby et al., 2004), deoxygenation of mangrove habitats is likely to affect the ecosystem services of adjacent habitats as well. Moreover, the factors that promote deoxygenation in mangrove ecosystems such as eutrophication, removal of mangroves and associated filtration capacity, and creation of shrimp farms have a number of well-recognized negative effects on human well-being (MEA, 2005b). Even with the apparent localized benefits of some activities such as shrimp farming, which offers substantial employment opportunity (e.g. 10,000 jobs in coastal Peru; Mialhe et al., 2013), the environmental costs grossly outweigh the economic benefits in any comprehensive economic analysis (Gunawardena & Rowan, 2005).

8.8.6 Implications of continuing ocean deoxygenation

8.8.6.1 Coral reefs

The continued decline of oxygen in the ocean is worrying because the recovery of reefs following hypoxic mass mortality events can take years (Dupont et al., 2010) to decades (Smith, 1975) due to the slow-growing nature of corals. Compared to many other types of disturbances on coral reefs (e.g. overfishing, crown-of-thorns starfish outbreaks, disease epidemics), the long-term effects of hypoxia on reefs are likely to be more severe because hypoxia simultaneously affects a broad range of taxa including consumers, habitat formers, and microbes (Altieri et al., 2017). Recolonization of some taxa (e.g. benthic algae, polychaetes, fishes) on coral reefs can be relatively rapid, while others (e.g. corals, echinoderms, molluscs) are slower to recover and may take decades (Banner, 1968; Dupont et al., 2010; Smith, 1975). Regardless of the rate of recovery, the community that establishes during recovery from a severe hypoxia event is unlikely to be identical to the community that preceded the deoxygenation due to hysteresis (Diaz & Rosenberg, 2008; Nelson et al., 2016). Whether a reef will shift from a coral-dominated to an algal-dominated state following a hypoxia-driven mass mortality of coral depends, in part, on whether sufficient grazing pressure is present (Kuempel & Altieri, 2017).



Figure 8.8.21 Mangroves converted to shrimp ponds contribute to hypoxic conditions in surrounding waterways and create ideal conditions for oxygen depletion within the ponds themselves. Image credit: Ilka Feller made possible by LightHawk.

8.8.6.2 Seagrass beds

Continued ocean deoxygenation is concerning because the effects of hypoxia will be compounded by climate change, which could accelerate rates of seagrass decline. There is some evidence that seagrass species can recover following prolonged deoxygenation and short-term, extreme anoxia events. For example, increases in seagrass coverage have been linked to significant reductions in anthropogenic nitrogen loads in subtropical Southwest Florida estuaries (Tomasko et al., 2005). Following an anoxic crisis that caused widespread seagrass mortality in Thau Lagoon in the French Mediterranean Sea in 1999, seagrass recovered to previous biomass levels within nine months through colonization by surviving seedlings (Plus et al., 2003). However, consecutive anoxic events are expected to deplete seed banks and limit recovery potential (Plus et al., 2003), particularly in long-lived meadow forming genera such as *Thalassia* that may take decades to recover following disturbance (Walker et al., 2007).

8.8.6.3 Mangrove forests

Global attention to the problem of mangrove destruction for shrimp aquaculture (Figure 8.8.21) has highlighted

abandoned ponds as an opportunity for mangrove restoration (McLeod & Salm, 2006). Cessation of shrimp production and restoration of tidal hydrology can alleviate eutrophication and anthropogenic hypoxia from these areas. However, in many areas of the world, mangrove forest destruction for shrimp aquaculture and other land uses continues unimpeded (Lee, 2016). Where shrimp aquaculture is unregulated or poorly regulated, ponds will continue to become anoxic and unsustainable, contributing to hypoxia in mangrove ecosystems and eutrophication in adjacent estuaries (Lee, 2016).

8.8.7 Conclusions / Recommendations

While this review reveals an alarming number of mechanisms and examples by which hypoxia has a negative impact on coral, seagrass, and mangrove habitats, the greater message is that deoxygenation in tropical ecosystems is poorly documented and so many impacts are likely as of yet unrecognized. The actual number of tropical hypoxic ecosystems is likely underestimated by an order of magnitude, and a notable proportion (13%) of coral reefs and associated tropical habitats globally are at risk of being or becoming hypoxic (Altieri et al., 2017) (Figure 8.8.22). Trends in shoreline development, habitat loss, and

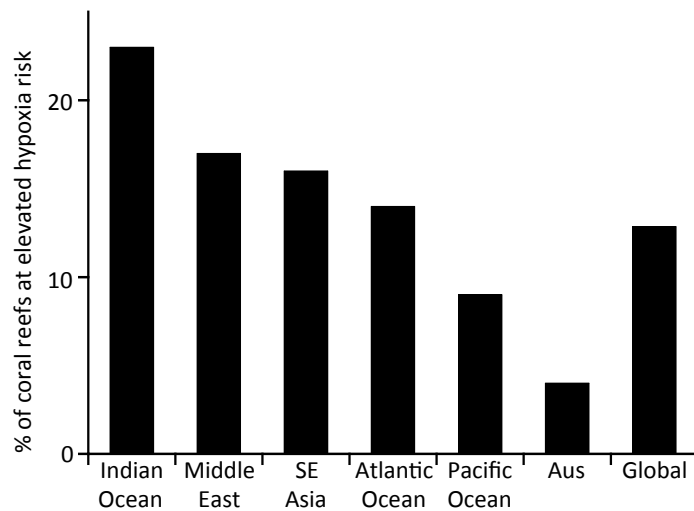


Figure 8.8.22 Percentage of coral reef ecosystems by ecoregions, and worldwide, at risk for hypoxia based on established databases of anthropogenic factors that contribute to hypoxia, including eutrophication and temperature, and coastal geomorphology that promotes stratification and limit exchange with the open ocean. From Altieri et al. (2017).

eutrophication in the tropics, combined with lessons learned from decades of hypoxia development in temperate ecosystems, suggests that the tropics are on a trajectory of increasing deoxygenation impacts but also that the effects are reversible if management efforts can be properly directed (Kemp et al., 2009). There are also some important distinctions regarding hypoxia in the tropics related to temperature, climate dynamics, and the dominant ecological role of biogenic habitats. The deficit of hypoxia research in the tropics and recent documentation of hypoxic events should motivate increased monitoring and research on the topic and its clear links to the well-being of human populations in tropical coastal areas. Below are several important themes to guide future research and management of ocean deoxygenation in tropical ecosystems.

8.8.7.1 Habitat interactions

The focus of this section has been on coral reefs, seagrass beds, and mangrove forests because of their critical role in tropical coastal ecosystems and their importance in mediating the effects of ocean deoxygenation. For simplicity corals, seagrasses, and mangroves are addressed separately in many of the subsections above. However, it is important to recognize that these three habitats often occur in close spatial association and are tightly linked through the exchange of energy, materials, and organisms (Gillis et al., 2014; van de Koppel et al., 2015) (Figure 8.8.23). As a consequence, the spatial configuration of these habitats can influence oxygen dynamics through the import/export of materials and the movement of water.

By reviewing these habitats in concert, there are also commonalities that become apparent owing to the structure and function of their foundation species: they are living organisms susceptible to ocean deoxygenation, they have the potential to modify oxygen conditions in and around their structures through their own metabolic gas exchange and modification of flow, and they play host to diverse communities and symbioses that are vulnerable to hypoxia. The generality and fundamental nature of these functions across habitat types suggests tropical ecosystems demand increased management and research to confront the ocean deoxygenation crisis. They also suggest that lessons learned in one habitat may apply to the others which should accelerate further development of a general understanding to govern management and direct future research.

8.8.7.2 Multiple-stressors

A multiple-stressor perspective (Breitburg & Riedel, 2005; Crain et al., 2008) should be applied to ocean deoxygenation in the tropics since hypoxia commonly co-occurs with other stressors. Two co-stressors that are particularly relevant are temperature and acidification because of their interactive physiological effects and their association with the origins of hypoxia, as evident in coral reefs (Nelson & Altieri, 2019). Increased temperatures often drive hypoxic conditions through a variety of mechanisms including decreased oxygen solubility in water and enhanced sediment and macrophyte respiration that consumes oxygen as observed in seagrass beds (Marsh et al., 1986; Zimmerman et al., 1989). The respiration that depletes

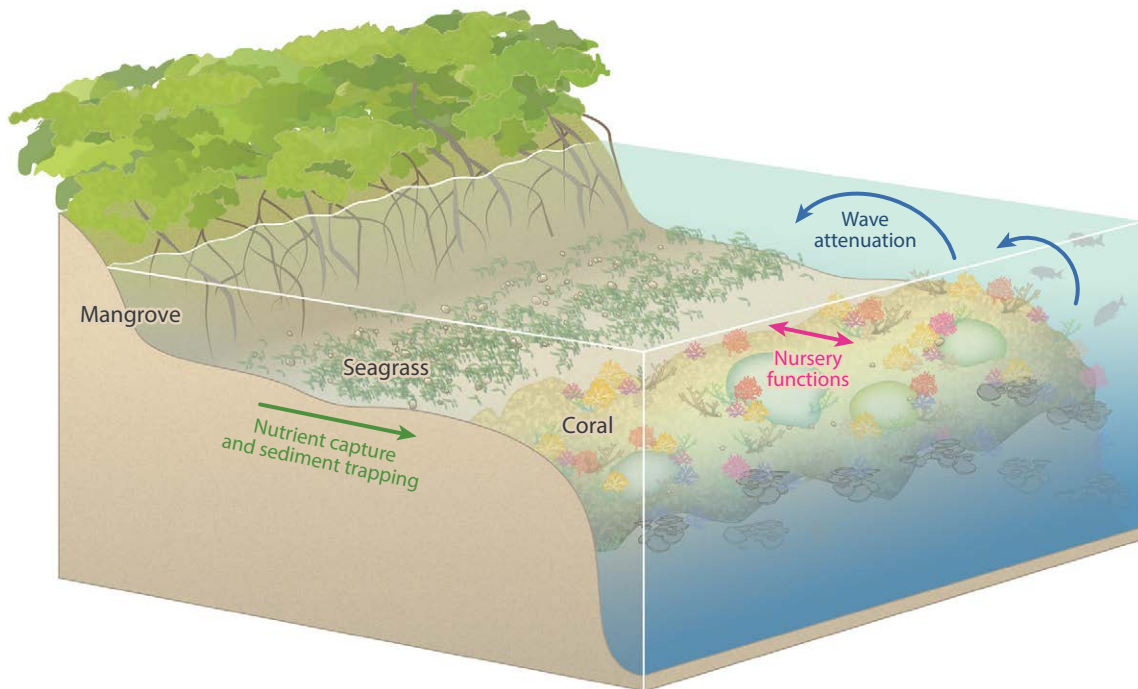


Figure 8.8.23 Various resource exchange and habitat modifications that connects coral reef, seagrass, and mangrove ecosystems. Inputs of nutrients and organic material, as well as the limited exchange from wave attenuation, contribute to oxygen dynamics in each. From van de Koppel et al. (2015).

oxygen also produces carbon dioxide which will locally drive down pH such that oxygen and pH often cycle together, as observed in mangroves (Gedan et al., 2017). The progression of climate change and ocean acidification, and increased vulnerability of organisms to hypoxia under elevated temperatures and increased acidity, suggests that the effects of continuing ocean deoxygenation on tropical marine organisms will become more severe with time.

The synergistic effects of temperature and hypoxic stress have been well documented in temperate organisms as higher temperatures lead to lower tolerance for hypoxia (Vaquer-Sunyer & Duarte, 2011) due in part to increased metabolic demands for oxygen and the oxygen limitation of thermal tolerance (Pörtner, 2010). A first step in developing a broader understanding of the synergisms between temperature and hypoxia tolerance in tropical ecosystems will be establishment of a basic quantitative assessment of their combined effect on mortality as has been done primarily for temperate species (Vaquer-Sunyer & Duarte, 2011). This would determine if the taxa that dominate tropical ecosystems differ in some consistent way, perhaps because of differing evolutionary histories and/or prior exposures to hypoxic environments. Over 90% of documented hypoxic marine ecosystems are in areas predicted to experience over 2 °C warming by the end

of this century due to climate change (Altieri & Gedan, 2015). Many tropical species already exist near the edge of their tolerance to oxygen and temperature extremes with narrower tolerances for fluctuations than their temperate counterparts (Johannes & Betzer, 1975). As a consequence, estimates suggest that groups such as tropical seagrasses are at significant risk of local extinction due to combined thermal and low oxygen stress in areas that experience warming (Pedersen et al., 2016).

Ocean acidification (OA) is of particular concern in tropical ecosystems because of the dependence of coral reef construction on calcification that is negatively affected by declines in pH. While a large and growing body of research has considered the synergistic impacts of OA and climate change (Hoegh-Guldberg et al., 2017; Koch et al., 2013; Kroeker et al., 2013), far less has considered the interactions of OA and deoxygenation for coral reefs or other tropical ecosystems. Where they have been examined together experimentally, it was found that hypoxia and low pH acted synergistically to decrease photosynthesis and survivorship of corals (Weber et al., 2012). Dissolved oxygen and pH often co-vary where local respiration rates deplete oxygen and supply carbon dioxide, often reaching or exceeding values not expected in the open ocean for decades or centuries to come (Figure 8.8.24). This local production

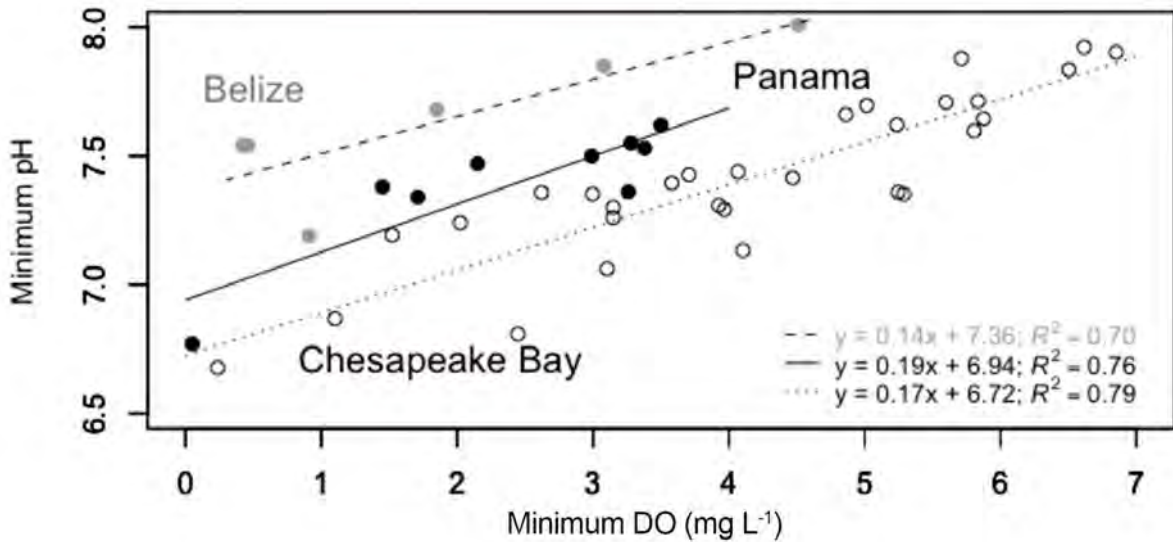


Figure 8.8.24 Correlation between oxygen depletion and pH depression in mangrove ponds. The relationship illustrates the common mechanism (i.e. aerobic respiration) that consumes oxygen and produces carbon dioxide and leads to co-occurring hypoxia and acidification stress. From Gedan et al. (2017).

of carbon dioxide and resultant respiration-driven acidification has the potential to exacerbate the ocean acidification driven by global process, and also offers an opportunity for comparative studies of variation in pH over relatively small spatial and temporal scales. On the other hand, consumption of dissolved carbon dioxide and production of oxygen through photosynthesis by tropical foundation species has the potential to locally counteract the effects of an acidified and hypoxic environment. For example, it has been hypothesized that seagrass beds might provide a local refuge for calcifying organisms such as corals by drawing down carbon dioxide within their canopies, and they may do the same for hypoxic stress if their super-saturation of

oxygen in the water column during the day provides at least temporary relief from hypoxic stress (Hendriks et al., 2014). Further research is needed to understand how the physiological effects of oxygen, temperature, and pH (along with salinity and other potential stressors) interact with one another and are modified by foundation species in the tropics.

8.8.7.3 Feedbacks and hysteresis

Mortality and shifts in community composition due to hypoxic conditions at the ecosystem scale can initiate further changes in biogeochemical processes and oxygen depletion. Known examples from tropical

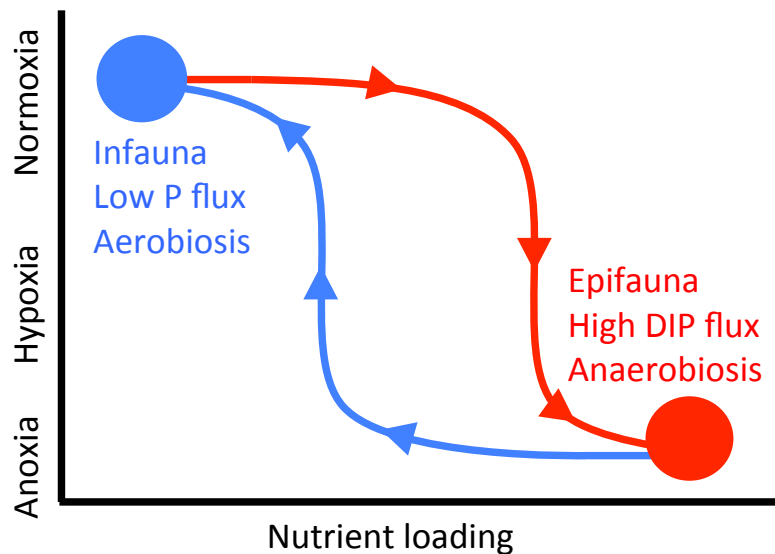


Figure 8.8.25 Diagram of hysteresis in hypoxic ecosystems. Due to feedbacks between oxygen concentration and changes in microbial processes, the return pathway (blue) can differ from the initial impact (red) such that the response to given level of driver can differ and be dependent on prior state. From Conley et al. (2009).

ecosystems include the production of organic material following hypoxia-induced seagrass mortality that fuels further oxygen depletion (Bjork et al., 2008), or the increase in coral death and algal production associated with anaerobic pathogens that further starve environments of oxygen (Dinsdale & Rohwer, 2011) (Figure 8.8.18). These feedbacks can lead to hysteresis in which achieving the threshold value for eutrophication needed to reverse hypoxic conditions may be lower and more difficult to achieve than values that initiated hypoxic conditions (Conley et al., 2009) (Figure 8.8.25). Studies of temperate soft sediment habitats have revealed other feedbacks between sediment oxygen conditions, microbial communities, nutrient cycling and availability, production of organic matter, and development of hypoxic conditions (Middelburg & Levin, 2009). Little is known about such shifts in biogeochemical process in tropical hypoxic ecosystems, and additional research on species tolerances and interactions (for both microbial and metazoan communities) will be necessary for elucidating the full suite of such feedbacks that further modify hypoxic conditions at the local scale.

8.8.7.4 Conclusion

Ocean deoxygenation is affecting tropical coastal ecosystems. Many identified hypoxic ecosystems are in countries at an early stage of economic development where lessons learned about links between agricultural intensification, water treatment, and hypoxia in advanced economies in temperate countries might inform

Deoxygenation in tropics, by the numbers:

- 75%: Percentage decline in coral diversity in a Panamanian hypoxic dead zone.
- 1,000,000: The number of dead coral reef fish following a single hypoxic event in Australia.
- 13%: Percentage of coral ecosystems worldwide at elevated risk from deoxygenation.
- 8.66 mg O₂ L⁻¹: Swing in dissolved oxygen concentration recorded in a mangrove pond over a 24-hour period from a low of 0.46 to a high of 9.12 mg O₂ L⁻¹.
- USD\$127 million: Value of ecosystem services loss from a single event of seagrass die-off associated with hypoxia in Florida.
- 370: Estimated number of undiscovered hypoxic ecosystems in the tropics.

management strategies to avoid future deoxygenation events (Kemp et al., 2009). The dependence of many tropical coastal societies on healthy coral reef, seagrass bed, and mangrove forest ecosystems for services including food provision, storm buffering, and tourism should be motivation for the international community to support the exchange of scientific capacity, management lessons, and intellectual capital. Given the apparent discovery deficit of hypoxic ecosystems in the tropics, it is urgent to document the extent of the problem and the consequences for ecological structure and function. Otherwise there is a risk that hypoxia will alter ecosystems before changes can be quantified, thus leading to “shifting baselines” (*sensu* Dayton et al., 1998) in which our understanding and management of some tropical ecosystems will be distorted by first observations in a degraded state.

8.8.8 References

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8.9 The significance of ocean deoxygenation for Elasmobranchs

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Summary

- All of the >1000 species of sharks, skates and rays are obligate water-breathers with comparatively high absolute oxygen demands being relatively large-bodied, active predators. With broad distributions across aquatic habitats exhibiting large variations in physico-chemical variables including oxygen concentration indicates elasmobranch physiology, behaviour and ecology to be strongly influenced by oxygen depletion.
- Many elasmobranchs show rapid behavioural responses to hypoxic water by increased activity associated with avoidance. Nonetheless, elasmobranchs also appear capable of withstanding mild hypoxia with circulatory and/or ventilatory responses, perhaps even for extended periods. However, such strategies may be insufficient to endure moderate, progressive or prolonged hypoxia or anoxia.
- As water temperatures rise with climate warming most elasmobranchs (as ectotherms) will exhibit elevated metabolic rates and will be increasingly less able to tolerate the effects of even mild hypoxia associated with ocean deoxygenation. Thus, sustained hypoxia in warmer coastal waters is likely to lead to shifts in elasmobranch distributions.
- Expansion of oxygen minimum zones (OMZs) of the open ocean in particular are predicted to have significant population-level implications for pelagic elasmobranchs as they become habitat compressed into surface layers by shoaling hypoxic water.
- Surface layers overlying OMZs appear to be space use hotspots of pelagic sharks that may be increasingly likely to undergo significant 'habitat compression' (reduced habitat volumes) with expanding OMZs, potentially increasing their susceptibility to surface fisheries, e.g. long-lining, leading to further risks of over-exploitation especially of threatened species such as shortfin mako (*Isurus oxyrinchus*).
- A priority for conservation is to mitigate ocean deoxygenation effects on elasmobranchs, such that future catch rates are controlled in the light of climate change rather than for exploitation to be exacerbated by ocean oxygen losses.

Ocean hypoxia effect	Potential consequences
Large-scale transport of oxygen depleted water, or eutrophication-induced hypoxia, in shallow water ecosystems may overlap entire movement ranges of individuals of less active species.	<ul style="list-style-type: none"> Leads to mortality of individuals from species with limited daily range (limited daily movement distances) or those exhibiting pronounced fidelity to particular locations, e.g. home range, spawning grounds.
Declining oxygen concentrations in current habitats may result in species-specific shifts in distribution and abundance patterns as well as changes to vertical niche.	<ul style="list-style-type: none"> Shifts in upper-trophic level relationships between elasmobranch predators and their prey, altering food web structure and stability. Spatial redistribution of coastal and open-ocean elasmobranchs both horizontally and vertically changing the location and intensity of interactions with fisheries with consequences for catch rates and management.
Shoaling hypoxic layers may result in species-specific vertical movement constraints and compression of vertical habitat into surface waters.	<ul style="list-style-type: none"> Altered geographic and vertical overlap with prey distributions that establish more persistent space-use hotspots of pelagic elasmobranchs closer to the surface Increased susceptibility to capture by surface fishing gears, e.g. long-lining.
The North Atlantic Ocean is projected to undergo large decreases in oxygen content within the upper water column, and in intermediate waters (100 – 1000 m) associated with OMZs.	<ul style="list-style-type: none"> Species occurring in this region, including currently overfished as well as internationally protected sharks, are predicted to undergo exposure to large declines in oxygen and pronounced shoaling of hypoxic layers of OMZs.

8.9.1 Introduction

The elasmobranchs (sharks, skates and rays; Subclass Elasmobranchii, literally “plate gills”) are cartilaginous fishes that, like the majority of all other fish, are obligate water-breathers reliant upon extracting oxygen from the surrounding water to meet metabolic demands. There are over 1,000 extant species of elasmobranch that arose sometime during *c.* 400 million years of independent evolution, with the main living families having first appeared sometime between the Permian and Jurassic Periods (~250–150 million years ago) (Young, 1981). Over that time elasmobranchs have evolved to occupy a very broad range of habitats within aquatic ecosystems worldwide: they are distributed in freshwater and estuarine systems and in the oceanic pelagic realm and the deep sea (to at least 4,500 m depth; Kyne & Simpfendorfer, 2010), and from polar Arctic seas (but not the Antarctic) in water temperatures of ~2 °C (Watanabe et al., 2012) through to low latitude coral reefs circumglobally (~30 °C). This broad distribution across aquatic habitats that exhibit large spatial and temporal variations in physico-chemical variables, including oxygen concentration, coupled with the relatively large body size and active predatory lifestyle of elasmobranchs indicates the physiology,

behaviour and ecology of sharks, skates and rays are likely to be strongly influenced by oxygen depletion.

Understanding how elasmobranchs will be affected by ocean deoxygenation is important not only for assessing the potential for altered distributions and abundance in relation to climate-driven changes (Deutsch et al., 2015), but also in determining how such environmentally induced changes may interact with commercial fisheries potentially to exacerbate exploitation rates. Life-history traits such as slow growth, late maturity and low fecundity make elasmobranchs less resilient to fishing pressure than bony fishes (Field et al., 2009). Many sharks, skates and rays are highly valued worldwide by fisheries and over-harvesting in some regions has led to declines in the population levels of numerous species (Baum et al., 2003; Ferretti et al., 2010; Worm et al., 2013) (Table 8.9.1). There is particular concern that target- and by-catch fisheries are depleting populations below sustainable levels where recovery may not be possible, or at best may be very slow, even if fishing pressure is removed (Field et al., 2009; Sims et al., 2018). An increasing number of elasmobranchs are being listed on the International Union for the Conservation of Nature (IUCN) Red List of threatened species, with some larger species of greater economic value now being listed on the Convention of International Trade in



Figure 8.9.1 Bull shark *Carcharhinus leucas*. © James Lea.

Endangered Species (CITES) (Dulvy et al., 2014) (Table 8.9.1). The conservation of elasmobranch populations may become increasingly difficult in the face of multiple pressures such as the expansion of industrialized fisheries, climate-driven changes in the ocean such as deoxygenation and, for many species, little or no sustainable management of stocks (Sims et al., 2018; Sims & Queiroz, 2016; Sims & Simpson, 2015).

Levels of dissolved oxygen in open ocean and coastal waters have been decreasing since at least the middle of the 20th century (Breitburg et al., 2018). Models predict climate-driven ocean warming and reduced ventilation of the deep ocean will lower levels of dissolved oxygen (DO) in the ocean by 1–7% by 2100, with *in situ* observations suggesting reductions of >2% since 1960 (Breitburg et al., 2018; Schmidtko et al., 2017). Permanent oxygen minimum zones (OMZ) across the world's ocean are increasing in area and volume as a result, with unknown consequences for ecosystems and biodiversity (Gilly et al., 2013; Mora et al., 2013; Stramma et al., 2008). Potential impacts may be particularly significant for large, active oceanic predators with high absolute oxygen demands because available habitats will become reduced, concentrating them further in surface waters where they may be more vulnerable to fisheries (Gilly et al., 2013; Prince & Goodyear, 2006; Prince et al., 2010; Stramma et al., 2011).

The effects of ocean deoxygenation on sharks, skates and rays is examined by considering what is known about their spatial overlap with hypoxic regions of the open ocean, including the so-called oxygen minimum zones, their physiological and behavioural responses to low oxygen concentrations, and how such responses may affect their vulnerability to open ocean fisheries.

8.9.2 Elasmobranchs and ocean deoxygenation

Dissolved oxygen (DO) has a major role in shaping marine ecosystems by determining the spatio-temporal distributions of all water-breathing marine organisms including fish (Gilly et al., 2013; Levin & Bris, 2015). Elasmobranchs are principally a marine taxon (only ~5% of species occur in fresh water) with the majority of species having range distributions associated with estuarine, coastal and shelf ecosystems. In shelf environments, naturally occurring processes such as seasonally high temperatures reducing oxygen solubility of water, and seasonal upwelling transporting oxygen-poor waters into shallow areas where respiration may further reduce DO, can both lead to chronic, episodic or prolonged hypoxia or anoxia in inner-shelf waters (<50 m depth) (Chan et al., 2008; Grantham et al., 2004) and estuarine habitats (Heithaus et al., 2009). Oxygen depleted water in shallow-water systems can also occur due to eutrophication-induced hypoxia (Breitburg et al., 2018; Diaz & Rosenberg, 2008). Both natural and anthropogenic-induced hypoxia have been recorded to change the distribution and abundance of fishes (Breitburg et al., 2018; Chan et al., 2008; Diaz & Rosenberg, 2008). Hypoxic waters occurring in shallow shelf areas have important consequences for major fisheries since some fish appear to respond by 'escaping' oxygen-poor environments, for example disappearance of rockfish (*Sebastes* species) from rocky reefs in the north-east Pacific Ocean during an anoxia event (Chan et al., 2008). OMZs intercepting shelf slopes in deeper water (>600 m) and oceanic seamounts far from continental landmasses can also result in dramatic changes in benthic and demersal fish vertical distributions (Chan et al., 2008; Wishner et al., 1990). However, hypoxic waters affecting the distributions, behaviour and ecology of sharks, skates and rays *in situ* are poorly documented by comparison, despite such events potentially overlapping the range distributions of many species. It is possible that large-scale coastal deoxygenation could result in mortalities of individuals of less active or wide-ranging elasmobranch species that are unable to move beyond the affected area, as has been observed for bony fish exposed to upwelling-driven nearshore hypoxia (Grantham et al., 2004). Nevertheless, the few studies that have been undertaken indicate large, active sharks appear to select habitats that are generally not oxygen depleted. For example, a comprehensive survey of bull sharks (*Carcharhinus leucas*) (Figure 8.9.1) in a subtropical

Table 8.9.1. Examples of threatened species of pelagic sharks with geographic distributions known to occur in waters above OMZs or in other areas projected to undergo oxygen losses over the coming decades. CITES: Convention on International Trade in Endangered Species of Wild Fauna and Flora; CITES 'II' denotes Appendix II listing with the year it was effective from. Data were accessed from the website of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (<<http://www.iucnredlist.org/>>; accessed May 2018).

Scientific name (common name)	Global IUCN Red List classification	Year of IUCN assessment	Population trend	Management measures	CITES listing effective from
Carcharhiniformes					
<i>Carcharhinus falciformis</i> (Silky shark)	Vulnerable A2bd	2017	Decreasing	Retention bans and live release are in place for all vessels operating under ICCAT and WCPFC management. IATTC and IOTC has prohibited retention of Silky Sharks on purse seine vessels, limited longline vessel bycatch.	II (2017)
<i>Carcharhinus galapagensis</i> (Galapagos shark)	Near Threatened	2003	Unknown	No management known to be in place.	
<i>Carcharhinus leucas</i> (Bull shark)	Near Threatened	2009	Unknown	No specific management programmes known. Managed in the U.S. east coast shark fisheries as part of the "large coastal" groups of species.	
<i>Carcharhinus longimanus</i> (Oceanic whitetip shark)	Vulnerable A2ad+3d+4ad	2015	Decreasing	Subject to protections under all the world's tuna-focused Regional Fishery Management Organisations (RFMOs). EEZs: Listed on U.S. Endangered Species Act. Protected in New Zealand.	II (2013)
<i>Galeocerdo cuvier</i> (Tiger shark)	Near Threatened	2009	Unknown	No specific conservation or management measures in place. EEZs: US Atlantic and Gulf of Mexico this species is managed under a Fisheries Management Programme.	
<i>Prionace glauca</i> (Blue shark)	Near Threatened	2009	Unknown	No species-specific catch limits or other protections in place in international waters for this species. Managed in EEZs of Canada, Mexico, USA (Atlantic, Gulf of Mexico) and New Zealand waters.	
<i>Sphyrna lewini</i> (Scalloped hammerhead)	Endangered A2bd+4bd	2007	Unknown	EEZs: Included in U.S. Large Coastal Shark complex management unit.	II (2014)
<i>Sphyrna mokarran</i> (Great hammerhead)	Endangered A2bd+4bd	2007	Decreasing	No known species-specific conservation measures in place. EEZs: Managed as a Large Coastal Shark on U.S. Highly Migratory Species Fishery Management Plan.	II (2014)
<i>Sphyrna zygaena</i> (Smooth hammerhead)	Vulnerable A2bd+3bd+4bd	2005	Decreasing	ICCAT region: Banned retention, trans-shipment, landing, storage, and sale of species in the family Sphyrnidae. EEZs: Managed as a Large Coastal Shark on U.S. Highly Migratory Species Fishery Management Plan.	II (2014)
Lamniformes					
<i>Alopias pelagicus</i> (Pelagic thresher)	Vulnerable A2d+4d	2009	Decreasing	IND: Prohibited to retain, transship or land in IOTC waters.	II (2017)
<i>Alopias vulpinus</i> (Common thresher)	Vulnerable A2bd+3bd+4bd	2009	Decreasing	ATL: Prohibited to target in ICCAT waters. IND: Prohibited to retain, transship or land in IOTC waters.	II (2017)
<i>Carcharodon carcharias</i> (Great white shark)	Vulnerable A2cd+3cd	2009	Unknown	EEZs: Protection in waters of Australia, EU, South Africa, Namibia, Israel, New Zealand, Malta and USA.	II (2005)
<i>Isurus oxyrinchus</i> (Shortfin mako)	Vulnerable A2abd+3bd+4abd	2009	Decreasing	N ATL: ICCAT 2017 Shortfin Mako Stock Assessment concludes "overfished and undergoing overfishing" and recommends zero TAC. Starting 2018 in NATL ICCAT waters can only retain if brought alongside dead (hence 'live release'). MED: Retention, transshipment, landing, display or sale prohibited. EEZs: Management in Australia, Canada, Chile, EU, New Zealand, USA.	
<i>Isurus paucus</i> (Longfin mako)	Vulnerable A2bd+3d+4bd	2006	Decreasing	No management measures in place for this species.	
<i>Lamna nasus</i> (Porbeagle)	Endangered A1abd	2006	Decreasing	EEZs: Management plans in waters of Canada and USA. Managed by quotas in New Zealand.	II (2014)

estuary in Florida, USA, showed they were highly responsive to reduced DO, being much more frequently caught in waters where DO was $>2.50 \text{ ml O}_2 \text{ L}^{-1}$ (Heithaus et al., 2009). Furthermore, Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) show little tolerance to hypoxia and move away from warm ($22 - 24 \text{ }^\circ\text{C}$) waters with reduced oxygen concentration ($\sim 2.86 \text{ ml O}_2 \text{ L}^{-1}$) seasonally in the north central Gulf of Mexico (Parsons & Hoffmayer, 2005).

Among large predators such as the majority of elasmobranchs, how variations in oxygen concentrations may alter behaviour and structure distributions in shelf seas has not been the subject of extensive studies (Heithaus et al., 2009). The impacts of ocean deoxygenation on elasmobranchs urgently requires more research given the environmental changes projected (Levin, 2018), and in addition to the high levels of exploitation of sharks, skates and rays in fisheries spanning coasts to the open ocean (Dulvy et al., 2014; Worm et al., 2013). In this context, the effects of expanding OMZs on pelagic shark and ray ecology and exploitation rates is emerging as a critical issue needing to be addressed given the potential for widespread population impacts that may already be occurring (Queiroz et al., 2016).

8.9.3 Ocean oxygen minimum zones

Global climate change has led to declines in DO in the ocean interior (ocean deoxygenation) that are predicted to continue (Keeling et al., 2010; Schmidtko et al., 2017). Therefore, the effects on marine biota are likely to be profound in regions projected to have significant oxygen concentration changes, such as in permanent OMZs where long-term DO declines are acute (Gilly et al., 2013) (Figure 8.9.2). Vast expanses of the world's ocean show strong vertical changes in oxygen levels (oxyclines), where DO initially decreases to low levels before rising again at greater depths (Gilly et al., 2013; Schmidtko et al., 2017). This reduction in DO delimits the OMZ, typically defined by concentrations of $20\text{--}90 \mu\text{mol O}_2 \text{ kg}^{-1}$ ($<0.47\text{--}2.11 \text{ ml O}_2 \text{ L}^{-1}$) and lower, and located in the depth range 200–800 m (Gilly et al., 2013). OMZs are globally distributed and comprise $\sim 5\%$ of ocean volume (~ 10 million km^3). They are associated with lower O_2 ventilation, increasing surface stratification and high primary production coupled with enhanced mesopelagic (200–1000 m) decomposition (Diaz & Rosenberg, 2008). However, as core oxygen values in the OMZ decline with ocean deoxygenation, the vertical

extent of the hypoxic layer thickens, that have resulted in geographic and vertical OMZ expansions over the past 50 years (Gilly et al., 2013; Stewart et al., 2014; Stramma et al., 2008).

Low-oxygen concentration water characterizing OMZs is seriously hypoxic for the vast majority of marine organisms (Vacquer-Sunyer & Duarte, 2008) prompting an urgent need to understand responses of marine biota to OMZ geographic and vertical expansions (Rosa & Seibel, 2008). Effects may include alteration of microbial processes that are key to nutrient cycling and gas fluxes (Levin & Bris, 2015), changing predator-prey dynamics (Stewart et al., 2013), and shifts in distributions, abundance and vulnerability of ecologically and commercially important fish species (Deutsch et al., 2015; Gilly et al., 2013; Prince & Goodyear, 2006; Prince et al., 2010; Stramma et al., 2011). OMZ expansion is accompanied by shoaling of the upper boundaries of the OMZs (Stramma et al., 2008) and this, in particular, is hypothesized to hold significant implications for fish ecology and fisheries (Gilly et al., 2013; Stramma et al., 2011), including, presumably, oceanic elasmobranchs. As OMZs shoal, acute oxygen gradients are expected to compress the habitat of pelagic fish against the layer of hypoxic water (Prince & Goodyear, 2006; Prince et al., 2010; Stramma et al., 2011) (Figure 8.9.2). This raises an important question: will expanding volumes of oxygen-depleted water, such as expanding OMZs, 'compress' oceanic sharks and rays in surface layers above expanding hypoxic waters, reducing their habitat space and potentially increasing their susceptibility to surface fisheries? Furthermore, if surface waters above OMZs are preferred habitats for pelagic elasmobranch foraging, given that prey species may be similarly habitat compressed, will these waters act as a 'habitat trap', further exacerbating interactions with surface fisheries?

Ocean deoxygenation occurring in oceanic regions away from continental landmasses will affect fewer elasmobranch species because only about 2.5% are oceanic (Compagno, 2008). However, if the preferred habitats of oceanic species such as the blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*) and giant manta ray (*Manta birostris*) (Figure 8.9.3), for example, are centred in areas where ocean deoxygenation occurs, then impacts may be significant for these threatened species. Oceanic sharks and rays are large-bodied predators that are also of high value to commercial, high-seas fisheries for their fins, meat and, in the case of *M. birostris*, their gill rakers. Hence, given

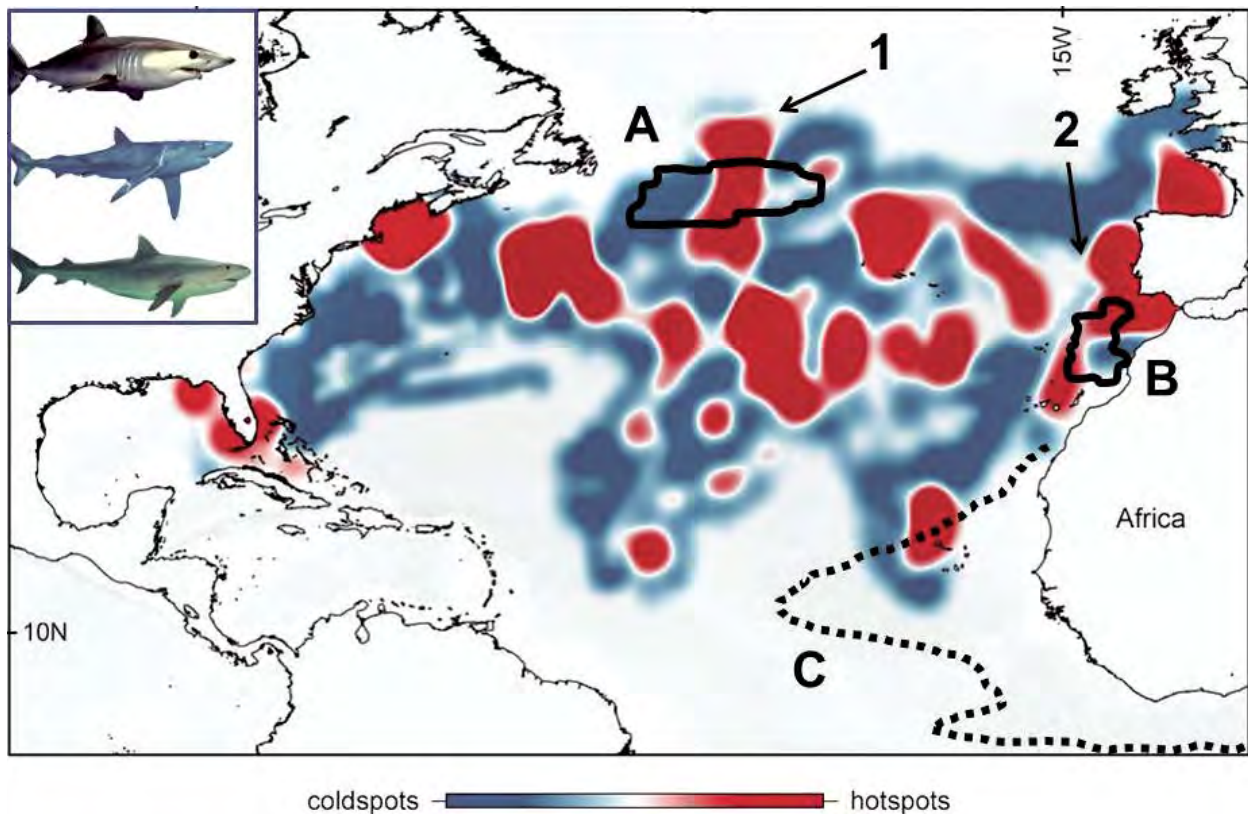


Figure 8.9.2 Oceanic space use hotspots of satellite-tracked pelagic sharks (shortfin mako, blue, tiger – shown in inset panel) overlapping with example areas of significant ocean deoxygenation in the North Atlantic. (A) Area projected from models to have O_2 losses of $>45 \mu\text{mol L}^{-1}$ (black lines), and (B) with losses of $30\text{--}40 \mu\text{mol L}^{-1}$, by 2090–99 compared to 1990–99 levels (mapped from Bopp et al., 2013). (C) Spatial extent of the eastern tropical Atlantic (ETA) OMZ as represented by the $3.5 \text{ ml O}_2 \text{ L}^{-1}$ at 100m contour (dashed black line). Shark hotspot map redrawn from Queiroz et al. (2016) where a higher cluster density (Z score) signifies a space-use hotspot. Shark images provided by Jeremy Stafford-Deitsch (mako, blue) and James Lea (tiger).

the relatively slow life-history traits, commercial value and significant catch rates of oceanic elasmobranchs, these are species for which there is particular conservation concern. But what evidence is there that preferred habitats of oceanic shark and ray overlap hypoxic zones in the open ocean?

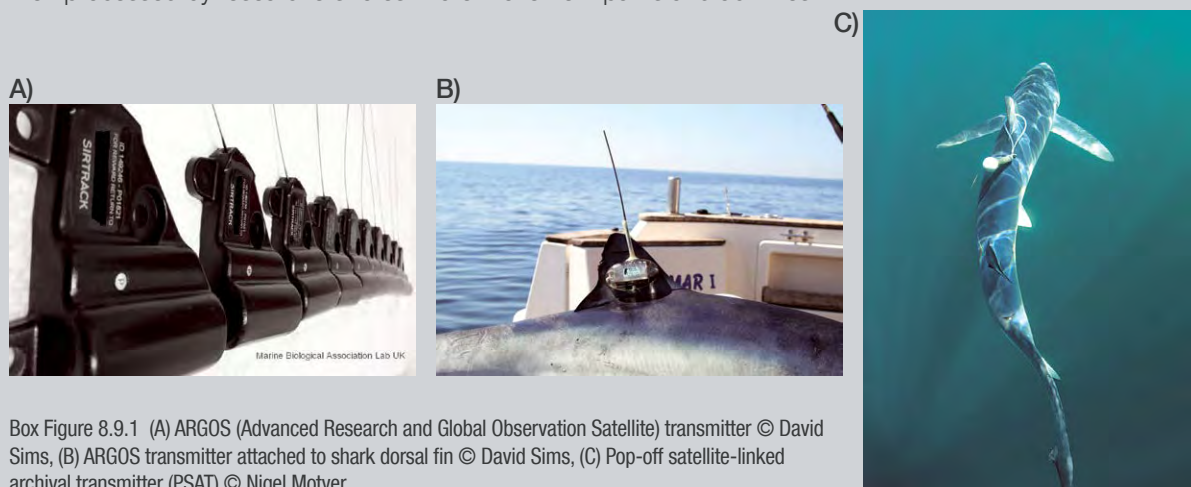
Only with the recent advances in miniaturized electronic tags for tracking fish at sea (Sims, 2010) have ocean-basin scale distributions of large oceanic sharks been possible to resolve at the fine-scale for multiple species over long-time periods (Block et al., 2011; Queiroz et al., 2016). Before then, elasmobranch distributions were generally understood only from fisheries-dependent catch data, which may not accurately represent actual population distributions. Satellite tracking of horizontal and vertical movements of large numbers of oceanic elasmobranchs has transformed understanding of spatial distributions over time, enabling the potential for impacts from ocean deoxygenation to be examined for the first time. For example, a recent study in the north Atlantic Ocean tagged over 100 individual pelagic sharks from six species (*P. glauca*; *I. oxyrinchus*; longfin

mako *I. paucus*; tiger shark, *Galeocerdo cuvier*; great and scalloped hammerheads, *Sphyrna* spp.) in both shelf and oceanic tagging locations and satellite tracked their movements for over 8,000 days (Queiroz et al., 2016). It showed that pelagic sharks occupy predictable habitat hotspots of high space use (Figure 8.9.2) that are persistent over years and characterized by strong sea-surface temperature gradients; movement modelling demonstrated these were preferred over other available habitats (Queiroz et al., 2016). Several of these multi-species hotspots of space-use overlap large-scale ocean areas with OMZs, in addition to areas that are projected to have among the highest rates of oxygen loss over the next century. For instance, a key pelagic shark hotspot in the North Atlantic occurs where the Gulf Stream flows into the North Atlantic Current and converges with the cold Labrador Current (arrowed 1; Figure 8.9.2). It appears to be an important foraging area for large sharks that undertake deep dives ($>1000 \text{ m}$) apparently to feed on deep-water cephalopods (Sims, 2017). Ocean modelling projects that a large-scale area of the North Atlantic overlapping this important pelagic shark space use hotspot (area A; Figure 8.9.2) will have

Box 8.9.1**Tracking elasmobranchs**

Two types of electronic tag are used to track long-distance movements of sharks and other marine vertebrates. The first is an ARGOS (Advanced Research and Global Observation Satellite) transmitter (Box Figure 8.9.1A) that emits ultra-high frequency radio signals when the tag and antenna attached to a shark's first dorsal fin breaks the sea surface (Box Figure 8.9.1B), with these signals being detected by Argos receivers on polar-orbiting satellites that relay the data to ground stations. Geographic positions of the tag are computed in near-real time and are available to researchers via a web portal.

The second is a pop-off satellite-linked archival transmitter (PSAT) that is attached to the fin or body (Box Figure 8.9.1C) which records swimming depth, water temperature and light intensity, before releasing from the shark at a pre-programmed time, floating to the surface and relaying data to overpassing ARGOS receivers. Data are then processed by researchers to estimate movement paths and activities.



Box Figure 8.9.1 (A) ARGOS (Advanced Research and Global Observation Satellite) transmitter © David Sims, (B) ARGOS transmitter attached to shark dorsal fin © David Sims, (C) Pop-off satellite-linked archival transmitter (PSAT) © Nigel Motyer.

Tags are small, weighing only about 50 – 160 g depending on battery size, and can be attached rapidly, within a couple of minutes. Tagging procedures require institutional, and in some countries governmental, training and approval to reduce the potential of injury to tagged animals.

one of the most dramatic oxygen losses for the North Atlantic of $>45 \mu\text{mol O}_2 \text{ L}^{-1}$ ($>1.03 \text{ ml O}_2 \text{ L}^{-1}$) by 2090-99, compared to 1990-99 levels (Bopp et al., 2013). This is not the only pelagic shark hotspot likely to be exposed to deoxygenation; for example, a hotspot between the Iberian Peninsula and north-west Africa (arrowed 2; Figure 8.9.2) occurs in an area projected to lose 30 – 40 $\mu\text{mol O}_2 \text{ L}^{-1}$ by 2090-99 (area B; Figure 8.9.2). Oxygen loss in large-scale ecosystems of the open ocean away from OMZs, are proposed to be driven by multiple contributing factors, including increased warming of surface waters, increased stratification, enhanced productivity and increased microbial respiration rates (Levin, 2018). Furthermore, a shark space use hotspot overlaps the eastern tropical Atlantic (ETA) OMZ (area C; Figure 8.9.2). Although the O_2 concentration in the ETA OMZ is significantly higher than in Pacific and Indian Ocean OMZs where the O_2 level can approach zero (Gilly et al., 2013), the decline in O_2 content has been

most intense in the ETA OMZ where OMZ thickening (leading to shoaling) has been relatively fast, increasing by 85% in 40 years, which may have the potential for large increases in the area of hypoxic regions (Stramma et al., 2008). The co-occurrence of pelagic shark space use hotspots in areas of high projected oxygen loss has, at present, unknown consequences for sharks given the paucity of specific studies.

Despite few specific studies to date on large pelagic fish and OMZs (Prince & Goodyear, 2006; Prince et al., 2010; Stramma et al., 2011), those that have been undertaken provide a background to assess how sharks may respond to ocean deoxygenation. It is suggested that a DO concentration of $\sim 3.5 \text{ ml O}_2 \text{ L}^{-1}$ represents a hypoxic threshold that induces stress in tropical pelagic fish such as tunas and billfishes, whereas levels $< 1.5 \text{ ml O}_2 \text{ L}^{-1}$ probably represent a below lethal threshold for continuous exposure in istiophorid

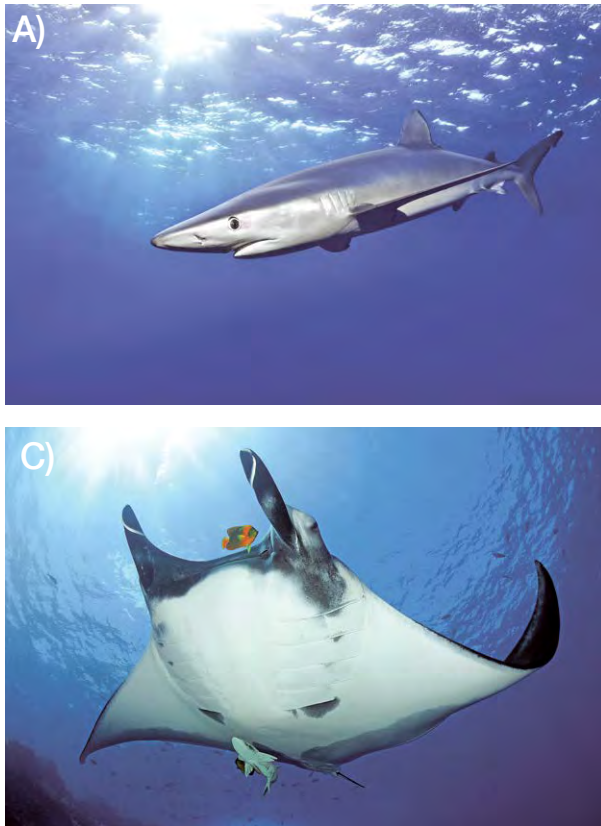


Figure 8.9.3 (A) Blue shark *Prionace glauca* off the Azores; (B) shortfin mako off New Zealand; (C) giant manta ray with shark suckers *Remora remora* and clarion angelfish *Holocanthus clarionensis*. (A) © Broker / Alamy stock photo; (B) © Richard Robinson / Alamy stock photo; (C) © Helmut Corneli / Alamy stock photo.

billfishes (Prince & Goodyear, 2006). A principal result of studies using electronic tags to track horizontal and vertical movements of tropical pelagic fish such as blue marlin (*Makaira nigricans*) and sailfish (*Istiophorus platypterus*) associated with OMZs has been that they undergo 'habitat compression' (Figure 8.9.4A) through restriction in depth distribution generally to layers above $3.5 \text{ ml O}_2 \text{ L}^{-1}$, to about 50 - 100 m depth in the ETA OMZ (Prince et al., 2010; Stramma et al., 2011). If large pelagic elasmobranchs are similarly restricted by low DO levels then habitat compression is likely to occur for them also as OMZs expand with continued ocean deoxygenation. In this way, expanding OMZs could act as a 'habitat trap': sharks and rays may benefit from increased habitat compression that may also act on hypoxia-intolerant prey species (e.g. small pelagic fish, epipelagic cephalopods) that become increasingly aggregated in surface waters by shoaling hypoxic water (Gilly et al., 2013), potentially increasing feeding opportunities for elasmobranchs (Figure 8.9.4B). Thus, sharks and rays showing preferences to aggregate for enhanced foraging opportunities in reduced habitat volumes above OMZs may be more vulnerable to capture by fishers because

they remain there longer (the "shooting fish in a barrel" analogy). Therefore, the OMZ 'habitat trap' hypothesis (Figure 8.9.4B) may ultimately further exacerbate population declines and pose significant threat to pelagic sharks and marine ecosystems. But is there broad and direct evidence that elasmobranchs specifically avoid oxygen depleted waters? Clearly, knowing this has implications for assessing susceptibility to fisheries because if elasmobranchs are tolerant to hypoxia then habitat compression from ocean deoxygenation may be less severe and, thus, risk of capture by fisheries may be lower for them compared to tropical tunas for example.

8.9.4. Physiological responses

Pelagic sharks have relatively high oxygen demands so encountering oxygen depleted waters of the open ocean may lead to metabolic stress. Among vertebrates, elasmobranchs are relatively large bodied, which confers on them higher absolute oxygen requirements than smaller bodied taxa (Payne et al., 2015; Sims, 1996). Elasmobranchs are also generally highly mobile predators and scavengers, predominating as upper-trophic-level predators in the ecosystems in which they occur. They have a key role in the structure and functioning of such systems, for example by regulating the abundance of prey populations that acts to stabilize trophic interactions across complex marine foodwebs (Heithaus et al., 2008). Naturally, the capacity for movement and activity among elasmobranchs varies with individual lifestyle, extending from slower-moving, ectothermic benthic species such as catsharks (e.g. *Scyliorhinus* spp.) and skates (*Raja* spp.) (Figure 8.9.5) that can lie motionless on the sea bed for many hours each day (Wearmouth et al., 2014), to the highly active, oceanic pelagic sharks such as the shortfin mako (Figure 8.9.3B) that swim at high speed, can traverse ocean basins and possess morphological adaptations such

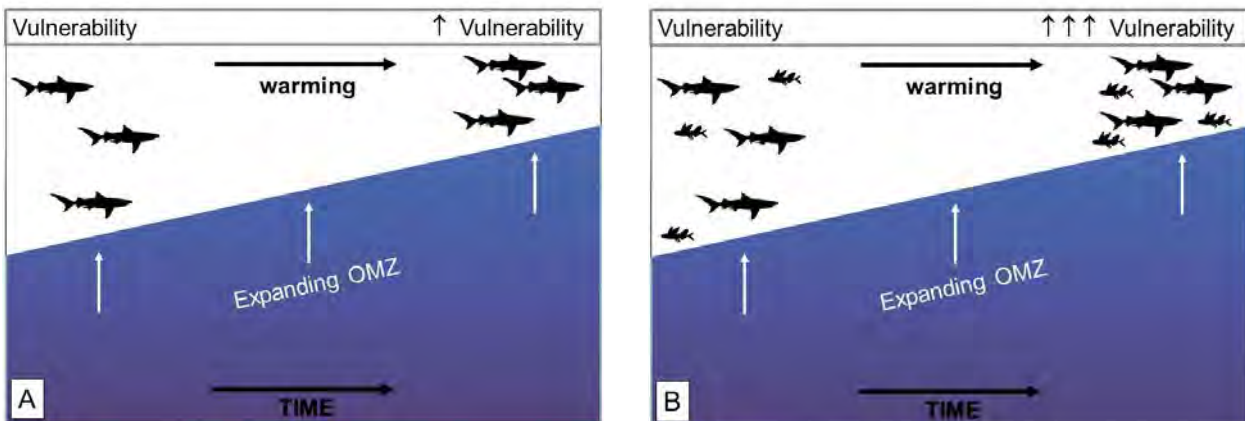


Figure 8.9.4 Scenarios of how ocean deoxygenation in oxygen minimum zones will potentially affect pelagic sharks. Schematic of the habitat trap hypothesis. (A) The concept of fish habitat compression from expanding OMZs increasing vulnerability leads to (B) the 'habitat trap' hypothesis, whereby habitat compression combined with predator and prey aggregation increases predator relative vulnerability to fisheries capture as predators remain in above-OMZ for extended periods. Shark and fish silhouettes from www.iconspng.com.

as endothermy, where body temperature is maintained some 4–6 °C above ambient (Bernal et al., 2010).

For elasmobranchs exposed to hypoxia that are unable to move due to physical environmental constraints, e.g. hypoxic water overlaps their entire preferred habitat or activity space, then physiological mechanisms must be employed to compensate for oxygen limitation (Jensen et al., 1994). Direct measurements of ventilatory responses of fishes indicates they can be considered oxygen regulators, that are able to maintain or even increase oxygen uptake in hypoxic conditions, or oxygen conformers, that immediately reduce their oxygen uptake as oxygen levels decline (Fritsche & Nilsson, 1994). It has been proposed that bony fishes are mainly oxyregulators, whereas most elasmobranchs are oxyconformers (Fritsche & Nilsson, 1994). However, elasmobranch ventilatory responses to hypoxia appear varied, including having been shown to increase upon exposure to low oxygen concentrations (Di Santo et al., 2016; Metcalfe & Butler, 1984). Little skate (*Leucoraja erinacea*) embryos for example, that develop within immobile egg-cases attached to substrata associated with the sea bed, maintain constant levels of oxygen uptake above $\sim 2.90 \text{ ml O}_2 \text{ L}^{-1}$ ($\sim 45\%$ air saturation in water at 15 °C) that are driven by increased tail-beat frequency that pumps more water through the egg-case (Di Santo et al., 2016). However, below this critical threshold oxygen consumption declines abruptly with increasing levels of hypoxia despite maintenance of elevated tail-beat frequency. Furthermore, temperature has a profound effect on the responses of the relatively inactive elasmobranch species (Butler & Metcalfe, 1988). For instance, at the lower temperature of 7 °C hypoxia has little effect on the lesser-spotted catshark

Scyliorhinus canicula of temperate north-east Atlantic shelf seas (Figure 8.9.5A), whereas at 12 °C it exhibits reductions in oxygen uptake and heart rate that are even more severe at higher temperatures (Butler & Metcalfe, 1988; Butler & Taylor, 1975). In general, therefore, relatively inactive elasmobranchs from temperate waters are considered to regulate oxygen uptake during hypoxia at low ambient temperatures (oxyregulation). At higher temperatures, that induce higher metabolic rates in ectotherms (decreasing aerobic scope), they exhibit an oxyconformity response, with lowered oxygen uptake matching hypoxic conditions (Butler & Metcalfe, 1988) and perhaps a progressively greater reliance on anaerobic metabolism (Di Santo et al., 2016). This suggests that as water temperatures rise with climate warming, many elasmobranchs may be less able to tolerate the effects of progressive hypoxia associated with ocean deoxygenation.

An obvious response of mobile aquatic animals exposed to hypoxia should be to avoid it and move to normoxic waters (Jensen et al., 1994). However, hypoxia can inhibit spontaneous activity in catshark (*S. canicula*), indicating that this species responds to hypoxia by reducing the demand for oxygen when it is at low ambient levels (Metcalfe & Butler, 1984). Reduction in activity when exposed to hypoxia also occurs in the Florida smoothhound shark (*Mustelus norrisi*) that is capable of ventilating while resting motionless, like other bottom-living elasmobranchs (Carlson & Parsons, 2001). Induced inactivity in response to hypoxia will lower oxygen consumption rate, thereby reducing oxygen demand and compensating for low ambient oxygen concentrations during hypoxia (Jensen et al., 1994). However, that some elasmobranchs may not

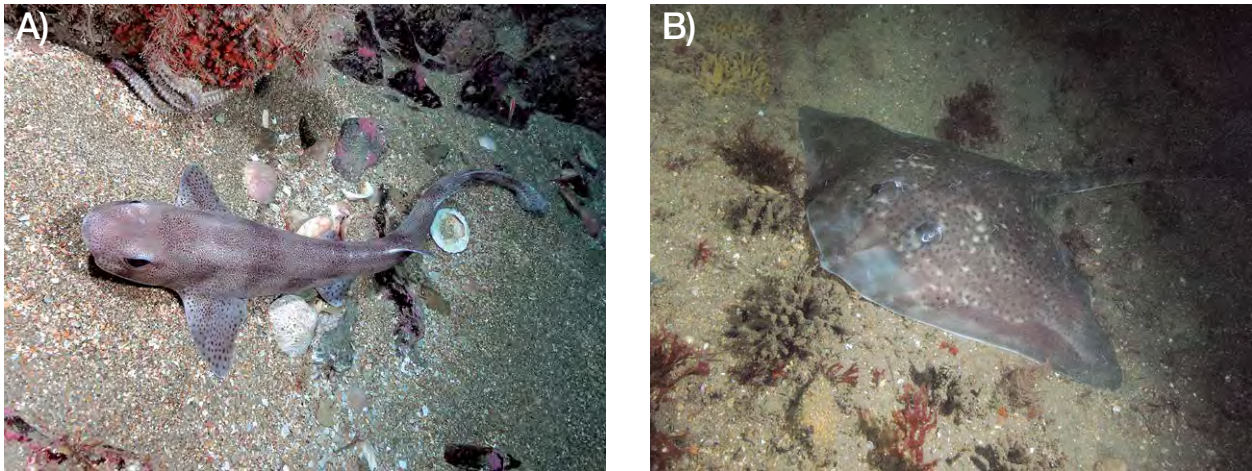


Figure 8.9.5 Distributions of smaller bodied elasmobranchs may be shifted by ocean deoxygenation in coastal waters. (A) the small spotted catshark, *Scyliorhinus canicula*, is common in north-east Atlantic and Mediterranean shelf seas and reaches a maximum length of 0.7 m. It has been shown to be an oxyregulator when exposed to mild hypoxia, but an oxyconformer with increasing hypoxia, indicating it will move to avoid moderate and strongly hypoxic waters resulting in potential distributions shifts. (B) a thornback ray, *Raja clavata*, occurs in the north-east Atlantic, Mediterranean and off north Africa growing to a maximum length of 1.3 m. It utilizes a broad range of habitats from estuaries to open ocean that may become more prone to deoxygenation in the future. © Keith Hiscock.

necessarily move away from hypoxia and developing embryos in egg-cases on the sea bed are unable to, implies compensatory mechanisms should be present to maintain critical oxygen uptake.

Among small-bodied, less active sharks such mechanisms appear to be present as physiological responses to severe oxygen stress. For the less active, temperate elasmobranchs that have been studied in detail, hypoxia causes a general circulatory response (Satchell, 1961) elicited, in *S. canicula*, by externally located O_2 receptors apparently distributed diffusely in the branchial (gill) cavities and innervated by cranial nerves (Butler et al., 1977). The circulatory response in general comprises an increase in the ventilation volume of water passed across the gills accompanied by a reduction in heart rate (bradycardia) and by an increase in cardiac stroke volume (volume of blood pumped from the ventricle per beat) (Butler & Metcalfe, 1988). During moderate hypoxia the ventilation volume is increased by up to 50% (Metcalfe & Butler, 1984). Nonetheless, it appears that this increase is insufficient to maintain partial pressures of oxygen in arterial blood as the inspired oxygen partial pressures decline (Butler & Taylor, 1975). Similarly, bradycardia and increased stroke volume only act to maintain overall cardiac output such that once a reduction in the venous concentration of oxygen no longer matches the decrease in arterial oxygen concentration, oxygen uptake falls (Butler & Metcalfe, 1988; Butler & Taylor, 1975). Butler et al. (1979) found that *S. canicula* were unable to survive prolonged exposure to severe hypoxia ($<2.30 \text{ ml } O_2 \text{ L}^{-1}$) whereas

developing embryos within egg-cases recovered after variable periods of hypoxia and up to 12 h anoxia (Diez & Davenport, 1987). Similarly, the sluggish, bottom-dwelling electric ray (*Torpedo marmorata*) (Figure 8.9.6) that is found in European shelf seas shows a significant increase in ventilation frequency and amplitude during hypoxia, and similar to catsharks, extreme hypoxia can be endured for many hours (Fritsche & Nilsson, 1994; Hughes, 1978). These studies indicate many inactive elasmobranchs from temperate waters are capable of withstanding mild hypoxia with circulatory responses, perhaps even for extended periods, however, such strategies may be insufficient to endure moderate, progressive or prolonged hypoxia or anoxia for periods greater than a day. Collectively, these observations suggest that deoxygenation occurring in temperate, coastal waters is highly likely to result in shifts in



Figure 8.9.6 *Torpedo ray Torpedo marmorata*. © Martin Habelnetzel / Alamy stock photo.

distributions of elasmobranchs arising from avoidance movements away from persistent hypoxic habitats. In the absence of avoidance, however, and where oxygen depleted waters entirely overlap the daily movement ranges of less active species it is possible mortalities could occur.

In tropical waters, the epaulette shark (*Hemiscyllium ocellatum*) is one of the few elasmobranchs that appears able to tolerate extreme hypoxic conditions for long periods in its natural habitat of shallow coral reefs (Nilsson & Renshaw, 2004). This shark tolerates repeated exposure to severe hypoxia (5% of normoxia) and even anoxia at 25 – 30 °C (Wise et al., 1998) during tidal fluctuations that at low tide cut-off the warm, shallow reef platform water (where it forages) from the surrounding ocean. In the isolated reef platform water at low tide the respiration of organisms trapped in this fixed volume of water lowers oxygen concentration to <20% air saturation (<1.3 ml O₂ L⁻¹) (Nilsson & Renshaw, 2004). A comparative study demonstrated that the critical oxygen tension, P_{crit} , at which an animal transitions from being an oxyregulator to an oxyconformer, was much lower for the hypoxia-tolerant epaulette shark than a hypoxia-sensitive shovel-nose ray (*Aptychotrema rostrata*), probably due to a significantly greater haemoglobin O₂ binding affinity in the shark (Speers-Roesch et al., 2012a). In addition, among elasmobranchs it was evident that the variation in hypoxia tolerance was not solely determined by differences in O₂ uptake and transport, but also by tissue-specific metabolic responses, such as metabolic depression associated with lower tissue lactate concentrations, for example (Nilsson & Renshaw, 2004; Speers-Roesch et al., 2012b). In contrast, exposure of the spurdog shark (*Squalus acanthias*) to severe hypoxia (5% air O₂ saturation for 4 h; ~0.30 ml O₂ L⁻¹) leads to reduction in active gill homeostatic processes, such as urea retention, ionoregulation, and an osmoregulatory compromise due to increased functional gill surface area (Zimmer & Wood, 2014). Overall therefore, it appears that most elasmobranchs can be considered to be only weak oxyregulators, principally elicited via circulatory responses, and across a relatively narrow range of temperatures. However, in a few species, like the epaulette shark, severe hypoxia may be regularly tolerated for extended periods, with oxyregulation persisting down to very low oxygen tensions through physiological adaptations in cardiovascular function and metabolic responses of the heart and other tissues.

There appear to be few studies documenting anaerobiosis (respiration without oxygen) in elasmobranchs exposed to hypoxia, even though it is feasible that sharks and rays may enter OMZs for instance, to feed on slow-moving, hypoxia-tolerant prey species, such as deep-water cephalopods (Rosa & Seibel, 2008; Seibel, 2011; Seibel et al., 2014), and which would be possible through use of anaerobic metabolic pathways. Interestingly, the hearts of the few elasmobranchs so far studied in this context have been identified to be well equipped biochemically for sustained periods of anaerobiosis (Sidell & Driedzic, 1985; Tota, 1999), with the catshark *Scyliorhinus stellaris* showing little cardiac ultrastructural damage even during periods of anoxia (Helle et al., 1983; Tota, 1999).

In the context of open ocean deoxygenation such as that observed in permanent OMZs, an important question is whether threatened pelagic sharks vulnerable to commercial exploitation are tolerant of hypoxia, or even short-term anoxia. Expanding midwater OMZs are likely to have the most pronounced effects on species with high metabolic oxygen demands. Oceanic sharks in the family Lamnidae are large, fast-swimming apex predators with high oxygen demands arising from cardiovascular and respiratory specializations (e.g. large gill surface areas, high mitochondrial densities, larger heart mass, increased muscle capillary density and myoglobin concentration) and swimming muscle physiology (red muscle endothermy) that maintain body temperatures above ambient, potentially expanding both horizontal and vertical niches (Bernal et al., 2010). These adaptations for a high O₂ uptake lifestyle suggest endothermic mako sharks may be intolerant of hypoxia, but it remains an open question how high-performance fish like this may be affected by hypoxic waters in the absence of experimental physiological studies of the type undertaken on smaller, less active elasmobranchs (Payne et al., 2015). However, behavioural responses of smaller bodied coastal pelagic sharks have been measured under controlled laboratory conditions in response to hypoxia. For large sharks that have not been studied under experimental conditions, DO has been measured or estimated in habitats through which shark movements have been tracked. Both these approaches provide insight into how pelagic sharks may respond to low oxygen, and thereby how they may interact with OMZs and other deoxygenated habitats that may influence their ecology and risk of capture.

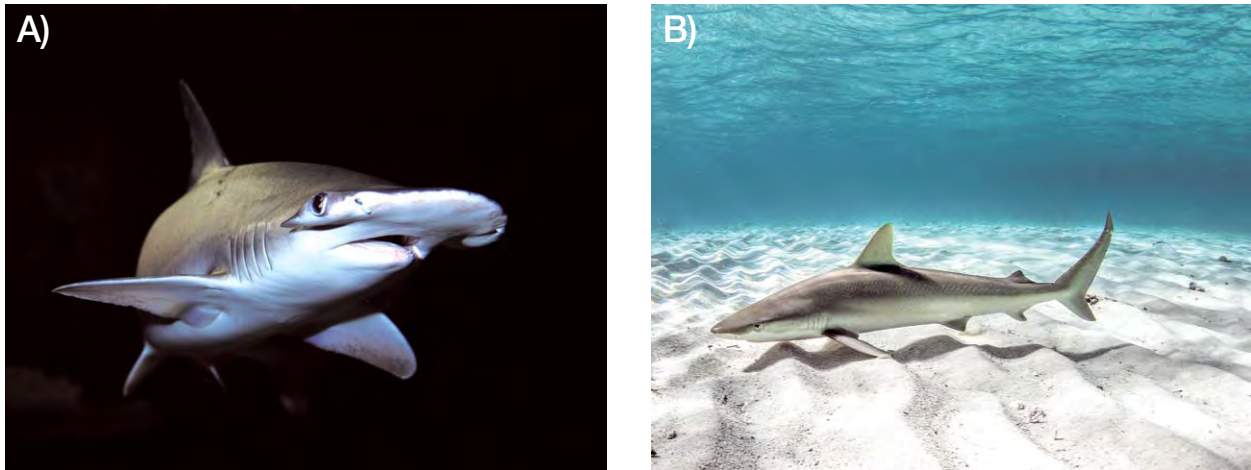


Figure 8.9.7 Ram ventilating sharks – (A) bonnethead *Sphyrna tiburo* and (B) blacknose *Carcharhinus acronotus*. © (A) Mark Conlin / Alamy stock photo; (B) Ken Kiefer / Alamy stock photo.

8.9.5 Behavioural responses

Many pelagic sharks and rays are obligate ram-ventilators that extract oxygen from water by swimming forwards with an open mouth to pass water across the gills. Under conditions of hypoxia therefore, elasmobranchs must increase mouth gape, swimming speed, or both, to increase ventilation volume and maintain oxygen uptake rate (Carlson & Parsons, 2001). Coastal ram-ventilating bonnethead (*Sphyrna tiburo*) and blacknose (*Carcharhinus acronotus*) sharks (Figure 8.9.7) exposed to hypoxic conditions ($\sim 1.80 - 2.43 \text{ ml O}_2 \text{ L}^{-1}$) in laboratory respirometers have been observed to increase swimming speed, mouth gape and oxygen consumption rate (Carlson & Parsons, 2001). These were responses similar to those seen in other ram-ventilating species of fish such as skipjack and yellowfin tunas. In sharks, the behavioural response of increased mouth gape during hypoxia has been proposed as a mechanism for maintaining oxygen delivery (Carlson & Parsons, 2001), which is supported by measurements for *S. tiburo* showing changes in oxygen content of water during swim trials caused no significant changes in either blood oxygen content or haematocrit (the ratio of the volume of red blood cells to the total volume of blood) (Carlson & Parsons, 2003). This suggests obligate ram-ventilating pelagic sharks may be able to tolerate minor or perhaps moderate levels of hypoxia.

That open-ocean pelagic sharks may be capable of withstanding moderate hypoxia, at least for short periods, is suggested by tracking studies where spatial movements have been related to modelled DO data that are estimated for the surface and at-depth environments visited by the sharks. For example, tracking shortfin

mako sharks in the eastern tropical Pacific (ETP), the world's largest OMZ, indicated those individuals generally remained in waters with $>3.0 \text{ ml O}_2 \text{ L}^{-1}$, rarely encountering water with $<2.0 \text{ ml O}_2 \text{ L}^{-1}$, although on very deep dives they may have reached water with $1.25 \text{ ml O}_2 \text{ L}^{-1}$ (Abascal et al., 2011; Vetter et al., 2008). In another study, great white sharks *Carcharodon carcharias* offshore in the ETP were typically associated with dissolved oxygen concentrations of $>3 \text{ ml O}_2 \text{ L}^{-1}$ with an estimated minimum O_2 level of $0.3 \text{ ml O}_2 \text{ L}^{-1}$ during occasional dives to near 1000 m (Nasby-Lucas et al., 2009). Similarly, the dive profile of a single scalloped hammerhead shark *Sphyrna lewini* in Baja California indicated it may have entered depths where modelled oxygen indicated waters were extremely hypoxic ($<0.5 \text{ ml O}_2 \text{ L}^{-1}$) (Jorgensen et al., 2009).

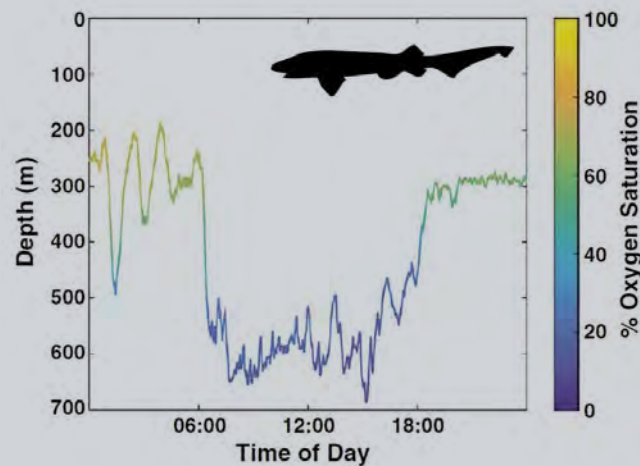
The studies discussed above were limited to using modelled DO data from oceanographic datasets to assess potential oxygen levels along paths taken by tracked sharks. Hence, actual DO in the habitats



Figure 8.9.8 Great white shark *Carcharodon carcharias*. © Wilyam Bradberry / Shutterstock.com.

Box 8.9.2**Measuring ocean oxygen with shark ‘oceanographers’**

Dissolved oxygen (DO) data can now be measured along the paths of elasmobranchs. DO-depth-temperature recording tags with the potential capability for data retrieval via ARGOS satellites have been developed and trialled on sharks and seals (Baillleul et al., 2015; Coffey & Holland, 2015). Box Figure 8.9.2 shows the tag-recorded swimming depth of a six-gill shark, *Hexanchus griseus*, and the dissolved oxygen concentration of water encountered over a 24 hr period (from Coffey & Holland, 2015). The trace illustrates that during daylight hours the shark was in deep waters between about 450 and 700 m depth and oxygen saturation of ~10–50%.



Box Figure 8.9.2 Swimming depth of a tagged six-gill shark and the environmental dissolved oxygen concentration recorded by the tag along its track. Figure credit (Coffey & Holland, 2015) available under the terms of the Creative Commons Attribution 4.0 International Licence (www.creativecommons.org/licenses/by/4.0/). The six-gill shark silhouette has been added to original made available by phylopic.com with credit to Tony Ayling (vectorized by T. Michael Keeseey) under the terms of the Creative Commons Licence (www.creativecommons.org/licenses/by-sa/3.0/).

As DO sensing tags become readily available, in the future they will no doubt improve our understanding of how elasmobranchs respond to climate-driven warming and deoxygenation occurring in the ocean. They will also make elasmobranchs ‘animal oceanographers’ with the tags they carry collecting very large quantities of DO data during horizontal and vertical excursions over huge areas. These data can be provided to oceanographic databases to help improve predictions of climate changes generated by atmosphere-ocean system models.

selected by sharks could be different to the values supposed. Direct measurements are needed to assess more accurately how pelagic sharks will respond to hypoxia. Important recent developments are data-logging tags capable of measuring dissolved oxygen and swimming depth for recording directly the DO levels experienced by free-ranging marine predators (e.g. Baillleul et al., 2015), including sharks (Coffey & Holland, 2015). The new tag used to track sharks provided DO concentration measurements highly correlated with vertical profiles obtained simultaneously from ship-borne instruments. Deployment on two bluntnose sixgill sharks (*Hexanchus griseus*) off Hawaii, Pacific Ocean, recorded oxygen saturations as low as 9.4% of normoxia for short durations (few mins) during dives to

nearly 700 m depth (Coffey & Holland, 2015). Although *H. griseus* (Figure 8.9.9) are large, generally slow moving sharks with lower metabolic rates than the high oxygen demand pelagic sharks, the new tag results confirm that moderate to extreme hypoxia may not necessarily be a barrier to space use of large sharks, although the time spent in those zones may be limited to short excursions.

8.9.6 Population impacts of deoxygenation and fishing

A major concern is how ocean warming, deoxygenation and fisheries exploitation may interact to impact elasmobranch populations. The available evidence indicates that elasmobranchs are well equipped

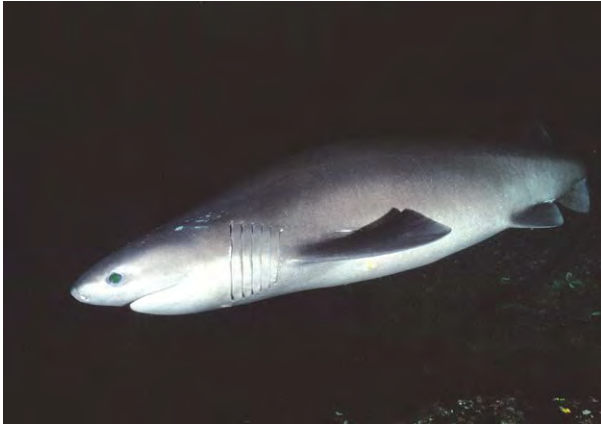


Figure 8.9.9 Bluntnose sixgill shark *Hexanchus griseus*. © Kelvin Aitken / WWPics / Alamy stock photo.

physiologically to detect hypoxia and, being mobile species, will generally be able to avoid them and move to normoxic waters. If, however, 'escape' to normoxic waters is less feasible (i.e. it is too far away for instance) or is not desired (e.g. greater foraging opportunities occur in a hypoxic zone), then elasmobranchs can exhibit behavioural and physiological responses to hypoxia. Where large-scale hypoxic zones occur and persist in shallow water systems, the habitat space of

smaller-bodied species such as benthic sharks and skates (Figure 8.9.5A, B) may be overlapped significantly by hypoxic waters that may result in movements and distribution shifts for affected species. This is largely because elasmobranchs are only weak oxyregulators that show oxyconformity responses with increasing levels of hypoxia and at the higher temperatures that are predicted in the future, with few species being tolerant to progressive or prolonged severe hypoxia. For shelf fisheries it seems likely, therefore, that expanding deoxygenation coupled with rising sea temperatures may result in periodic shifts in elasmobranch distributions which, if shifted to areas with higher fishing intensity, may result in exposure of populations to greater risks of capture.

The available studies indicate that pelagic sharks generally spend much of the time above stress thresholds of hypoxia, but behavioural responses to hypoxia and directly measured and modelled DO data along shark tracks suggest periodic entry into hypoxic zones may occur for some species. This supports the hypothesis that expanding OMZs will cause 'habitat

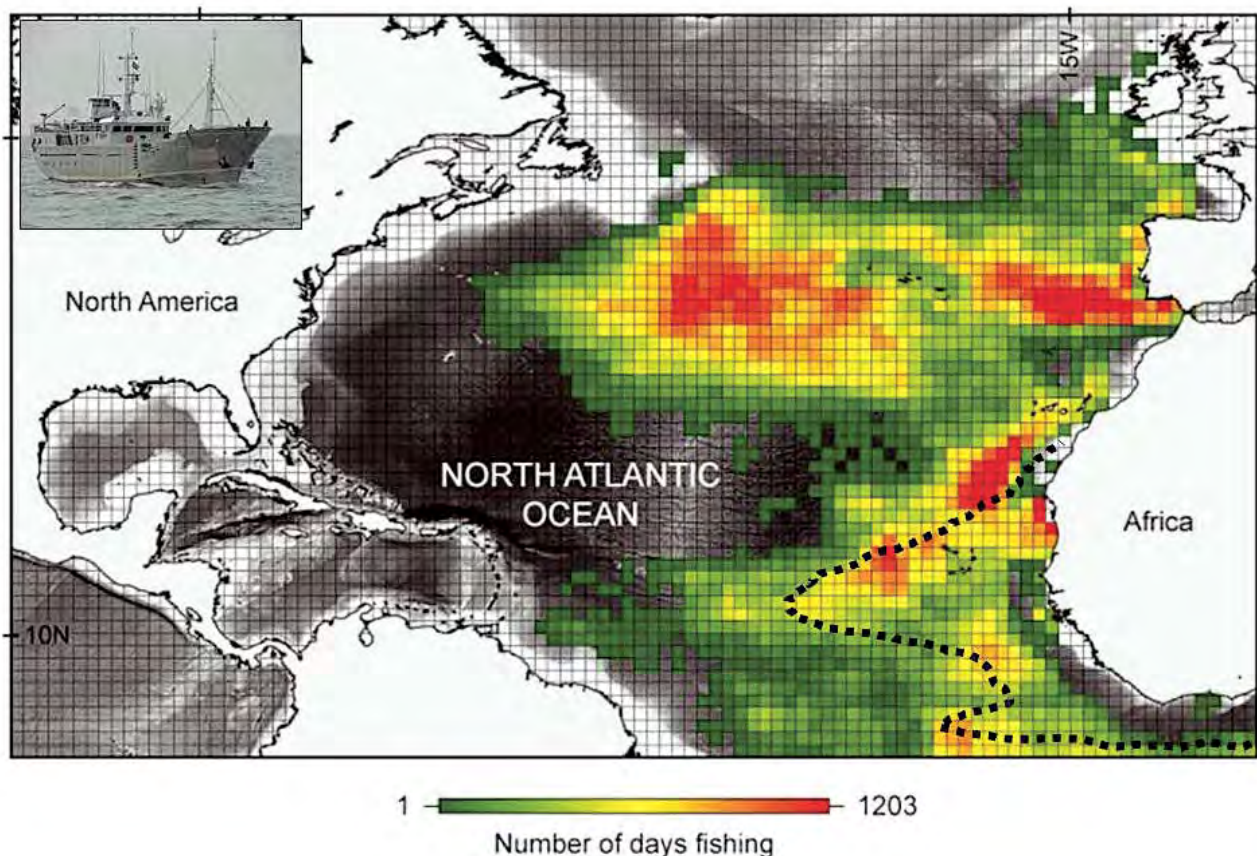


Figure 8.9.10 Exploitation hotspots of the Spanish and Portuguese surface-longline fleets shows co-occurrence of persistent, year-round hotspots covering a major part of the eastern tropical Atlantic (ETA) OMZ. Dashed black line represents the $3.5 \text{ ml O}_2 \text{ L}^{-1}$ at 100m as an indicator of the spatial extent of the ETA OMZ. Note the fishing hotspots located along the OMZ. Fishing effort map redrawn from Queiroz et al. (2016) where warmer colours denote greater effort (days) per grid cell.

compression' of pelagic sharks by generally limiting vertical range to surface layers above $\sim 3.5 \text{ ml O}_2 \text{ L}^{-1}$ for example (Figure 8.9.4A). Similarly, there is evidence that pelagic sharks show habitat preferences for surface waters above intermediate-depth OMZ areas (100 – 1000 m) (Queiroz et al., 2016). Shark space use hotspots in such areas (Figure 8.9.2) may characterize preferred foraging areas for sharks because hypoxia-intolerant prey may also be restricted to surface layers with reduced vertical space use (Sims, 2017). This supposes that expanding OMZs could be considered as 'habitat traps' for pelagic sharks (Figure 8.9.4B). Research on this topic is needed because habitat compression into surface layers together with habitat trapping of pelagic sharks, will potentially increase their risk of capture by surface fisheries such as pelagic longlines. This is because habitat compression and trapping will result in reduced habitat volumes and persistent higher densities of sharks in surface waters above OMZs, theoretically leading to greater spatial overlap of sharks with surface fishing gear such as longlines. A recent study identified a fishing hotspot of the Spanish and Portuguese longline fleets above the eastern tropical Atlantic OMZ that was persistent for most of the year (Queiroz et al., 2016) (Figure 8.9.10). The spatial co-occurrence of a pelagic shark hotspot and a fishing hotspot in surface waters above an OMZ suggests greater catches are possible compared to many adjacent normoxic areas. This argues the need for specific management of elasmobranch populations occurring in areas where OMZs and other deoxygenated habitats occur. Where these are also subjected to intense fishing exploitation indicates risks of overfishing are likely to become more marked as OMZs expand in the future and further compress pelagic elasmobranch habitats.

The degree to which hypoxic waters are entered by pelagic sharks will also likely vary species by species and will need to be considered in the context of the management and conservation of pelagic sharks (Sims et al., 2018). Understanding the responses of different shark species to OMZs for example is important because predictions about future habitable space available to an endothermic species may be inappropriate to extrapolate to ectothermic species. For instance, the cardiovascular and respiratory specializations of the warm-bodied shortfin mako shark contrasts with the blue shark, which is ectothermic and lacks some of these adaptations, suggesting their responses to low DO may be different. As a warm-bodied, fast swimming shark, the shortfin mako may be an elasmobranch

that is most likely to become habitat compressed above OMZs, where it is possible they may remain for extended periods feeding on a greater abundance of habitat compressed prey.

Many elasmobranch species are in decline as a result of overexploitation by fisheries (Baum et al., 2003; Dulvy et al., 2014; Ferretti et al., 2010; Worm et al., 2013), particularly from fleets operating in open ocean areas such as the high seas which remain largely unregulated with regards to shark catches (Campana, 2016; Queiroz et al., 2016). The effects of ocean deoxygenation on species is only likely to add to the impacts on already threatened populations. For example, the shortfin mako shark occurs broadly in areas currently undergoing ocean deoxygenation (Queiroz et al., 2016) and in areas projected to undergo significant oxygen loss over the next 50 – 100 years (Bopp et al., 2013; Levin, 2018) (Figure 8.9.2). However, in the North Atlantic where significant oxygen losses are predicted, shortfin mako is already being overfished (ICCAT, 2017a), with little or no management in place that will halt the decline and promote stock rebuilding (ICCAT, 2017b; Sims et al., 2018). Therefore, there is the potential for widespread habitat compression to occur through ocean deoxygenation that will likely exacerbate population decline by potentially increasing interactions between sharks and fishing gear (Figure 8.9.4). Moreover, the shortfin mako is unlikely to be an isolated example. Many other pelagic shark species form space use hotspots in the same ocean areas as makos (Queiroz et al., 2016) and are similarly classified as threatened according to IUCN criteria (Table 8.9.1). For instance, in the North Atlantic blue, tiger, silky (*Carcharhinus falciformis*), oceanic whitetip (*C. longimanus*) and smooth hammerhead (*Sphyrna zygaena*) sharks which are already threatened by fisheries overexploitation (Queiroz et al., 2016) overlap with existing OMZs or other areas projected to undergo oxygen loss. (Figure 8.9.2) (Table 8.9.1). This suggests that the interaction of ocean deoxygenation effects and shark fisheries will be broad across both species and regions.

A priority for both scientific research and policy will be to understand how expanding hypoxia affects the most threatened elasmobranchs, and to identify the conservation measures needed to mitigate ocean deoxygenation effects on elasmobranchs, such that future catch rates are controlled in the light of climate change rather than for exploitation to be exacerbated by ocean oxygen losses.

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8.9.7 References

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8.10 The significance of ocean deoxygenation for ocean megafauna

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Summary

- Marine mammal distribution is primarily driven by prey availability. Therefore, community-wide impacts on gilled species affect the behaviour of marine mammals. Coastal hypoxia is increasing in areas of critical marine mammal habitat. There are approximately 48 species of marine mammal in the hypoxia-affected regions of the Northern California Current System, Black Sea, Baltic Sea, and Gulf of Mexico.
- Coastal hypoxia events lead to shifts in distribution, mobility, predator avoidance, and mortality of gilled animals. Severe or prolonged hypoxia can lead to shifts in food webs, with the potential for impacting foraging success of marine mammals. Increased ocean warming, and the resultant decreases in oxygen availability suggest an imminent pattern of worsening hypoxia worldwide.
- These patterns may lead to increased pressure for marine mammal species that are already threatened or endangered. Conversely, increased rates of predation on gilled species incapacitated or spatially compressed by hypoxia may benefit certain marine mammals. Direct links between coastal hypoxia and marine mammals may be difficult to quantify, but abundant nearshore marine mammals are excellent potential study species to begin understanding the various implications.
- Ocean deoxygenation drives offshore oxygen minimum zone (OMZ) expansion and shoaling. This expansion may positively affect the foraging efficiency of northern elephant seals, due to (1) their increased ability to feed on inactive prey, (2) decrease of diving costs in terms of both time and energy expenditure, and subsequent increased prey search time in the bottom phase of foraging dives, and (3) elevated prey density related to the compression of vertical prey distribution. Increased dependency on the prey in the OMZ (about 40% of total their prey) may lead to species composition changes within the mesopelagic community. Increased foraging efficiency by elephant seals may lead to further population increases, potentially resulting in large disturbance and shifts in the functioning of the mesopelagic ecosystem through top-down and trophic cascade effects.
- Sperm and beaked whales, typical deep divers in the mesopelagic zone, foraging on squids which inhabit the upper mesopelagic zone and often rest in the OMZ. Although foraging and vertical migration of squids remain unclearly defined, it is suggested that future shoaling of the OMZ will cause the vertical compression of this 'resting zone', consequently giving a foraging advantage to sperm whales and beaked whales feeding on squid.
- Increased foraging efficiency in habitats where the OMZ shoaling occurs will enhance the role of deep diving mammals in nutrient cycling, via altered nutrient pumping to surface waters from the OMZ, leading to increased productivity and nutrient flux to depths. This increased flux could ultimately affect oxygen consumption as a result of microbial respiration and nitrification in the oxygen limited zone, leading to further expansion of the OMZ.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen concentrations in nearshore region produce community-wide impacts on gilled species.	<ul style="list-style-type: none"> • Altered foraging behaviour and spatial habitat use of marine mammals. There are approximately 48 species of marine mammals in the hypoxia-affected regions of the Northern California Current System, the Black Sea, the Baltic Sea, and the Gulf of Mexico. • Shifts in distribution, mobility, predator avoidance, schooling behaviour, and mortality of gilled animals. Severe or prolonged hypoxia can lead to shifting marine community composition, and may potentially impact foraging success of marine mammals. • Increased pressure for marine mammal species, that are already threatened or endangered, to adapt to a changing regime. Conversely, increased predation success on gilled species incapacitated or spatially compressed by hypoxia may benefit certain marine mammals.
Decreasing oxygen concentrations and shoaling in offshore regions impact resting zones of mesopelagic prey.	<ul style="list-style-type: none"> • Increased shoaling may positively affect the foraging efficiency of marine mammals due to (1) their increased ability to successfully feed on inactive or incapacitated prey, (2) decreased diving costs (shallower dives) and increased allotment of search time in the bottom phase of foraging dives, and (3) elevated prey densities related to the vertical and horizontal compression of prey fields. • Increased dependency on the prey in the OMZ (northern elephant seals: about 40%) may lead to species composition and functional changes within the mesopelagic community. • Increased foraging efficiency may lead to population increases (i.e. northern elephant seal), potentially resulting in large functional shifts within the mesopelagic ecosystem. • Future shoaling of the OMZ may provide foraging advantages to sperm whales and beaked whales feeding on squid within these zones. • Increased foraging efficiency will enhance the role of deep-diving mammals in the nutrient cycling of the OMZ via nutrient pumping, leading to increased productivity and nutrient influx to depths. This increased flux could ultimately increase oxygen consumption via microbial respiration and nitrification in the oxygen limited zone, leading to further expansion of the OMZ.

8.10.1 Introduction

Loss of oxygen in the water column may not physiologically affect air-breathing marine mammals, but these animals respond to changes in prey availability as driven by oceanographic factors, including ocean deoxygenation, which makes the threat of increased global deoxygenation to marine mammals as yet unclear. The extent of ocean deoxygenation varies temporally and spatially according to the variability of the environment. Deoxygenation in nearshore areas is very complex due to the influence of land-based inputs and human activities. Severe deoxygenation in the environment has the capacity to affect marine mammals due to changes in prey abundance caused by hypoxic conditions (Chan et al., 2008; Diaz & Rosenberg, 2008; Steingass & Horning, 2017). Offshore deoxygenation occurs with

vertical shoaling of the oxygen minimum zone (OMZ) at a decadal scale as a consequence of global warming (Bograd et al., 2008; Emerson et al., 2004; Ito et al., 2016; Keeling et al., 2010; Stramma et al., 2010, 2012), and this may gradually affect the foraging behaviour of marine mammals.

Although it is difficult to provide a detailed explanation of the relationships between ocean deoxygenation and marine mammals, it is possible to provide (1) the general status of nearshore marine mammals in relation to deoxygenation, and (2) provide a scenario of how pelagic deep diving marine mammals could react to ocean deoxygenation adopting the elephant seal, (*Mirounga angustirostris*) (Figure 8.10.1A) and sperm whales, (*Physeter macrocephalus*) (Figure 8.10.1B) as models of offshore marine mammals.

8.10.2 Nearshore deoxygenation

In recent years, coastal hypoxia has increased in spatial extent, prevalence, and duration on a global scale (Diaz & Rosenberg, 2008). Nearshore coastal ecosystems represent a large percentage of fisheries productivity (Chan et al., 2008). However, ecosystem-scale consequences of coastal hypoxia are just beginning to be examined. Little is known regarding the impacts of deoxygenation events on marine predators, particularly mammals. While not directly reliant on the oxygen in the water column, marine mammals are susceptible to alterations in distribution, availability, behaviour, and mortality of their gilled prey. These effects have been initially examined through conceptual models simulating marine mammal foraging during hypoxia, (Steingass & Horning, 2017), ecosystem monitoring (Craig et al., 2001), and modelling mammal behaviour during related oceanographic studies (Hazen et al., 2013). However, these effects have not been well-studied in the wild.

There are an estimated 48 species of marine mammal (Table 8.10.1) in the hypoxia-affected regions of the Northern California Current System, Black Sea, Baltic Sea, and Gulf of Mexico that may be vulnerable to impacts from ocean deoxygenation.

Table 8.10.1 Marine mammal species (n = 48) inhabiting areas impacted by major hypoxic zones. (Barlow et al., 2010; Becker et al., 2012; Carretta et al., 2017; Ciesielski et al., 2004; Das et al., 2003; Klinowska, 1991; Koschinski, 2001; Natoli et al., 2008; Van de Vijver et al., 2007; Verfuß et al., 2007; Viaud-Martinez et al., 2008; Wells & Scott, 1999; Würsig, 2017) GoM = Gulf of Mexico; CCS = California Current System; BLT = Baltic Sea; BLK = Black Sea

Scientific Name	Common Name	Classification	Region
<i>Balaenoptera acutorostrata</i>	Minke whale	Cetacea	CCS GoM
<i>Balaenoptera borealis</i>	Sei whale	Cetacea	CCS GoM
<i>Balaenoptera edeni</i>	Bryde's whale	Cetacea	CCS GoM
<i>Balaenoptera musculus</i>	Blue whale	Cetacea	CCS GoM
<i>Balaenoptera physalus</i>	Fin whale	Cetacea	CCS GoM
<i>Berardus bairdii</i>	Baird's beaked whale	Cetacea	CCS
<i>Delphinus capensis</i>	Long-beaked common dolphin	Cetacea	CCS GoM
<i>Delphinus delphis</i>	Short-beaked common dolphin	Cetacea	BLK CCS GoM
<i>Eschrichtius robustus</i>	Gray whale	Cetacea	CCS
<i>Eubalaena glacialis</i>	Northern Atlantic right whale	Cetacea	GoM
<i>Feresa attenuata</i>	Pygmy killer whale	Cetacea	GoM
<i>Globicephala macrorhynchus</i> (not confirmed)	Short-finned pilot whale	Cetacea	CCS GoM
<i>Globicephala melas</i>	Long-finned pilot whale	Cetacea	GoM

8.10.2.1 Trends and impacts - nearshore

Marine mammal distribution is primarily driven by prey availability. Therefore, community-wide impacts on gilled species affect the behaviour of marine mammals. Coastal hypoxia is increasing in areas of critical marine mammal habitat (Chan et al., 2008; Conley et al., 2011; Rabalais et al., 2009; Zaitsev, 1992). The severity of these events varies seasonally, but events have recently reached anoxia (<0.5 ml O₂ L⁻¹) or near-complete loss of oxygen, to the point of being unable to sustain gilled animals. In such cases, mass mortality of prey could reduce the ability of mammals to find food.

Coastal hypoxia events lead to shifts in distribution, mobility, predator avoidance, and increased mortality of gilled animals. Severe or prolonged hypoxia can lead to shifts in food web function (Rabalais et al., 2009), with the potential for impacting foraging success of marine mammals. These effects are predicted to increase in the future (Checkley Jr. & Barth, 2009; Gilbert et al., 2010; Grantham et al., 2004; Pierce et al., 2012; Rabalais et al., 2009; Steingass & Horning, 2017).

<i>Grampus griseus</i>	Risso's dolphin	Cetacea	CCS GoM
<i>Kogia breviceps</i>	Pygmy beaked whale	Cetacea	CCS GoM
<i>Kogia sima</i>	Dwarf sperm whale	Cetacea	CCS GoM
<i>Lagenodelphis hosei</i>	Fraser's dolphin	Cetacea	GoM
<i>Lagenorhynchus obliquidens</i>	Pacific white-sided dolphin	Cetacea	CCS
<i>Lissodelphis borealis</i>	Northern right whale dolphin	Cetacea	CCS
<i>Megaptera novaeangliae</i>	Humpback whale	Cetacea	CCS GoM
<i>Mesoplodon</i>	Mesoplodont beaked whales	Cetacea	CCS
<i>Mesoplodon bidens</i>	Sowerby's beaked whale	Cetacea	GoM
<i>Mesoplodon densirostris</i>	Blainville's beaked whale	Cetacea	GoM
<i>Mesoplodon europaeus</i>	Gervai's beaked whale	Cetacea	GoM
<i>Orcinus orca</i>	Killer whale	Cetacea	CCS GoM
<i>Peponocephala electra</i>	Melon-headed whale	Cetacea	GoM
<i>Phocoena phocoena</i> <i>Phocoena phocoena relicta</i> <i>Phocoena phocoena vomerina</i>	Harbour porpoise	Cetacea	BLT BLK CCS
<i>Phocoenoides dalli</i>	Dall's porpoise	Cetacea	CCS
<i>Physeter macrocephalus</i>	Sperm whale	Cetacea	CCS GoM
<i>Pseudorca crassidens</i>	False killer whale	Cetacea	GoM
<i>Stenella attenuata</i>	Pantropical spotted dolphin	Cetacea	GoM
<i>Stenella clymene</i>	Clymene dolphin	Cetacea	GoM
<i>Stenella coeruleoalba</i>	Striped dolphin	Cetacea	CCS GoM
<i>Stenella frontalis</i>	Atlantic spotted dolphin	Cetacea	GoM
<i>Stenella longirostris</i>	Spinner dolphin	Cetacea	GoM
<i>Steno bredanensis</i>	Rough-toothed dolphin	Cetacea	GoM
<i>Tursiops truncatus</i>	Common bottlenose dolphin	Cetacea	BLK CCS GoM
<i>Ziphius cavirostris</i>	Cuvier's beaked whale	Cetacea	CCS GoM
<i>Arctocephalus townsendi</i>	Guadalupe fur seal	Pinnipedia	CCS
<i>Callorhinus ursinus</i>	Northern fur seal	Pinnipedia	CCS
<i>Eumatopias jubatus</i>	Steller sea lion	Pinnipedia	CCS
<i>Halichoerus grypus</i>	Grey seal	Pinnipedia	BLT
<i>Mirounga angustirostris</i>	Northern elephant seal	Pinnipedia	CCS
<i>Phoca hispida</i>	Ringed seal	Pinnipedia	BLT
<i>Phoca vitulina</i>	Harbour seal	Pinnipedia	BLT CCS
<i>Zalophus californianus</i>	California sea lion	Pinnipedia	CCS
<i>Enhydra lutris</i>	Sea otter	Mustelidae	CCS
<i>Trichechus manatus</i>	West Indian manatee	Sirenia	GoM

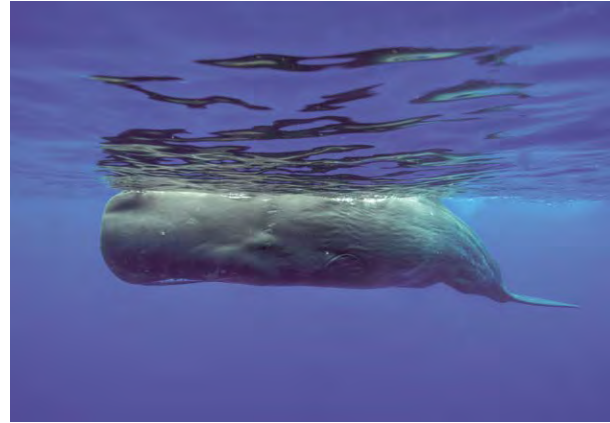


Figure 8.10.1 (A) Elephant seal (*Mirounga angustirostris*). © MZPHOTO.CZ / Shutterstock.com; (B) Sperm whale (*Physeter macrocephalus*). © wildest animal / Shutterstock.com.

8.10.2.2 Ecosystem consequences – nearshore

A number of fish species consumed by marine mammals, and affected by hypoxia, are also important fisheries species. Domenici et al. (2000, 2002) showed that swim speeds, schooling behaviour, and predator avoidance of Atlantic herring (*Clupea harengus*) (Figure 8.10.2) are all affected by hypoxia. During the most severe oxygen depletion, swim speed decreased until schooling was completely disrupted, leading to decreased predator avoidance capabilities. In lesser sandeel (*Ammodytes tobianus*), moderate hypoxia increased burrowing. As hypoxia continued to increase, the number of fish in the water column doubled, and diel burrowing cycles were disrupted by severe hypoxia (Behrens & Steffensen, 2007; Behrens et al., 2010). All of these behavioural modifications point to increased susceptibility to predation.

Greater understanding of the effects of coastal hypoxia on marine mammals can be obtained through rigorous monitoring of diet, behaviour, spatial distribution and abundance. Direct links between coastal hypoxia and marine mammals remain difficult to quantify, but abundant nearshore marine mammals are likely excellent study species to begin unravelling this issue.

8.10.2.3 Implications of continuing ocean deoxygenation

Increased ocean warming, and the resultant decreases in oxygen retention ability of sea water suggest an imminent pattern of worsening hypoxia worldwide. This pattern may lead to increased pressure on marine mammals that are already threatened or endangered. Conversely, increased rates of predation on gilled

species incapacitated or spatially compressed by hypoxia may benefit certain marine mammals. While initially beneficial for opportunistic or generalist species of mammals, hypoxia-driven ecosystem shifts or faunal collapse may result in irreversible trends limiting marine mammal distribution and populations growth and resilience.

8.10.3 Offshore deoxygenation

8.10.3.1 Deoxygenation and foraging behaviour of offshore marine mammals

The capacity of sea water to retain dissolved oxygen universally decreases with increasing temperature (Keeling et al., 2010). Ocean warming simultaneously reduces the water density and stratifies the upper water column; this leads to decreased oxygen transport to subsurface waters and subsequent reduction in the flux of oxygen into the interior ocean (Keeling et al., 2010). These mechanisms suggest offshore deoxygenation may not directly affect offshore marine mammals foraging in shallow waters, such as baleen whales. However, decadal climatic changes have caused deoxygenation events which present as shoaling of the upper boundary of the OMZ or OMZ expansion, in global marine systems, including the North Pacific, Atlantic, eastern tropical Pacific, and Arabian Sea regions (Andreev & Watanabe, 2002; Bograd et al., 2008; Emerson et al., 2004; Gilly et al., 2013; Ito et al., 2016; Keeling et al., 2010; Stramma et al., 2010, 2012). Although the definition of OMZ varies with the physiological tolerance of organisms and ecosystems to hypoxia (e.g. $<20 \mu\text{mol O}_2 \text{ kg}^{-1}$ or $0.5 \text{ ml O}_2 \text{ L}^{-1}$ in the Pacific region), OMZs have generally expanded globally in the last 50 years (Gilly et al., 2013). Furthermore oxygen levels continue to decline, for example Stramma et al. (2008) describe a



Figure 8.10.2 Large adult male killer whale stalking herring in shallow water off Norway. © Nature Picture Library / Alamy stock photo.

rate of decline ranging from $0.09 - 0.34 \mu\text{mol O}_2 \text{ kg}^{-1} \text{ year}^{-1}$ within the 300 - 700 m depth range in the tropical ocean regions of the eastern Atlantic and the equatorial Pacific.

While there are limited qualitative and quantitative data regarding how marine mammals react to changes in prey conditions in relation to OMZ expansion, there have been consistent changes in mesopelagic foraging behaviour of the northern elephant seal in the eastern North Pacific where the OMZ has expanded (shoaled) (Andreev & Watanabe, 2002), showing evidence that OMZ expansion enhances foraging efficiency of an air-breathing predator. There is also evidence of changes in the diving behaviour of squid-feeding beaked and sperm whales, species that may act as model species to provide simple predictions of how these whales may react to ocean deoxygenation through squid feeding.

8.10.4 Ecological and biogeochemical consequences for northern elephant seals from ocean deoxygenation

Northern elephant seals migrate twice a year, undertaking post-breeding and post-moulting migrations to the north-eastern Pacific (from 38° to 60° N and from the

coast to 172.5° E; Le Boeuf et al., 2000; Robinson et al., 2012), during which they dive to depths of 400 - 600 m (maximum depth: 1735 m; Robinson et al., 2010). Elephant seals dive continuously both day and night, diving to shallower depths at night and deeper depths during the daytime, showing an apparently diel pattern (Figure 8.10.3).

Daytime foraging in the OMZ and OLZ (oxygen limited zone; $20 - 60 \mu\text{mol}$; Gilly et al., 2006) accounts for about 40% of their total feeding, as measured by jaw motion suggesting the importance of daytime foraging despite increased dive depths and thereby reduced foraging efficiency. The high dependency of elephant seals on prey found within the OMZ and OLZ during the day may relate to increased efficiency of capturing prey residing in the OMZ and OLZ at >600 m depth in order to avoid predation pressure in the oxygen rich zone. Gilled animals within the OMZ demonstrate lower metabolic rates making their capture easier (Childress & Seibel, 1998; Naito et al., 2013; Seibel, 2011). Although the mechanistic details are not fully understood, marine hypoxia allows seals to consume large amounts of prey in the OMZ and OLZ due to increased foraging efficiency (roughly estimated total and daytime amounts (i.e. from OMZ): $210,000 \text{ t year}^{-1}$ and $84,000 \text{ t year}^{-1}$

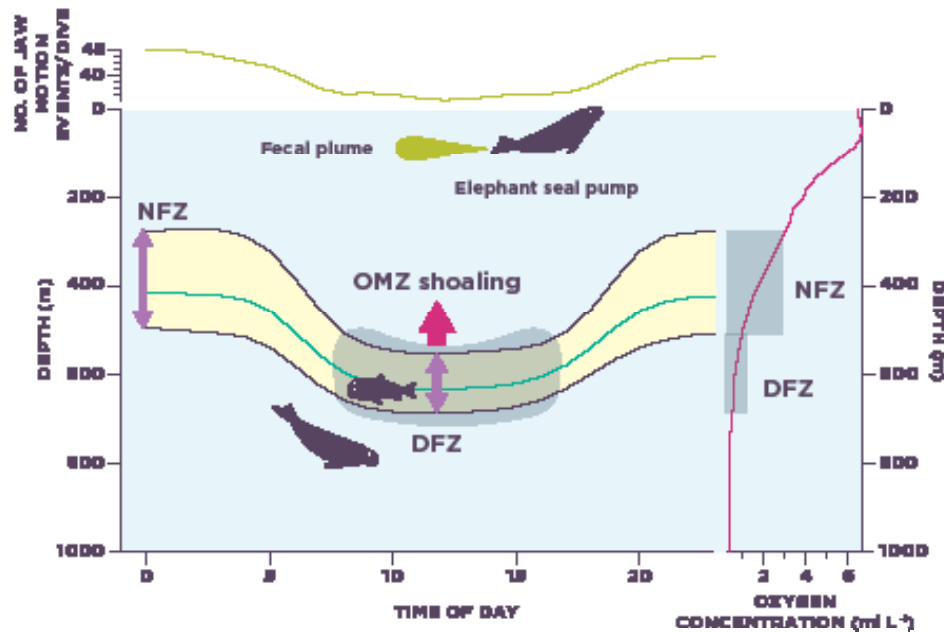


Figure 8.10.3 Typical diel pattern of diving and foraging behaviour based on jaw motion activity of northern elephant seal in the north-eastern Pacific, and typical vertical distribution of oxygen in the region. NFZ and DFZ denote the Night-time Foraging Zone and the Daytime Foraging Zone respectively. These zones of foraging were determined by the depth ranges between average minimum and maximum depth of jaw motion events in every hour during post breeding migration of a seal (Total no. of foraging dives: 6408, Seal ID: PB-1015). Boxes in the vertical oxygen distribution profile indicates depth and oxygen content ranges of NFZ and DFZ.

respectively based on the daily consumption rate: 3% of body mass (Naito et al., 2013), average body mass: 200 kg (assumed value), estimated number of foraging days: 200 (Le Boeuf et al., 2000), approximate population size: 175,000 (Weber et al., 2000) which underlies the important role of seals in structuring the mesopelagic ecosystem. Further shoaling of the OMZ and OLZ in the future may enhance seal foraging efficiency due to (1) increase of inactive prey, (2) decreased diving cost enabling an increase of prey search time during the dive bottom phase, and (3) increased prey density due to vertically-compressed oxygenated habitat (Gilly et al., 2013). These may further increase the dependency of feeding in the expanded OMZ during the day as compared to night-time foraging, which as a result may decrease. A large modification of the day/night dependency ratio (i.e. from the present approximate day to night ratio of 4:6) may trigger an ecological disturbance, ultimately changing the species composition of the deep-sea community as prey composition may differ between day and night (Naito et al., 2017). Enhanced foraging efficiency could elevate the population fitness and breeding rate of elephant seals, leading to a potential long-term increase in population and thereby top-down modification of their terrestrial breeding habitats. However, any future increase of this population in relation to ocean deoxygenation is uncertain, as carrying capacity at breeding sites may also limit

population trends. While long term population increases of elephant seals has been reported (6% increase year⁻¹; Weber et al., 2000), how this increase relates to ocean deoxygenation remains to be confirmed.

The unexpectedly high dependency of elephant seals on prey in the OMZ may have an unprecedented effect on nutrient cycling in relation to OMZ expansion. While an important function of nutrient pumping to the surface water by baleen whales has been reported (Lavery et al., 2010; Roman & McCarthy, 2010), no biological pump information from the OMZ has been reported. Elephant seals, as deep-water foragers, may serve a similar



Figure 8.10.4 Dall's porpoise *Phocoenoides dalli* in south-east Alaska. © Minden Pictures / Alamy stock photo.



Figure 8.10.5 Cuvier's beaked whale (*Ziphius cavirostris*). © Nature Picture Library / Alamy stock photo.

function as nutrient cyclers. Foraging within the OMZ is particularly important in biogeochemical cycling, since prey extraction from the OMZ and subsequent nutrient delivery to the surface in the form of a faecal plume and urine is relatively large allowing seals to play a driving role in this cycle. The pump effect of feeding by elephant seals and other marine mammals enhances the productivity of surface waters (Lavery et al., 2010). Although the quantitative details are not known, it is predicted that increased future productivity will lead to an increase in the export of organic matter to subsurface waters, as a result of deoxygenation in subsurface waters (Gilly et al., 2013) driven by an increase in oxygen consumption by microbial respiration and nitrification, combined with the stratification and surface water warming effects.

8.10.5 Deoxygenation and foraging behaviour of toothed whales

Toothed whales (odontocetes) are dependent upon the mesopelagic zone as their major foraging zone (Belta, 2015); pelagic porpoises and dolphins (small Delphinidae) (Figure 8.10.4) tend to forage in the upper part of the mesopelagic zone, while whales of the Physeteridae, Ziphiidae and large Delphinidae (Figure 8.10.5) dive very deep to forage in the lower part of

the mesopelagic zone (Aoki et al., 2007; Belta, 2015; Clarke, 1996; Miller et al., 2004; Ohizumi et al., 2003; Tyack et al., 2006). Among toothed whales, diving and foraging behaviour of sperm whales and some beaked whales have been investigated extensively, and the results indicate that they hunt and consume squids using an echolocation system in the lower part of the mesopelagic zone, often foraging at deeper depths than elephant seals (Aoki et al., 2007; Blanco & Raga, 2000; Clarke, 1996; Kawakami, 1980; Miller et al., 2004; Ohizumi et al., 2003; Santos et al., 2000; Tyack et al., 2006). This suggests that a key to understanding sperm whale response to ocean deoxygenation is through quantitative understanding of squid behaviour in relation to the OMZ. Although squid forage in the euphotic zone, they are well-adapted to the low oxygen environment and utilize the OMZ to forage and rest (Gilly et al., 2006). These resting squid may give whales a large advantage in foraging. Davis et al. (2006) monitored diving behaviour of sperm whales and the jumbo squid, *Dosidicus gigas*, which rests in the upper boundary of the OMZ (>300 m depth) after feeding on myctophid fish in warmer shallow waters in the Gulf of California. Consistent dive depths of sperm whales foraging for jumbo squid suggested that the OMZ expansion compresses the distributional range of squids allowing whales to forage upon them

more efficiently. Compared to sperm whales within the shallow OMZ in the Gulf of California, other populations of sperm whales often dive to deeper depths (400-1000 m) in zones with no apparent OMZ, including the North Atlantic, Gulf of Mexico, Ligurian Sea, Kumano coast of Japan, and Ogasawara Islands (Aoki et al., 2017; Watwood, 2006). These differences in foraging depth suggest that sperm whales and beaked whales may in fact experience a large advantage to foraging within areas of OMZ shoaling, due to greater efficiency in feeding upon squid. As with elephant seals, increased efficiency of foraging by toothed whales could lead to significant disturbance and disruption to the marine ecosystem through top-down effects leading to a trophic cascade (Estes & Palmisano, 1974) of ecosystem function in the future.

Toothed whales may have a similar deep biological pump function which affects biogeochemical cycling as in the case of the northern elephant seal, but the details of this pump function are as yet not clearly understood. Further investigations detailing the relationship between marine mammals and mesopelagic deoxygenation are necessary to enable a clear understanding of how ocean warming is affecting the deep sea ecosystem.

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8.11 The significance of ocean deoxygenation for the physiology of marine organisms

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Summary

- Breathing water is hard work, making the physiological performance and behavioural repertoire of marine organisms heavily dependent on their capacity to extract oxygen from the ambient sea water.
- There is no such thing as an oxygen threshold above which everything is fine and below which survival is at risk and conservation measures should be implemented. Ocean deoxygenation affects marine organisms as soon as it departs from full aeration, with downstream consequences on their activities and capacity to face natural contingencies. The target for conservation strategies should be, therefore, preserving the aeration of marine waters. This being said, it must be recognized that naturally hypoxic ecosystems exist in nature, supporting species with unique physiological and behavioural features. These poorly oxygenated ecosystems must be identified and preserved as they also contribute to biodiversity.
- Present-day deoxygenation of the ocean favours hypoxia tolerant species at the expense of hypoxia sensitive ones. This is illustrated by shifts in the species composition of marine communities.
- In the short term, marine organisms can respond to ocean deoxygenation through changes in their physiology and behaviour. Alteration in feeding behaviour and distribution pattern are classically observed, potentially leading to reduced growth and to more difficulties completing their life cycle.
- In the medium term, epigenetic processes may provide marine populations with a rapid way to acclimate to the rapidly changing oxygenation state. However, this developing field of biological sciences is too recent to fully evaluate the contribution of epigenetic responses to marine organisms' adaptation to ocean deoxygenation.
- Changes in the phenology (timing of life stage-specific events) of marine species, in relation with ocean deoxygenation have not been observed. However, deoxygenation generally co-occurs with other environmental disturbances (ocean warming and acidification) which are also liable to affect marine species' life-cycle. The lack of understanding of their interactions and synergies currently restricts our ability to assess marine populations' capacity to phenologically respond to ocean deoxygenation.
- In the long term, adaptation through natural selection may occur in species with short generation time. This is, however, more difficult to envisage in most commercial fish species which are characterized by long generation time. Between now and 2100, approximately 80 generations of sardine (*Sardina pilchardus*; age at first maturity: 1 year) but only 10-15 generations of Atlantic cod (*Gadus morhua*; age at first maturity: 5 to 8 years) will follow one another. These numbers of generations are relatively modest and cast some doubts on the capacity of commercial fish species in particular, to adapt to the fast-changing ocean conditions.
- Large inter-individual and inter-specific variation in tolerance to reduced oxygen availability exists in nature. This diversity in marine species' responses makes them challenging to comprehend. Moreover, synergies with other environmental stressors, whether natural or anthropogenic such as, ocean warming and acidification, add to this difficulty.
- Over the last 30 years, marine biologists and physiologists have made tremendous efforts to gain understanding of how marine animals respond to environmental conditions and, in particular, to reduced oxygen availability. Despite all these efforts there is still a long way to go and intensifying collaboration between physiologists, ecologists, modellers and managers is key to providing policy makers and marine resources' managers with fully operational, science-based information.

Ocean deoxygenation effect	Potential consequences
Reduced oxygen availability in the water ventilated over the respiratory surfaces (gills, skin).	<ul style="list-style-type: none"> • Reduced diffusion of oxygen across the epithelium of the respiratory organs (gill, skin). • Less oxygen transported to the cells by the internal circulatory fluid (blood, extracellular fluid).
Reduced oxygenation of the circulatory fluid.	<ul style="list-style-type: none"> • Reduced oxygen diffusion from the circulatory fluid into the cells. • Reduced oxygen availability in the cellular power houses (mitochondria).
Reduced oxygen diffusion into mitochondria.	<ul style="list-style-type: none"> • Reduced energy production in the form of ATP.
Reduced ATP production.	<ul style="list-style-type: none"> • Reduced capacity for activities. • Prioritization of functions by reallocating blood flow among the various organs. • Prioritization at the expense of non-essential (non-life sustaining) activities such as growth and reproduction.
Reduced growth and reproduction.	<ul style="list-style-type: none"> • Increased risk of predation. • Reduced survival. • Altered recruitment. • Altered population production (biomass) and demography.
Altered recruitment, production and demography.	<ul style="list-style-type: none"> • Altered ecosystem functioning. • Altered ecosystem services.

8.11.1 Introduction

For thousands of years, marine organisms have been a staple of the diet of many coastal human populations, as well as a determining factor of their health and wealth. Yet, proper knowledge about how environmental conditions influence the distribution and abundance of this important food source is relatively recent. As an example, only 70 years ago, a French naval historian presenting the state of scientific knowledge on the reproduction of Atlantic cod suggested that *“une certaine destruction est nécessaire, car, si tous les oeufs éclosaient et si tous les poissons arrivaient à l'état adulte, le monde serait mis en péril au bout de quelques générations et l'océan risquerait de se combler.”* [a certain destruction is necessary or, if all eggs hatched and if all fish grew to adult stage, the world would be in danger after a few generations and the oceans would be filled (translation by the authors)] (Lacroix, 1949). This poor perception of, and lack of basic knowledge about, how environmental conditions influence marine organisms appeared even more clearly in the late 1980s and early 1990s when population statistics and models did not anticipate the collapse of crucial fish stocks such as the Western Atlantic cod stocks (Atkinson et al., 1997; Chouinard & Fréchet, 1994; Rose et al., 1994, 2000; Taggart et

al., 1994). Faulty models, poor data and non-science-based management decisions allowed for overfishing (Rose, 1997; Steele et al., 1992; Walters & Maguire, 1996), but the role of environmental variables was also mistakenly dismissed (Hutchings & Myers, 1994; Myers et al., 1996). Nowadays, fortunately, the key role played by the environment in determining marine organisms' activities and performance is taken more broadly into account, with large efforts being devoted to increasing current understanding of their physiology and behaviour (McKenzie et al., 2016). The recent controversy about the influence of ocean warming on fish body size and its possible ecological consequences provides a perfect illustration of the issues and challenges that the scientific community is facing in this regard (Cheung et al., 2013; Lefevre et al., 2017; Pauly & Cheung, 2017). In that case, the question was whether an unfavourable gill surface area to body mass ratio makes big fish less likely to survive global warming, shifting the composition of fish populations in favour of smaller individuals.

Among all the environmental factors that are liable to affect marine organisms, water temperature and oxygenation are certainly the most potent. With remarkable exceptions such as some sharks and tunas, as well as the opah (Figure 8.11.1), heat moves

Box 8.11.1 A case study, the Atlantic cod

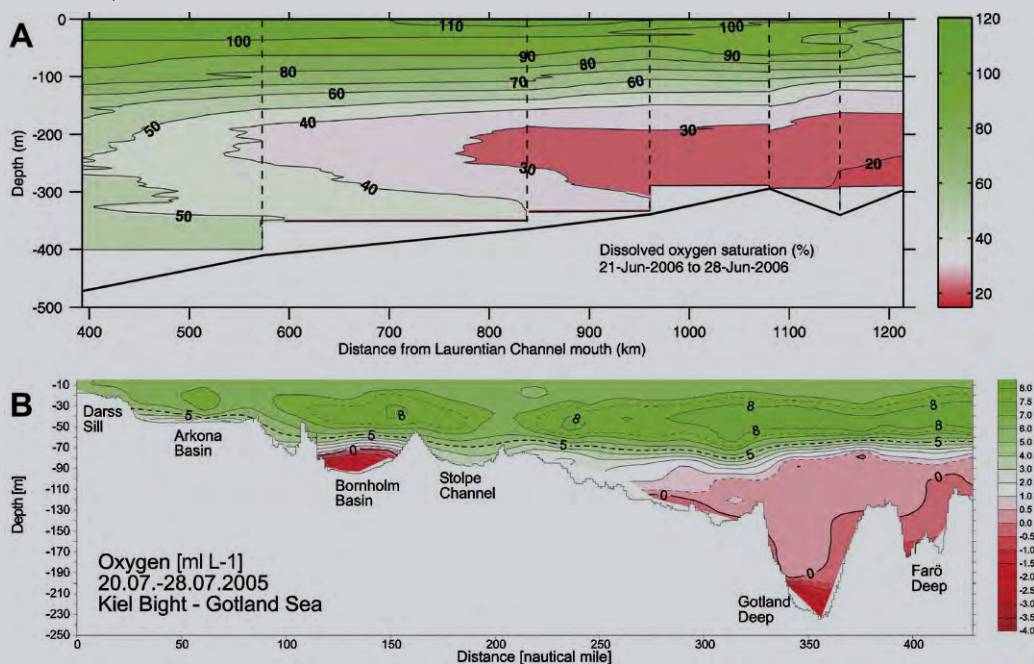
Atlantic cod (*Gadus morhua*) is a major source of food and wealth on both sides of the North Atlantic. In at least two regions of its distribution area, the Baltic Sea and the Gulf of Saint Lawrence, cod is faced with severely deoxygenated water (Chabot & Claireaux, 2008; Chabot & Gilbert, 2008) with oxygen levels less than 30% of air equilibration over extended areas. Physiologists have shown that 20-30% aerated water allows cod to meet minimal, life sustaining oxygen requirements but that it is not enough to cover the oxygen demand associated with activities such as feeding, escaping a predator or coping with a disease (Claireaux et al., 2000; Plante et al., 1998; Schurmann & Steffensen, 1997).



Box Figure 8.11.1.1 Atlantic cod (*Gadus morhua*). © Richard Larocque DFO.

Even when not life-threatening, water deoxygenation has a range of negative effects on cod. For instance, the growth rate of cod starts to decline as soon as ambient oxygenation drops below 70% of full aeration. This is due to decreased food consumption caused by a reduced ability to cover the additional demand for oxygen caused by digestion (Chabot & Dutil, 1999; Jordan & Steffensen, 2007). This is confirmed by laboratory experiments and field observations which show that cod avoid less than 70% saturated waters (Chabot & Dutil, 1999;

Claireaux et al., 1995; Dutil et al., 2007; Herbert & Steffensen, 2005; Johansen et al., 2006; Schurmann & Steffensen, 1994).



Box Figure 8.11.1.2 Vertical profile of dissolved oxygen along a longitudinal transect in (A) the Estuary and Gulf of St. Lawrence and (B) the Baltic Sea. Note the different oxygen units and colour scales, A: from 0 to 100% sat; B: from 0 to 8 ml L⁻¹. Hypoxia is more severe in the Baltic Sea, with negative oxygen concentrations resulting from the combination of anoxia and elevated concentrations of hydrogen sulphide. Anoxia is not observed in the Estuary and Gulf of St. Lawrence. Modified from Fennel et al. (2008).

The Gulf of St. Lawrence is characterized by three deep channels (depth >175 m; Box Figure 8.11.1.2A) through which dense Northwest Atlantic water progresses upstream. As it moves towards the head of the channels, this already deoxygenated water (circa 60%) is further depleted of its oxygen due to the respiration by living organisms and decomposition of organic matter by micro-organisms (Genovesi et al., 2011; Gilbert et

al., 2005; Thibodeau et al., 2006). When reaching the head of the channels, the most extreme deoxygenation conditions are observed, with 18-25% of full saturation.

Since the 1980s, the distribution area of Atlantic cod in the Gulf of St. Lawrence has shrunk severely as a result of overfishing (Castonguay et al., 1999; Chouinard & Fréchet, 1994; Myers et al., 1996) combined with a very cold period which is suspected to have increased natural mortality (Dutil et al., 1999). In recent years, signs of recovery have been observed (DFO, 2017), but it is likely that the poor oxygenation of the deep waters will prevent cod from returning to their full historical distribution (Chabot, 2004; D'Amours, 1993; Gilbert et al., 2007).

The Baltic Sea is a shallow body of water (average 55 m) with several deeper basins connected by channels (Box Figure 8.11.1.2B). Water exchange between the Baltic Sea and the North Sea is limited by sills situated in the Danish Strait where maximum depth varies between 7 and 18 m (Matthäus & Schinke, 1999). Baltic surface waters are brackish (salinity of 6-8 ‰) and they flow out into the North Sea unimpeded over the sills. Occasionally, denser oxygenated waters from the North Sea travel in the opposite direction, passing over the sills into the Baltic. Because of the sills, these inflows of oxygenated water only happen during strong and long-lasting westerlies (Matthäus & Schinke, 1999). Between inflows, oxygen progressively decreases in the deep basins, resulting in severe hypoxia or even anoxia (Matthäus & Schinke, 1999). During the period 1880 to 1976, inflow events occurred regularly. Since then, however, the number of major events has been decreasing, with only one per decade since the 1990s (Morholz et al., 2015). As a result, the deep basins of the Baltic Sea have been deoxygenated and even anoxic for most of the time since the 1970s (Fennel et al., 2008; Laine et al., 2007).

As in the Gulf of St. Lawrence, the presence of cod in the deep basins of the Baltic Sea is conditioned by the water oxygen level. During the 1960s and 1970s, these basins were relatively well oxygenated and were inhabited by cod (Laine et al., 2007; Uzars, 1994). During the 1980s, however, cod vacated the deep basins, switching from a benthic to a pelagic lifestyle and also diet (Tomkiewicz et al., 1998; Uzars, 1994). Moreover, deoxygenated water caused severe egg mortality (Nissling & Westin, 1991; Nissling et al., 1994; Wieland et al., 1994) as an oxygen level above 20% of full saturation is required for proper cod egg development. Since the 1980s, the reproductive volume available to Baltic cod has been shrinking and it is, nowadays, limited to the Bornholm Basin (MacKenzie et al., 2000).



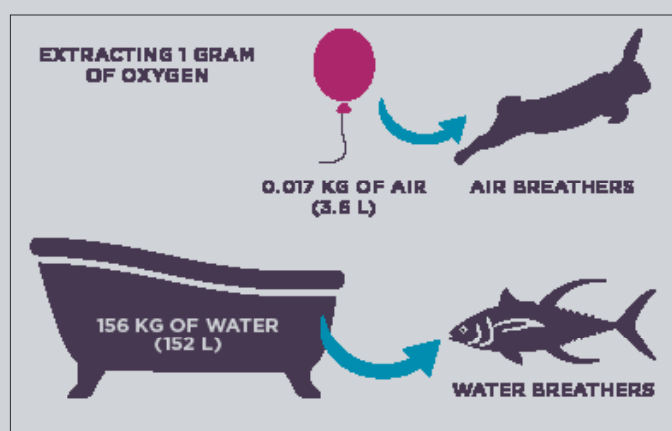
Figure 8.11.1 The opah (*Lampris guttatus*) has whole-body endothermy keeping it ~5 °C warmer than the surrounding environment. © Paulo Oliveira / Alamy stock photo.

so readily between the body of marine organisms and the surrounding water that their internal temperature is typically very close to that of the environment. The first consequence of this is that through controlling the rate of internal chemical reactions, water temperature sets the pace of ectotherms' metabolism and, therefore, influences all aspects of their physiology, behaviour and life cycle. As a result, water temperature is generally considered as the most pervasive dimension of oceanic creatures' ecological niche, as well as a key to understanding their distribution, migration and reproduction.

Beside adequate thermal conditions, the vast majority of marine animals also require properly oxygenated water to survive and thrive. Oxygen is required to fully extract and use the energy ingested as food or stored as reserves. By comparison, reactions that proceed without oxygen (anaerobic metabolic pathways) are approximately 15 times less efficient at accomplishing this task than processes which take place in the presence of oxygen

Box 8.11.2 Breathing in water

Breathing is much more difficult in water than in air. First, there is ~30 times less oxygen in sea water than in air (at 15 °C, 8.2 and 280 mg O₂ L⁻¹ in water and air, respectively) (García & Gordon, 1992; Schmidt-Nielsen, 1997). Second, sea water is ~850 times denser and ~60 times more viscous than air (Chemical Rubber Company, 1984; Wiesenburg & Little, 1988). This means that water breathers must work harder than air breathers to move one litre of medium over their respiratory organs. Third, a much greater volume of water is required to extract the same quantity of oxygen than from air. For instance, to obtain 1 g of O₂ it takes 125 kg of sea water but only 0.0044 kg of air (ratio 28400:1). The most obvious consequence of this is that water breathers cannot afford to regulate their body temperature as this would require much more energy and oxygen. As a compensatory measure, water breathers are equipped with highly efficient respiratory systems which allow them to extract up to 80% of the oxygen present in the medium they breathe (Hughes & Shelton, 1962) while some air breathers barely reach 27% (Altman & Dittmer, 1971). As a result, the ratio of the mass of water to the mass of air that must be ventilated to extract 1 g of O₂ is 9176:1, or 156 kg of water for 0.017 kg of air (Box Figure 8.11.2.1).



Box Figure 8.11.2.1 Breathing in water: Relative ventilatory volume to extract 1 gram of oxygen in water breathers and air breathers.

(aerobic metabolic pathways; du Plessis et al., 2015). This multiplier effect of oxygen explains why, through evolution, marine species have developed a whole range of respiratory systems aimed at transferring oxygen from the ambient water into the cells. In many aquatic breathers, respiratory systems include gill arches which support gill lamellae. As water moves across the gills, a continuous positive O₂ pressure gradient allows the passive diffusion of O₂ from the water to the body fluids (Davis, 1975; Hofmann et al., 2011; Perry & McDonald, 1993). A more or less developed circulatory system then distributes O₂ among the various organs and tissues (Perry & McDonald, 1993). Once in the cell, oxygen is transferred to the cellular power houses, the mitochondria, where it is used to produce adenosine triphosphate (ATP), the chemical fuel of most cellular activities.

The fact that the temperature of oceanic waters fluctuates both spatially and temporally is a readily perceived phenomenon. Harder to envisage, however, is that the ocean's oxygen level also varies to a very

large extent. The terms normoxic, hyperoxic, hypoxic and anoxic are classically used to describe a water mass with regard to its oxygen condition. A classic example to illustrate these terms is that of a tide pool situated high on a rocky shore. At high tide, the water in the pool is vigorously stirred and it is, therefore, fully aerated. This fully air-equilibrated or air-saturated water is termed normoxic (100% sat). At low tide, however, water oxygenation in that pool can vary greatly. During the day, for instance, photosynthesizing algae result in oxygen production that can elevate oxygenation well above air-saturation levels. In such a case, the water is described as being hyperoxic. During the night, in contrast, respiration by organisms present in the pool can drive the oxygen level below full air-saturation, resulting in hypoxic or even anoxic water as saturation reaches 0%.

Deoxygenated or hypoxic conditions are very common in aquatic ecosystems, occurring when dissolved oxygen is removed through respiratory or chemical processes

faster than it is replenished through, for example, exchange with the atmosphere, photosynthesis or advection of oxygen-rich water. In oceanic and coastal environments, stratification of the water column is the most commonly observed limiting factor for the diffusion of oxygen from the surface to deep layers. Eutrophication also leads to low levels of dissolved oxygen, as the increased primary production resulting from nutrient loading contributes to increased detritus deposition and oxygen consumption by the microorganisms involved in their degradation (Bourgault et al., 2012; Breitburg et al., 2009; Cloern, 2001; Diaz & Rosenberg, 1995; Gray et al., 2002; Kemp et al., 2009; Rabalais, 2009; Rabalais et al., 2010; Zhang et al., 2010a). In the context of contemporary climate change and resulting ocean warming, it has also to be borne in mind that oxygen solubility in water is temperature dependent - the warmer the water the less oxygen it can dissolve. This close relationship between temperature and oxygen solubility is one reason why these two environmental factors will be considered jointly herein (McBryan et al., 2013).

The major effects of ocean deoxygenation on the physiology of marine organisms are explored, and implications in terms of conservation and management are identified. The section essentially focuses on fish, but the notions and concepts presented are broadly shared among all marine water breathers. Firstly, key mechanisms that make water-breathing organisms vulnerable to ocean deoxygenation are summarized. Secondly, the main physiological and behavioural responses of marine animals to ocean deoxygenation are highlighted and the resulting impacts on populations and communities are explored. Finally, key challenges and opportunities for conservation of marine species under deoxygenated marine water conditions are discussed.

8.11.2 Mechanisms of ambient oxygen effects: the case of a marine fish

One aspect of metabolism is to convert food material or stored reserves into a form of energy usable to power cellular activities. Adenosine triphosphate, or ATP, is used by virtually all forms of life to store and transfer energy. However, synthesizing ATP efficiently requires oxygen, which must be acquired from the environment (Nelson, 2016). Through evolution, the respiratory and circulatory systems of aquatic organisms have evolved to fulfil this function over a range of ambient oxygen

levels which extends from above air saturation, down to levels below which oxygen-demanding activities are not sustained and death occurs (Chabot et al., 2016).

The concept of a limiting oxygen level curve (LOL-curve) is very useful to describe the gradual limitation imposed by declining ambient oxygen on a fish's ATP production and ensuing capacity for activities (Claireaux & Chabot, 2016; Neill & Bryan, 1991; Neill et al., 1994). The LOL-curve in an idealized fish is presented in Figure 8.11.2. The x-axis represents the range of oxygen levels that this fish may encounter in its environment. When expressed in terms of percentage of air-saturation, this range extends from more than 100% in a vegetated hyperoxic environment, to 0% (anoxia) as observed in a highly eutrophic water body. The y-axis represents, on an arbitrary scale, a range of observable metabolic rates, classically expressed as an oxygen uptake per unit of time and per unit of body mass. Note that, through evolution, respiratory and cardio-circulatory systems have evolved to maximize oxygen uptake when water is fully aerated (100% air saturation).

There are two important points on Figure 8.11.2: the standard metabolic rate (SMR) and the maximum sustainable metabolic rate (MMR). Briefly, SMR quantifies the minimum oxygen requirement to support life-sustaining activities and maintenance processes, whereas MMR estimates the maximum rate at which oxygen can be supplied to activities (Claireaux & Chabot, 2016). The area bounded by SMR and MMR indicate the confines within which an organism's activities must take place.

On the basis of this general framework, consider a typical fish living in a water body where oxygen availability gradually declines. At first (from point *a* to point *b*), the fish initial metabolic rate (*c*.220) is maintained by increasing water flow through the mouth and opercula (ventilation) and by augmenting blood flow in the gill lamellae (perfusion). At point *b*, however, these regulatory measures reach their limit and ambient oxygen availability becomes insufficient to sustain the fish's initial oxygen demand. Point *b* is termed the limiting oxygen level (LOL; *c*.25% air saturation). As the ambient oxygen level continues to fall, the fish then enters a second phase of the response, during which non-obligatory activities are progressively reduced to align the fish's metabolic oxygen demand with the availability of oxygen in the environment. This is achieved via behavioural adjustments such as, reduced swimming

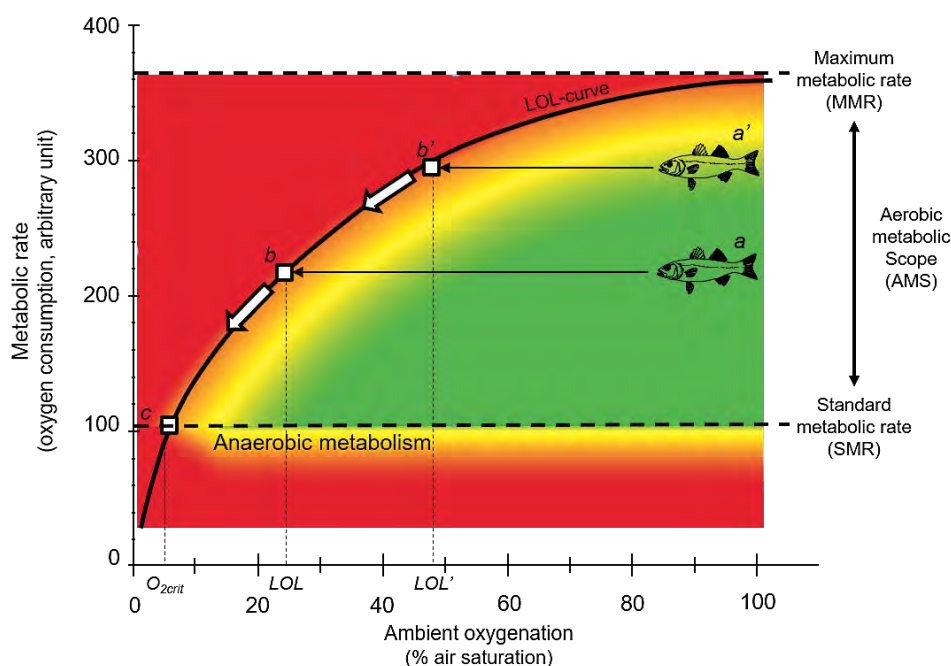


Figure 8.11.2 Influence of ambient oxygenation (% air saturation) upon the aerobic metabolic capacity of an idealized fish (unit less). MMR: maximum sustainable metabolic rate. SMR: standard metabolic rate. LOL-curve: continuum of limiting oxygen levels. The vertical distance between the LOL-curve and SMR represents the aerobic metabolic scope at the ambient oxygen saturation considered. The series a-b-c and a'-b'-c figure the paths of change in metabolic rate in a hypothetical fish in two physiological states and exposed to a progressive deoxygenation of the surrounding water. a and a': initial metabolic rate in normoxia. b and b': indicate the points where the corresponding limiting oxygen levels are reached (LOL and LOL'). c: indicates the critical oxygen level (O_{2crit}) i.e. the minimum oxygen level required to sustain life sustaining activities (SMR).

activity (Domenici et al., 2000; Herbert & Steffensen, 2005; Poulsen et al., 2011; Schurmann & Steffensen, 1994) or reduced food ingestion (Buentello et al., 2000; Chabot & Dutil, 1999; Pichavant et al., 2000, 2001). As the fish's metabolic rate becomes oxygen dependent and "travels" from b to c, a redistribution of blood flow among tissues and organs is also observed (Axelsson et al., 2002), resulting in functional impairments such as reduced swimming capacity (Dutil et al., 2007) and slower digestion (Jordan & Steffensen, 2007; Zhang et al., 2010b). At point c (~8% air saturation), MMR equals SMR, i.e. only oxygen demand supporting short-term survival can be met. The oxygen level corresponding to point c is classically termed the critical oxygen saturation (O_{2crit}). If the ambient oxygen level declines below O_{2crit} , the fish will engage in anaerobic ATP synthesis and survival will then depend on its capacity to establish a proper balance between ATP demand and production.

If that same fish was now heavily engaged in digestion (a'), its oxygen demand would be 30% higher than previously (~300), making it more susceptible to reduced oxygen availability. In the event of a decline in ambient oxygen, that metabolic rate would indeed only be maintained until ~48% air saturation i.e. the corresponding LOL (b'). If water oxygen level was to

decline below 48% air saturation, blood allocation to the digestive tract would then progressively be decreased and the animal's metabolic rate would follow the same path as before, dropping monotonically until O_{2crit} (c).

In summary, LOL values form a continuum, the LOL-curve (solid line in Figure 8.11.2), which extends from MMR measured in normoxia down to O_{2crit} . The vertical distance between the LOL-curve and SMR defines the aerobic metabolic scope (AMS), which delineates the metabolic boundaries within which all aerobic activities must be undertaken and are prioritized when ambient deoxygenation occurs (Fry, 1971). Note that activities include all energy-requiring work, which not only means mechanical work, but also growth, regulation of the internal milieu, gonad maturation, or fighting diseases and other stresses. The lower the ambient oxygen availability, the smaller AMS and, therefore, the lesser the capacity of fish to allocate oxygen to these activities. Reciprocally, the higher the metabolic demand for oxygen, the higher the corresponding LOL and, therefore, the sooner the limitation in case of decreasing oxygen availability in the environment i.e. $LOL' > LOL$ on Figure 8.11.2. For this reason, Fry (1971) called dissolved oxygen a limiting factor for metabolic rate.

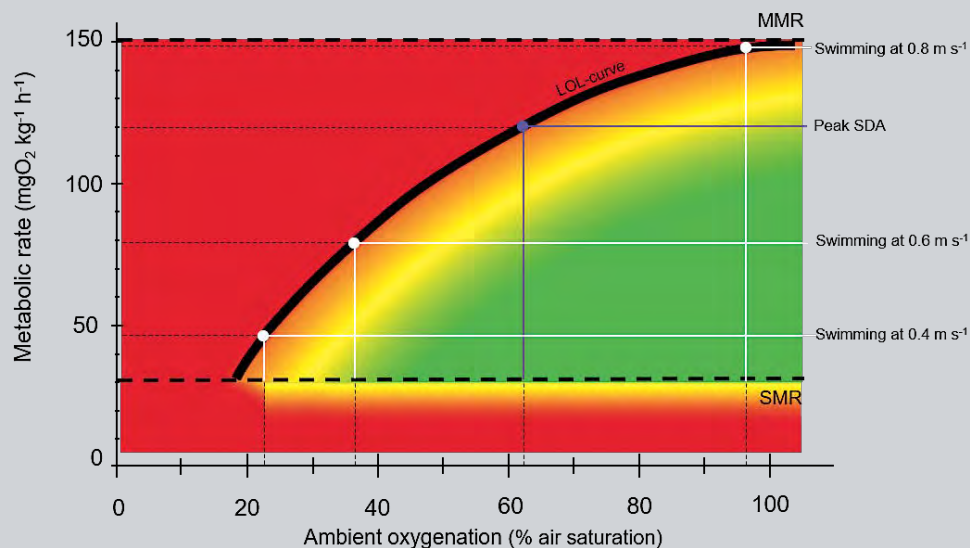
Box 8.11.3 A case study, the European sea bass (*Dicentrarchus labrax*)

Understanding the limitations imposed by ocean deoxygenation on organisms' activities and performance has been a challenging issue since the very early days of animal physiology. In those days, gaining new knowledge about the mechanisms involved in hypoxia tolerance was the main objective. In recent decades, however, new challenges emerged, such as those related to the increasing pressure from human activities upon marine ecosystems. From this perspective, contemporary climate change and related ocean warming, acidification and deoxygenation are particularly hot topics for marine biologists. Faced with these new challenges, animal physiologists responded by adopting a drastic change in approach, moving from mechanistic (reductionist) orientated investigations to increasingly integrative studies aimed at understanding how the physiological influences of the environment propagate across the biological organization scale to eventually affect population-level (dynamic, production, evolution) and ecosystem-level (food web, biodiversity, resilience) processes. In this context, the notions of aerobic metabolic scope and limiting oxygen level proved to be effective tools (Claireaux & Lagardère, 1999; Claireaux & Lefrançois, 2007; Fry, 1947, 1971; Marras et al., 2015; Neill & Bryan, 1991; Neill et al., 1994).



Box Figure 8.11.3.1 European sea bass (*Dicentrarchus labrax*).
© imageBROKER / Alamy stock photo.

In the Atlantic Ocean, the distribution of the European sea bass (*Dicentrarchus labrax*; Box Figure 8.11.3.1) extends from the coast of Morocco to the South of Norway. The species is also present in the Mediterranean Sea as well as in the Black Sea. The sea bass is a eurytherm and euryhaline fish, capable of withstanding temperatures from 2 °C to 36 °C and salinities from 0‰ to 40‰. The sea bass is the target of commercial and recreational fisheries and Atlantic stocks are threatened, as indicated by the 32% lower total biomass in 2011-2012 compared with the three previous years. Accordingly, fishing restrictions have been put in place to preserve this stock (European Council Regulation, 2015).



Box Figure 8.11.3.2 Limiting effect of ambient oxygenation (% air saturation) upon the activities of 15 °C-acclimated European sea bass (*Dicentrarchus labrax*). Maximum sustainable metabolic rate (MMR) and standard metabolic rate (SMR) are indicated by the thick horizontal dotted lines. The thick solid line represents the limiting oxygen level-curve (LOL-curve). The thin white lines represent the metabolic rates associated with swimming at velocities of 0.4, 0.6 and 0.8 m s⁻¹ and indicate the corresponding minimum oxygen level required to do so (LOL). The thin blue line represents the peak metabolic demand for oxygen following a full meal (specific dynamic action; SDA) and also indicate the corresponding LOL.

Box Figure 8.11.3.2 illustrates the limiting effect of ambient oxygenation on two ecologically crucial activities of the European sea bass: swimming and feeding. Swimming capacity is a key determinant of this top predator's ecological performance (Claireaux et al., 2006). When acclimated to a water temperature of 15 °C, the maximum swimming speed of a 200 g sea bass is approximately 80 cm s⁻¹. The oxygen demand to sustain such a swimming speed is approximately 300 mg O₂ h⁻¹ kg⁻¹. Such a metabolic demand for oxygen can only be covered in fully aerated water (100% air saturation). As soon as ambient oxygenation departs from full aeration, sea bass maximum swimming velocity decreases, dropping to 60 cm s⁻¹ at 37% saturation and to only 40 cm s⁻¹ at 22% air saturation. The second most important activity considered in Box Figure 8.11.3.2 is feeding. A sea bass feeding maximally can ingest approximately 3% of its body mass in one meal. At 15 °C, digestion spreads over several days and will mobilize energy and, therefore, oxygen. The increased oxygen demand measured during digestion is termed the specific dynamic action (SDA) and it generally peaks 15-20 h post-feeding with peak oxygen demand during SDA attaining ~240 mg O₂ h⁻¹ kg⁻¹ (Lefrançois et al., 1998). The minimum ambient oxygen level necessary to allow such a rate of oxygen consumption is 60-65% air saturation. In a water body where the oxygenation level is less than 60% air saturation, sea bass cannot feed maximally, with consequences on growth and downstream impacts on size dependent performance such as, predator avoidance and reproductive capacity.

8.11.3 Responses of marine organisms to hypoxia

Over the past decades, the occurrence of hypoxic episodes in marine waters has increased drastically (Diaz & Rosenberg, 1995; Diaz, 2001), with an increase in the number of areas affected but also in the extension, severity and duration of these episodes (Breitburg et al., 2018; Chan et al., 2008; Conley et al., 2007; Stramma et al., 2008; Turner et al., 2008). Projections suggest that these circumstances will become even more common in the future (Breitburg et al., 2018; Keeling et al., 2010; Vaquer-Sunyer & Duarte, 2008).

As indicated earlier, coastal and oceanic waters are oxygenated from the surface, either directly, through oxygen transfer from the atmosphere, or from oxygen release by photosynthesising algae and phytoplankton. With the warming of the global ocean, however, surface waters absorb less oxygen due to reduced oxygen solubility (Carpenter, 1966). Moreover, when absorbed, the transfer of oxygen down the water column is made more difficult as warmer surface waters are lighter and are, therefore, less likely to sink and mix with deeper, colder water layers. In estuaries, where surface waters are generally less salty and therefore lighter than deeper water, the propensity to stratification is maximal, making benthic hypoxia an even more frequent event. This complex combination of biological and physical processes involving interactions between the “four spheres” (lithosphere, atmosphere, hydrosphere and biosphere) explains why ocean oxygenation is variable and why changes can stretch over years or even

decades (Long et al., 2016), making them difficult to predict. There exist four levels of marine organisms' response to deoxygenation: species specific variation in tolerance, acclimation, epigenetics and adaptation.

8.11.3.1 Species specific variation in tolerance to deoxygenation

There is a broad variability in the capacity of marine species to tolerate ambient deoxygenation. Although there can be quite a bit of variation among the species of a given group, fishes and crustaceans are generally viewed as the most sensitive groups to hypoxia. At the other end of the spectrum, cnidarians, a phylum which includes the jellyfish, is among the most hypoxia tolerant animal groups. The overall winners are priapulids, a phylum of unsegmented marine worms (Vaquer-Sunyer & Duarte, 2008).

All the components of the oxygen cascade system, from oxygen extraction at the respiratory surface, through to its utilization for ATP production by mitochondria, are liable to display species-specific features which can explain the broad inter-specific differences in hypoxia tolerance. These differences not only concern aspects of ventilation and oxygen diffusion across respiratory epithelium, but also features of the circulatory system as well as the presence, nature and functioning characteristics of the respiratory pigments. These differences not only contribute to segregate marine organisms' ecological niche, but also set the boundaries of their capacity to cope with environmental deoxygenation.

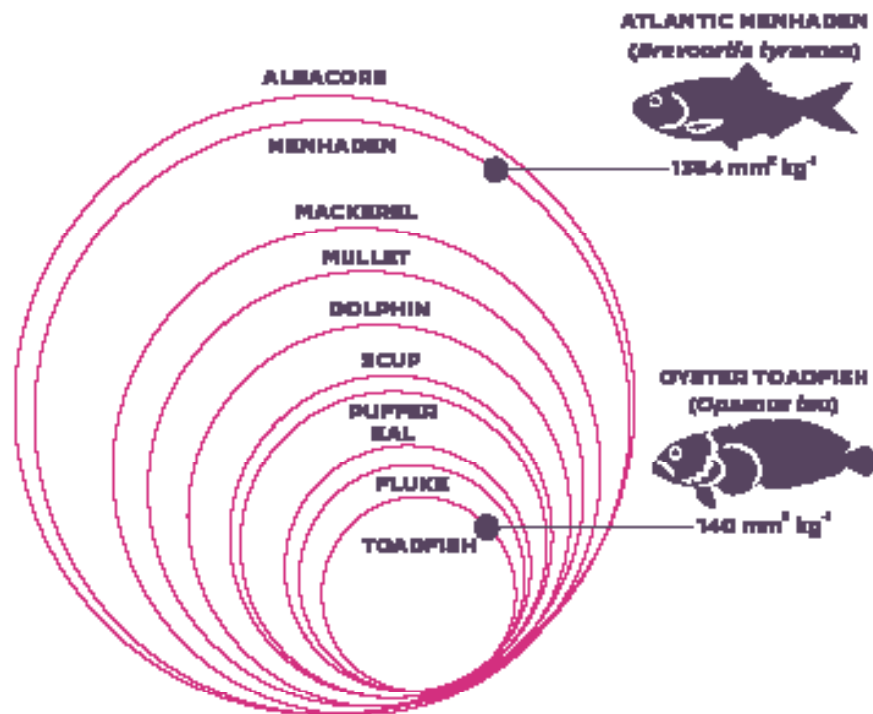


Figure 8.11.3 Relative gill areas of marine fishes (from Gray, 1954).

The surface of respiratory organs must be large enough to allow sufficient oxygen extraction from the water to sustain downstream activities. The link between oxygen extraction capacity and life style is especially clear in fish (Figure 8.11.3). When species of approximately the same body mass are compared, there is indeed a definite difference as illustrated by the streamlined, active menhaden (*Brevoortia tyrannus*) which has a gill surface area nearly ten times that of the sluggish toadfish (*Opsanus tau*) (Figure 8.11.4). The ecological significance of this relationship is twofold as it also implies that organisms with high metabolic demands for oxygen are also those that will be limited the most in case of ambient deoxygenation. As a result, gill surface area to body mass ratio is a convenient proxy to compare hypoxia tolerance among marine organisms (Childress & Seibel, 1998). Mass for mass, animals with large gills will tend to be more active but also less tolerant to hypoxia than fish with small gills.

The inter-specific variability in hypoxia tolerance affects both the position and shape of the LOL-curve, as well as the value of the O_{2crit} (Figure 8.11.2), with lower values of the latter being generally observed in intertidal species in comparison with fast swimming pelagic species (Richards & Lau, 2017). This difference is believed to represent an adaptation to hypoxic conditions, a more common feature of intertidal and coastal ecosystems. As previously discussed, the lower O_{2crit} , the lower the

oxygen threshold below which life sustaining activities are no longer covered aerobically and survival is at risk.

Blood oxygen affinity is also a primary determinant of hypoxia tolerance in marine organisms (Farrell & Richards, 2009; Mandic et al., 2009; Wells, 2009). It is generally quantified as P_{50} , which is the partial pressure of oxygen at which blood is 50% saturated with oxygen. Blood with a high affinity for oxygen has a low P_{50} , while animals with blood with a low P_{50} are more hypoxia tolerant. Tunas, for example, are active pelagic fish living in well aerated water bodies. Their blood oxygen affinities are relatively low, with P_{50} values ranging from 2 to 3 kPa (Brill & Bushnell, 1991; Jones et al., 1986; Lowe et al., 2000). The lugworm (*Arenicola marina*) (Figure 8.11.5), on the other hand, is endemic to shallow intertidal ecosystems chronically affected by severe hypoxic episodes and its blood has 20 times more affinity for oxygen than tunas, with a P_{50} of 0.1 to 0.2 kPa (Everaarts, 1986).

8.11.3.2 Acclimation

It is important that the concepts of acclimation and adaptation are defined. Adaptation is understood as the evolutionary process by which, through natural selection, a population's gene pool changes to accommodate new environmental conditions (Ownby et al., 2002). Acclimation, on the other hand, results from

behavioural, physiological, phenological and epigenetic adjustments made by an organism to minimize the effects of environmental disturbance.

8.11.3.2.1 Behaviour

Behaviour is the first line of defence when environmental conditions depart from optimum. Mobile organisms have the capacity to avoid hypoxic waters and this is generally associated with comparably higher oxygen thresholds than in less mobile and, *a fortiori*, sessile species. For example, fishes have been reported to move higher in the water column when bottom waters become hypoxic (Claireaux et al., 1995; Wu, 2002), and fishes and invertebrates can leave an area that has become hypoxic (Bell & Eggleston, 2005). These behavioural changes aiming at ensuring short term survival can have significant ecological implications. When exposed to progressive hypoxia, mullets (*Liza aurata* and *Mugil cephalus*) (Figure 8.11.6) perform aquatic surface respiration by which they rise to the surface to ventilate in the well-oxygenated layer of water in contact with air (Lefrançois et al., 2009; Shingles et al., 2005). However, although providing an advantage in hypoxic habitats, surfacing also exposes fish to significantly increased

risks of predation by birds (Domenici et al., 2007; Kersten et al., 1991; Kramer et al., 1983). Similarly, crustaceans have been reported moving to shallower areas to avoid hypoxic bottom waters, making them more vulnerable to predators (Bell et al., 2003). Furthermore, organisms moving out of hypoxic waters may occur in increased density in well aerated environments, intensifying inter- and intra-specific competition (Eby & Crowder, 2002; Eby et al., 2005). If these indirect costs become too high, and hypoxia is not too severe, marine organisms may also remain in hypoxic water instead of avoiding it (Bell & Eggleston, 2005). Another illustration of the ecological consequences of environmental hypoxia is that hypoxic water layers may act as predation refuges for forage species from active, oxygen-demanding predators which are thus less capable of active predation in deoxygenated water (Altieri, 2008; Anjos et al., 2008; Hedges & Abrahams, 2015).

Fast-moving organisms do not necessarily show a broader behavioural repertoire than those with restricted mobility. A whole range of behavioural responses have indeed been observed in benthic species. Polychaetes, annelids, crustaceans, bivalves, priapulids and anemones, for instance, leave their burrows and



Figure 8.11.4 The oyster toadfish (*Opsanus tau*) waits in its lair. © YAY Media AS / Alamy stock photo.



Figure 8.11.5 Lugworm (*Arenicola marina*) casts. © John M Baxter.

tubes, or reduce their burial depth, in the presence of hypoxia (Dyer et al., 1983; Nestlerode & Diaz, 1998; Neuenfeldt et al., 2009; Nilsson & Rosenberg, 1994; Pihl et al., 1992). Bivalves can also stretch their siphon upward into the water column to reach waters with higher oxygen concentration (Jorgensen, 1980). Some echinoderms stand immobile on their arm tips with the central disk elevated to avoid the hypoxic bottom water (Baden et al., 1990) while some gastropods can climb structures to reach waters with higher oxygen concentration (Vaquer-Sunyer & Duarte, 2008). Even sessile organisms can avoid frequently occurring or chronic hypoxia by avoiding them as larvae, before settling (positive oxytaxis; Lagos et al., 2015).

8.11.3.2.2 Physiology

The full coverage of the species-specific characteristics of oxygen homeostasis in marine organisms is beyond the scope of the present section. A general framework can, however, be laid down. Through evolution, a suite of physiological systems has developed to ensure optimal cellular oxygenation and downstream ATP production (Nilsson & Östlund-Nilsson, 2008). This physiological infrastructure for oxygen delivery includes an entry (respiratory surfaces), a transport vehicle (a

circulatory fluid, with or without respiratory pigments, possibly included in red blood cells), sets of highways and secondary roads (the vasculature) and a propulsion device (the heart). Moreover, regulatory mechanisms are provided by endocrine and neural pathways, the complexity of which increases with the accuracy of species-specific homeostatic requirements. When fish, for instance, are exposed to acute hypoxia, they reduce their heart rate, elevate gill vascular resistance, hyperventilate and increase ventilatory amplitude (Burlison & Smatresk, 1990 a, b; Burlison et al., 1992; Randall, 1982). Key to these reflex regulatory responses is oxygen-sensing which occurs through specialized chemoreceptor cells (Coolidge et al., 2008), the location of which is still a topic of active research. In fish, for instance, oxygen chemoreceptors have been located in the brain (Smatresk et al., 1986), the vasculature (Randall, 1982), the buccal and gill cavities (Milsom et al., 2002) and the gills (Burlison & Milsom, 1993; Laurent & Dunel, 1980; Reid & Perry, 2003; Sundin et al., 2000). It has also been shown that the receptors in the gills sense oxygen in the water flow as well as within the gill vasculature itself (Randall, 1982).

Metabolic adjustments to cope with reduced oxygen availability have also been reported, resulting in reduced



Figure 8.11.6 (A) Golden grey mullet *Lisa aurata* in the surf breaking on the shore. © Nature Picture Library / Alamy stock photo; (B) Flathead grey mullet *Mugil cephalus*. © Mark Conlin / Alamy stock photo.

activity (echinoderms and fish; Diehl et al., 1979; Herbert & Steffensen, 2005; Johansen et al., 2006) reduced feeding activity (fish, crustaceans, molluscs, and polychaetes; Bell et al., 2003; Chabot & Dutil, 1999; Llanso & Diaz, 1994; Tamai, 1993) and reduced metabolic rates (cnidarians and crustaceans; Harper & Reiber, 1999; Rutherford & Thuesen, 2005). Shifts to anaerobic metabolism over time scales of hours to days have also been reported in bivalves (Brooks et al., 1991; De Zwaan et al., 1993), polychaetes (Grieshaber and Volkel, 1998), oligochaetes (Dubilier et al., 1997), echinoderms (Ellington, 1975), and crustaceans (Anderson et al., 1994). Metabolic depression has also been reported in fish (Bickler & Buck, 2007). For a review see Vaquer-Sunyer and Duarte (2008) and Keeling et al. (2010). It has also been shown that hypoxia is an endocrine disruptor in fish, impairing reproduction (Wu et al., 2003). For instance, in the Gulf of Mexico, gonadal growth is impaired at hypoxic sites in both females and males Atlantic croaker (*Micropogonias undulatus*; Thomas & Rahman, 2018). At the cellular level, the effects of hypoxia are mediated by a family of proteins, the hypoxia inducible factors (HIF). These proteins, and in particular HIF-1, act as transcription factors and are regulated in the absence of oxygen. In fish it has been shown that hypoxia exposure which resulted in HIF-1 induction during embryogenesis are associated with enhanced hypoxia tolerance in subsequent developmental stages (Robertson et al., 2014).

8.11.3.2.3 Phenology

The life cycles of marine organisms are synchronized with periodic (e.g. tidal, seasonal) changes in their environment in such a way that their various phases e.g. hatching, metamorphosis or settlement, occur under the most favourable conditions. This synchronization

process is highly species-specific and occurs through an organism's sensitivity to environmental cues such as temperature, light or food availability (Edwards & Richardson, 2004). Through this process, the spawning season, for instance, is synchronized with ocean temperature so that the development of the early life stages takes place under the most favourable combination of salinity, temperature and food conditions (Asch, 2015; Greve et al., 2005; Koeller et al., 2009; Poloczanska et al., 2013).

To our knowledge, however, there exists no published report documenting phenological responses of marine species to environmental oxygen levels. Local episodes of hypoxia generally co-occur with other environmental disturbances which are also liable to trigger shifts in marine species' life-cycle. The lack of understanding of these interactions, their synergies and their impact on an organism's physiology clearly contributes to restrict present ability to assess a marine population's capacity to phenologically respond to ongoing ocean deoxygenation (McBryan et al., 2013).

8.11.3.2.4 Epigenetics

In marine organisms, embryonic and larval life stages are commonly associated with critical changes in morphology, physiology and behaviour, usually coupled with shifts in habitat and diet. During that period, environmental conditions strongly influence the development of embryos and larvae, affecting not only the performance of these young stages but also having consequences for later life stages (Vanderplancke, 2014; Zambonino et al., 2013, 2017). Moreover, being characterized by fast growth and rapid cell division, early life stages are also prone to epigenetic remodelling (Perera & Herbstman, 2011).



Figure 8.11.7 Zebrafish (*Danio rerio*). © Ian Grainger / Shutterstock.com

Epigenetics proposes that, through fine-tuned molecular mechanisms (DNA methylation, histone modification and non-coding RNA-associated gene silencing), environmental cues such as diet, past environmental conditions, exposure to contaminants or diseases can affect gene activation and expression. It also suggests that these functional modifications of the genes can accumulate throughout an organism's lifetime and, most importantly, can be passed onto the next generation. Epigenetics therefore makes the transition between phenotypic plasticity and genetic adaptation. For example, a beneficial transgenerational effect of parental hypoxic exposure on hypoxia tolerance of offspring has been demonstrated in the zebrafish (*Danio rerio*; Ho & Burggren, 2012) (Figure 8.11.7). This involvement of epigenetic mechanisms in the production of phenotypic diversity is crucial because it presents new possibilities

for species to rapidly respond to ongoing climate change and resulting ocean deoxygenation (Donelson et al., 2012). Negative epigenetic effects are also possible, such as reproductive impairments in future generations of medaka (*Oryzias melastigma*), a small fish inhabiting shallow lagoons and swamps, after parents were exposed to hypoxia (Wang et al., 2016). However, research on environmental and evolutionary epigenetics is at an early stage and its integration into evolutionary theory is far from possible at this time.

8.14.3.3 Adaptation

Adaptation is taken to mean the evolutionary process by which natural selection affects, over generations, the gene pool of a population so that this population remains adapted to its environment (Ownby et al., 2002).

Table 8.11.1 Generation time in some marine organisms (after Heron, 1972 in Anderson, 1981)

Organism	Order of magnitude of generation time
Bacteria	Few hours
Ciliates	Few days
Rotifers	1 to 3 weeks
Planktonic crustaceans	1 to 6 months
Bivalves	1 to 3 years
Commercial fish	1 to 10 years

While behavioural and physiological adjustments can be made within seconds to hours in case of changes in the environmental conditions, adaptation occurs over generations. Thus, a species' generation time will strongly determine its capacity to adapt to rapidly changing conditions - the shorter the generation time the higher the potential for rapid evolutionary adaptation (Table 8.11.1).

The pattern of the selective pressure is also a key determinant of the rate of a species' evolutionary process. Unfortunately, interactions between natural variability and anthropogenic climate change make it difficult to project future oxygenation conditions in the ocean. Even more open to conjecture are future oxygenation conditions in shallow coastal waters, where continental and marine biogeochemical processes are particularly intricate. As a result, the patterns of natural selection in these environments are particularly difficult to establish and marine organisms' evolutionary capacity to adapt to these new conditions is still uncertain. Between now and 2100, for instance, approximately 80 generations of sardine (Figure 8.11.8A) (*Sardina pilchardus*; age at first maturity: 1 year) but only 10-15 generations of Atlantic cod (Figure 8.11.8B) (age at first maturity: 5 to 8 years) will occur. If the complexity of the physiological infrastructure involved in homeostasis is considered, these numbers of generations are relatively modest and cast some doubts on the capacity of commercial fish species in particular, to adapt to the fast changing ocean conditions.

8.11.4 Interactions with other environmental drivers

With global climate change, ocean warming is combining with ocean deoxygenation and acidification

(Altieri & Gedan, 2015; Stortini et al., 2017) and this combination is likely to have synergetic impacts on marine ecosystems.

The interaction between warming and deoxygenation is perceived to be both strong and worrisome as both drivers are likely to co-occur in many coastal areas. As already mentioned, the vast majority of marine organisms are ectotherms, which means that their body temperature is that of the environment. Thus, ocean warming increases their metabolic rate and, therefore, will increase their need for oxygen. At the same time, oxygen solubility decreases as temperature increases (García & Gordon, 1992), making it more difficult for these species to meet their increased oxygen requirement.

Respiration is the main cause of environmental deoxygenation, and because respiration releases carbon dioxide (CO_2) in a nearly equivalent amount as to that of consumed oxygen (respiratory quotient c.0.8), environmental hypoxia generally occurs together with increased dissolved CO_2 (hypercapnia). However, CO_2 not only dissolves but also chemically reacts with water, altering its carbonate chemistry and lowering its pH. Consequently, deoxygenated deep waters are generally more acidic than oxygenated, surface waters (Burnett, 1997; Gobler et al., 2014; Melzner et al., 2012; Mucci et al., 2011). Note that the contemporary increase in anthropogenic CO_2 release in the atmosphere, and its diffusion into the ocean, potentially aggravates marine hypercapnia and the resulting acidification of marine waters.

Published reports suggest that early life-stages of bivalves display additive effects (increased mortality, reduced growth) when facing acidification and deoxygenation combined (Gobler et al., 2014). Similarly, two species of

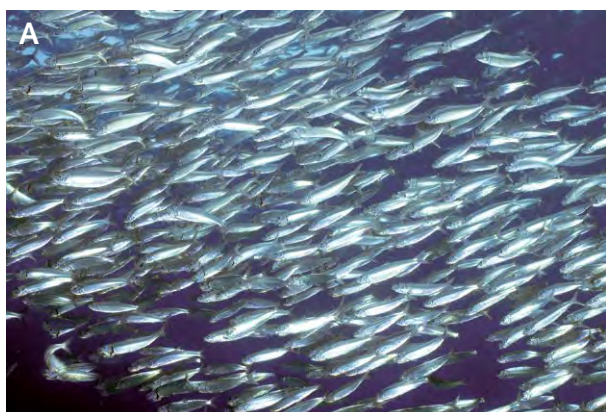


Figure 8.11.8 (A) Sardines (*Sardina pilchardus*). © BIOSPHOTO / Alamy stock photo; (B) Atlantic cod (*Gadus morhua*). © Paulo Oliveira / Alamy stock photo.

silversides (*Menidia menidia* and *Menidia beryllina*) have been shown to resort to surface respiration at a higher ambient oxygenation when pH is decreased, indicating lower hypoxia tolerance under acidified conditions (Miller et al., 2016). In cephalopods, environmental hypercapnia affects blood oxygen transport capacity because of the sensitivity of the oxygen-transporters (haemocyanin) to internal acid-base disequilibrium (Seibel, 2016). With rare exceptions (Cochran & Burnett, 1996; Gobler et al., 2014; Miller et al., 2016), published values of hypoxia tolerance have been typically obtained in CO₂ / pH conditions prevailing in surface waters. These values most likely underestimate the true sensitivity of marine species to ambient deoxygenation (Cochran & Burnett, 1996).

The gills of marine organisms are a multi-tasking organ involved in breathing, osmoregulation, acid-base regulation, feeding and excretion. Due to this functional linkage, a strong interaction between ion, water and gas exchange exists, termed the osmo-respiratory compromise (Claireaux & Dutil, 1992). Consequently the increased ventilation (water) and perfusion (blood) of the gills observed when oxygen availability is reduced, result in increased transepithelial movements of water and ions, putting additional load on homeostasis-related energy expenditure. This tight relationship between osmoregulation and ventilation pivots on a complex, species-specific and delicately tuned functional trade-off which remains to be fully investigated (Evans et al., 2005).

Contaminants, parasites and disease can also modulate the capacity of marine organisms to face environmental deoxygenation. Gills, for instance, are particularly vulnerable to water-borne contaminants (Farrell et al., 2004). Moreover, it has been shown that hypoxia reduced the ability of fish to metabolize contaminants and increased ROS production and resulting oxidative damage (Chiedek et al., 2007; Kreitsberg et al., 2013; Mustafa et al., 2012). Parasitized sticklebacks, *Gasterosteus aculeatus* and *Pungitius pungitius* displayed surface respiration at a higher level of dissolved oxygen than healthy individuals (Giles, 1987; Smith & Kramer, 1987). Eastern oyster *Crassostrea virginica* are also more prone to infection during hypoxic events, and it has been proposed that this is due to reduced immune competency (Breitburg et al., 2015). Increased susceptibility to disease and parasites during hypoxic episodes has also been demonstrated in fish (Boleza et al., 2001; Plumb et al., 1976).

8.11.5 Conclusions / Recommendations

As environmental conditions change in the ocean, so does the distribution of habitats that marine species can occupy (Cooke et al., 2014; Huey et al., 2012; Marras et al., 2015; McKenzie et al., 2016). Marine organisms respond to ocean deoxygenation in a number of ways, with physiological, behavioural and epigenetic adjustments, changes in distribution and, possibly, phenology, to evolutionary adaptation. The diversity of these potential responses, and their variability within and among species, makes them challenging to comprehend. Moreover, synergies with other existing pressures, whether natural or resulting from human activities such as, ocean warming and acidification, add to this difficulty. It is therefore crucial that the currently available knowledge base is increased and conveyed to policymakers and the general public to ensure that scientifically sound mitigation and conservation strategies are designed, agreed upon and implemented.

As has been seen, the constraints imposed on marine organisms by dwindling oxygen availability are relatively well understood. However, the propagation of their effects across biological organizational levels remains insufficiently understood to allow reliable projections of impacts upon marine ecosystems' structure, function and services. Over the last 30 years, marine biologists and physiologists have made tremendous efforts to overcome this sticking point, gaining a mechanistic, cause and effect, understanding how marine animals respond to reduced oxygen availability, and hence offering to enrich available models (Deutsch et al., 2015; Holt & Jørgensen, 2015; Jørgensen et al., 2012; Marras et al., 2015; Peck et al., 2016; Rose et al., 2018). Unfortunately, the contribution of this new knowledge to marine resource management is still largely incomplete and greater collaborations between physiologists, ecologists, modellers and managers are required if policy decisions with regard to fisheries management or marine protected areas, for example, are to be fully supported with science-based information (Bianucci et al., 2016; McKenzie et al., 2016; Stortini et al., 2017).

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Ocean deoxygenation: Impacts on ecosystem services and people

9

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Summary

- Effects of ocean deoxygenation on people remain understudied and inherently challenging to assess. Few studies address the topic and those that do generally include more readily quantified economic losses associated with ocean deoxygenation, exclude non-use and existence value as well as cultural services, and focus on relatively small, bounded systems in capitalized regions. Despite the lack of extensive research on the topic, current knowledge based in both the natural and social sciences, as well as the humanities, can offer useful insights into what can be expected from continued ocean deoxygenation in terms of generalized impact pathways.
- People receive benefits from ocean ecosystem services in the form of well-being (assets, health, good social relations, security, agency). Ecosystem services are translated to human well-being via social mediation, such that differences in levels of power and vulnerability determine how different social groups will experience hazards created by continued ocean deoxygenation. Despite not knowing the precise mechanisms of ocean deoxygenation-driven biophysical change, established social mechanisms suggest that ocean deoxygenation will exacerbate existing social inequities.
- Reductions in dissolved oxygen (DO) are generally expected to disrupt ecosystem functioning and degrade habitats, placing new challenges and costs on existing systems for ocean resource use. Coral reefs, wetlands and marshes, and fish and crustaceans are relatively more susceptible to negative effects of ocean deoxygenation. People reliant on these systems and animals may experience relatively more negative impacts. In the near-term, some hypoxia-tolerant species, particularly gastropods, may see benefits from reduced DO levels due to altered food webs, and potential increases in ecosystem services should be considered in adaptation strategies.
- People in low latitudes, coastal urban and rural populations, poor households in developing countries, and marginalized groups (such as women, children, and indigenous populations) are most vulnerable to the impacts of ocean deoxygenation. Communities where these characteristics overlap are uniquely vulnerable, notably coastal communities in low income developing countries (LIDCs).
- Improved understanding of nuanced impact pathways of ocean deoxygenation to human well-being outcomes will be of critical importance for effective planning in response to ocean deoxygenation going forward. Analyses of ecosystem services should consider the entire range of ecosystem service types, even where not quantifiable, in order to provide the information needed for proper planning, including how different groups of people will be impacted, based on their vulnerability to hazards caused by low DO levels. Transdisciplinary approaches to assess systems holistically present promising means for gaining policy-relevant knowledge of complex social-ecological system dynamics.
- Policies and actions aimed at adapting to and mitigating for ocean deoxygenation should focus on reducing the vulnerability of groups and individuals by addressing ultimate and proximate causes of high sensitivity and exposure to low DO hazards, and building adaptive capacity. Attention should be paid to the central role that social institutions play in mediating access to ecosystem services and the inherent inequities in the ways humans experience natural hazards.

Social and biophysical trends related to effects of low oxygen conditions	Potential consequences
Dissolved oxygen levels are lowest at low latitudes, eastern coastal margins, and coastal waters subject to eutrophication.	<ul style="list-style-type: none"> • Groups near to and reliant on these areas will be most at risk to resulting hazards. • Less proximal groups may also see risk due to biophysical teleconnections and socio-economic interconnectivity.
Persistence of low O ₂ zones varies over space and time.	<ul style="list-style-type: none"> • Some ecosystem services may see positive impacts in the short-term, but the trend is toward habitat degradation and reduced ecosystem services. • In the near-term, negative impacts may be lessened where localized low O₂ can be avoided by use of higher O₂ areas nearby.
Groups vary in their vulnerability to natural hazards.	<ul style="list-style-type: none"> • Groups with more exposure and sensitivity to hazards and less adaptive capacity will be more negatively impacted by reduced ecosystem services and less able to benefit from any enhanced ecosystem services. • The groups more exposed to hazards of environmental change are more dependent on local environmental quality and less able to mobilize resources to adapt. These same groups are typically those discriminated against or marginalized in societies, on the grounds of class, race and gender identities. • More vulnerable groups will be more negatively affected despite uncertainty in biophysical impacts. • Women, children, groups with restricted mobility, and those living in poverty are most vulnerable to low O₂ impacts. • Low O₂ impacts will further exacerbate existing social inequities.
Marine organisms and ecosystem subtypes are differentially impacted by low O ₂ .	<ul style="list-style-type: none"> • People reliant on ecosystem services from coral reefs, wetlands and marshes, fish, or crustaceans may see relatively greater hazards from low O₂. • People who benefit from ecosystem services supplied by mangroves, gastropods, or bivalves may experience relatively less hazard, and possibly see enhanced services in the near-term.
Impacts of low O ₂ may be enhanced by other stressors, such as ocean warming, acidification, and pollution.	<ul style="list-style-type: none"> • Impacts may be worse on people exposed to areas experiencing several stressors and people reliant on ecosystem subtypes sensitive to several stressors (e.g. coral reefs). • Impacts on people are more challenging to predict due to uncertainty around synergistic or combined impacts.
Ecosystem services and categories (provisioning, cultural, supporting, and regulating) differ in how they are affected by low O ₂ and mediated by social factors.	<ul style="list-style-type: none"> • Ecosystem service categories more reliant on animals for service provision (cultural, provisioning, and supporting) are likely to be more negatively affected by low O₂, thus will have relatively more impact on people. • Ecosystem service categories more reliant on access to certain places for provision (cultural, provisioning, and supporting) are more susceptible to social mediation of well-being outcomes, thus will have relatively less equitable impact on groups. • Regulating services are generally less susceptible to low O₂ and social mediation, thus will likely have relatively less impact, distributed more equitably.
Ecological interactions can lead to complex and less immediately apparent impacts of low O ₂ .	<ul style="list-style-type: none"> • Communities and economic sectors may see complex changes to resources as altered predator-prey and food web dynamics will likely lead to impacts on species not directly affected by low O₂. • Some groups may benefit from species that may see near-term benefits due to predator release or habitat shifts of prey.
Social and ecological positive feedbacks can exacerbate impacts of low O ₂ .	<ul style="list-style-type: none"> • Continued urbanization and movement toward coasts both contribute to ocean deoxygenation hazards via eutrophication and increase exposure of people to impacts, while reduced ecosystem services in rural coastal regions may propel further movement to urban areas in search of greater economic opportunity. • Low O₂-induced cyanobacteria blooms have a direct negative impact on human health when blooms are toxic and lead to further reduced O₂ causing run away from equilibrium.

9.1 Introduction

Knowledge of how ocean deoxygenation affects human communities is only just beginning to accumulate and less is known about specific impacts of deoxygenation on economies and societies than about the impacts of other facets of global environmental change, such as sea-level rise, ocean warming or even ocean acidification (e.g. Allison & Bassett, 2015). Assessing effects of environmental change on humans is challenging in that it requires understanding both the biophysical and social mechanisms of change; each represent gaps in knowledge in relation to decreasing levels of dissolved oxygen in the ocean (Cooley, 2012; Rabotyagov et al., 2014). Attention paid to climate change effects in the ocean already lags behind that paid to land-based impacts (Allison & Bassett, 2015) and ocean deoxygenation has only recently received substantial attention (Altieri et al., 2017). How reduced oxygen interacts with other biogeochemical stressors (e.g. pollution and ocean acidification) to affect marine systems is not well-understood (Cooley, 2012) and that lack of understanding will amplify uncertainty of potential impacts on human economic and social systems. There is, thus, a gap in knowledge around how ocean deoxygenation affects the benefits that ocean ecosystems provide for people (ecosystem services) and the ultimate impacts on human well-being.

While human impacts of ocean deoxygenation have not been substantially studied, research in the humanities and social sciences has been furthering our understanding of the impacts of environmental change on people since the rapid rise of the new inter-disciplines of environmental sociology, and, more recently, the environmental humanities (e.g. Castree, 2014; Catton & Dunlap, 1978; Cropper & Oates, 1992). Researchers in these fields have analysed socially differentiated impacts, feasibility and outcomes of a range of adaptation options, and the complex nature of support for and challenges to ongoing technical and political responses (Allison & Bassett, 2015). These insights into the character and mechanisms of environmentally-driven social change are largely absent from most “human dimensions” research in major earth (and ocean) system science programmes; such research is typically limited to endeavours to quantify aspects of societal impact — potential vulnerabilities to physical and biochemical changes, monetary value of threatened ecosystem services, and costs and benefits of various options for adaptation and mitigation action (Castree et

al., 2014). Asymmetrical use of available knowledge has led to gaps in our understanding of experienced and expected societal impacts of environmental change (including ocean deoxygenation) and ultimately impedes proper planning and policy development (Breitburg et al., 2018). By failing to engage meaningfully with social enquiry, environmental science had failed to account for the role of power relations and social difference in shaping who most impacts the environment and who is most impacted by environmental change. This is now being addressed by rise of environmental justice as a field of environmental studies as well as activism (Bullard, 2018).

Knowledge derived from qualitative and quantitative methods used in the natural sciences, social sciences, and humanities is here employed together with the ecosystem services for human well-being framework (MEA, 2005a), from ecological economics, and the Pressure and Release (PAR) Model (Blaikie et al., 1994), from political ecology, to evaluate the potential impacts of ocean deoxygenation on human societies. Ecosystem services comprise the range of benefits the natural environment provides to humans, which are translated into human well-being via social systems (MEA, 2005). Loss or reduction of a given ecosystem service may constitute a natural hazard or lead to increased impact of natural hazards. The Pressure and Release Model provides insights into how natural hazards (e.g. as a result of ocean deoxygenation) combined with human vulnerability (as a result of social factors) lead to the impacts experienced by communities (Blaikie et al., 1994; Wisner et al., 2004).

Using the combined ecosystem services and PAR framework, supplemented by qualitative insights from case-study research in the environmental social sciences and humanities, we can maximize usability of current knowledge in addressing a topic with few studies explicitly linking the chain of impacts from natural to social changes, as in the case of ocean deoxygenation to human well-being changes. Studies that have addressed this chain of impacts have generally performed partial assessments that analyse economic effects of ocean deoxygenation on industrial and recreational fisheries in developed countries (see Chapter 10), with only a few studies assessing ecosystem services and human well-being impacts more holistically (see Section 9.5). However, use of ‘transitive logic’ and the ecosystem services and PAR frameworks, allows for construction of generalized impact pathways. In other words, by

applying the mathematical concept of ‘transitivity,’ if $A = B$ and $B = C$, then $A = C$, we can effectively maximize application of current knowledge by connecting bodies of knowledge that describe individual steps of the process from ocean deoxygenation to human outcomes. As such, if we know (A) how ocean deoxygenation affects an ecosystem subtype, species, or biophysical process (in one or more general or specific ways), (B) the effects of those biophysical changes on ecosystem service provision, and (C) social mechanisms by which those changes in ecosystem service availability affect human well-being, we can assert generalized expectations for how reduced levels of dissolved oxygen may affect people in such circumstances. A selection of example impact pathways is described in Section 9.6.

In this chapter, we provide an overview of ocean ecosystem services (Section 9.2), introduce both the ecosystem services and PAR frameworks (Section 9.3), and describe generalized trends and variability in observed and expected ecosystem service and human well-being outcomes from ocean deoxygenation (Section 9.4). We present six case studies in which ocean deoxygenation has been tied to ecosystem service changes (Section 9.5) and summarize several generalized pathways through which ocean deoxygenation may impact people (Section 9.6). Lastly, we discuss the potential implications of continued ocean deoxygenation and necessary considerations for appropriately addressing impacts in a social, economic, cultural, and political context (Section 9.7).

Table 9.1 Marine ecosystem services identified in a range of publications and organized by the Millennium Ecosystem Assessment categories (Agardy et al., 2011; Barbier, 2017; Barbier et al., 2011; Cooley, 2012; MEA, 2005a; Orth et al., 2006; Palumbi et al., 2009). Cooley (2012) identified services thought to be susceptible to ocean deoxygenation (✓), susceptible to combined biogeochemical impacts of ocean deoxygenation, pollution, and ocean acidification (✓*), and tolerant of ocean deoxygenation (-). Some services identified in other publications were not included (NI) in Cooley’s (2012) assessment.

Regulating		Cultural	
Pollution & waste control	✓	Ceremonial & spiritual use	✓*
Flood & storm protection	✓	Aesthetic	✓*
<i>Regulation</i>		Science & education	✓*
• Air quality	-	Tourism & recreation	✓*
• Climate	-	Therapeutic use	NI
• Hydrologic cycle	-	Traditional use	NI
Human disease control	-	Bequest to future generations	NI
Erosion control	-		
Provisioning		Supporting	
<i>Food</i>		Biodiversity	✓*
• Fish	✓*	Nutrient cycling & fertility	✓*
• Invertebrates	✓*	<i>Biological regulation</i>	
• Plants	-	• Predator-prey relationships	✓*
• Mammals, birds	✓	• Keystone predators	✓*
Medicine & genetic resources	✓	<i>Habitat provision</i>	
<i>Ornamental resources</i>	✓*	• Nursery	✓
• Coral	✓*	• Breeding	✓
• Aquarium fish	NI	• Feeding	NI
• Shells	NI	Primary production	-
<i>Building materials</i>		Sediment formation & retention	?
• Fibre	?		
• Wood	✓		
• Lime, coral	-		
<i>Fuel & energy</i>			
• Timber	✓		
• Oil and gas	-		
• Wind, wave, thermal, tidal	NI		
Transport, trade & tourism	-		

Valuing ecosystem services

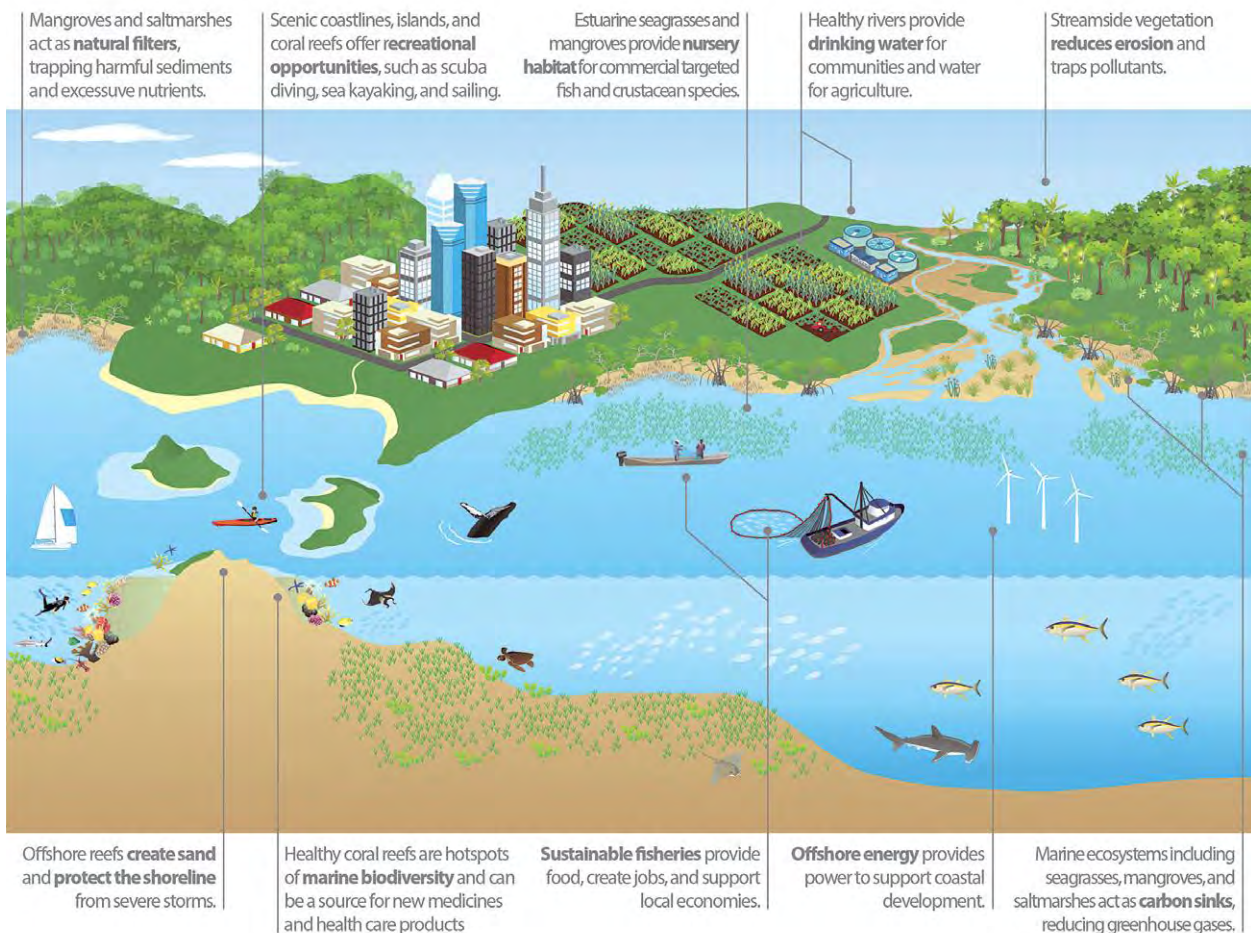


Figure 9.1 Ocean ecosystem services. Reproduced with permission from Agardy et al. (2011). Illustrator Tracey Saxby, Integration & Application Network, University of Maryland Center for Environmental Science.

9.2 Marine ecosystem services

Ecosystem services are the benefits humans derive from the use of an ecosystem (MEA, 2003). Benefits conferred from ecosystem services reach beyond monetary gains and include all services provided by the natural system that may not be easily seen or quantified yet are critically important to the continued existence of people and societies. Ecosystem services (Figure 9.1, Table 9.1) are typically grouped into four broad categories, defined by the Millennium Ecosystem Assessment (MEA, 2003):

i) *Provisioning services*, include material benefits derived from the use of an ecosystem's resources, for example, provisioning of food through fishing, gathering, and farming, production of energy via tidal energy technologies and offshore drilling, or generation of income through livelihood activities like transport, trade, and tourism.

ii) *Cultural services* are “non-material benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation, and aesthetic experiences.” These services include the cultural, therapeutic, historical, or religious values people derive from the ecosystem and contribute to their sense of place, quality of life and overall mental, emotional and spiritual health.

iii) *Regulating services* are those that play a role in regulation of large-scale biophysical processes such as climate and air quality. In the ocean, they include pollution and waste control, storm and flood protection, regulation of air quality, climate, and hydrologic cycling, human disease control, and erosion control.

iv) *Supporting services* are those that enable ecosystem function and continued contribution

Table 9.2 Summary of the relative magnitude of ecosystem services provided by different coastal system subtypes. Double asterisks (**) denote ecosystem subtypes that are negatively affected by all three biogeochemical stressors addressed by Cooley (2012): ocean deoxygenation, ocean acidification, and pollution. Adapted from MEA (2005a), Table 19.2.

Direct and Indirect Services	** Estuaries and Marshes	Mangroves	Lagoons and Salt Ponds	Intertidal	Kelp	Rock and Shell Reefs	Seagrass	** Coral Reefs
Food	●	●	●	●	●	●	●	●
Fibre, timber, fuel	●	●	●	●	●	●	●	●
Medicines, other	●	●	●	●	●	●	●	●
Biodiversity	●	●	●	●	●	●	●	●
Biological regulation	●	●	●	●	●	●	●	●
Freshwater storage and retention	●	●	●	●	●	●	●	●
Biochemical	●	●	●	●	●	●	●	●
Nutrient cycling and fertility	●	●	●	●	●	●	●	●
Hydrological	●	●	●	●	●	●	●	●
Atmospheric and climate regulation	●	●	●	●	●	●	●	●
Human disease control	●	●	●	●	●	●	●	●
Waste processing	●	●	●	●	●	●	●	●
Flood/storm protection	●	●	●	●	●	●	●	●
Erosion control	●	●	●	●	●	●	●	●
Cultural and amenity	●	●	●	●	●	●	●	●
Recreational	●	●	●	●	●	●	●	●
Aesthetics	●	●	●	●	●	●	●	●

of other categories of ecosystem services. In the ocean, they include nutrient cycling and fertility, biological relationship regulation, habitat provision, primary production, biodiversity, and sediment formation and retention.

Ecosystem service assessments frequently express the value of ecosystem services in monetary terms; however, such quantifications should be considered proxies to reflect potential contributions to human well-being, which is ultimately the measure of benefit from ecosystems that most reflects human-centred perspectives on the multiple ‘contributions of nature to people’ (Díaz et al., 2018). Such quantifications are also inherently imperfect as they cannot incorporate and value in monetary terms every benefit an ecosystem provides. For example, the ocean is estimated to provide US\$2.5 trillion annually in benefits to people as a “gross marine product” and have an “asset” base of US\$24 trillion (Hoegh-Guldberg et al., 2015). The magnitude of these estimates convey the importance of the ocean to people and still, they are considered to be conservative, as they do not include benefits produced from, but not by the ocean, such as offshore oil and gas or wind energy, or “intangible” benefits, such as climate regulation, oxygen production, or any cultural services (Hoegh-Guldberg et al., 2015). Non-use and existence values as well as cultural services are challenging to evaluate quantitatively (Cooley, 2012) and, as a result, are generally less-represented in ecosystem service assessments (MEA, 2005a).

All marine ecosystem subtypes provide services, though of varying type and magnitude (Table 9.2). Mangroves, coral reefs, and estuaries and marshes provide the largest relative magnitude of ecosystem services per unit area, followed by lagoons and salt ponds, intertidal zones, rock and shell reefs, seagrass, and kelp (Table 9.2) (MEA, 2005a).

9.3 Implications for human well-being

9.3.1 Deriving human well-being from ocean ecosystem services

Well-being is the ultimate value people derive from ecosystem services and consists of five primary qualities: (1) basic material for a good life, (2) health (mental and physical), (3) good social relations, (4) security, and (5) freedom of choice and action (MEA, 2005b). These components of well-being relate to personal and social functioning, and express what a person values doing or being (Sen, 1999). Importantly, definitions of well-being and its constituent parts are known to vary across communities and cultures (Harthorn & Oaks, 2003; Lupton, 1999; Nelkin, 2003). In particular, health is conventionally considered a physical quality, while many cultures, including many indigenous groups, consider psychological, social and cultural aspects of health as inherently inter-connected with physical health (Arquette et al., 2002; Garrett, 1999; Harris & Harper, 1997; Wolfley, 1998).

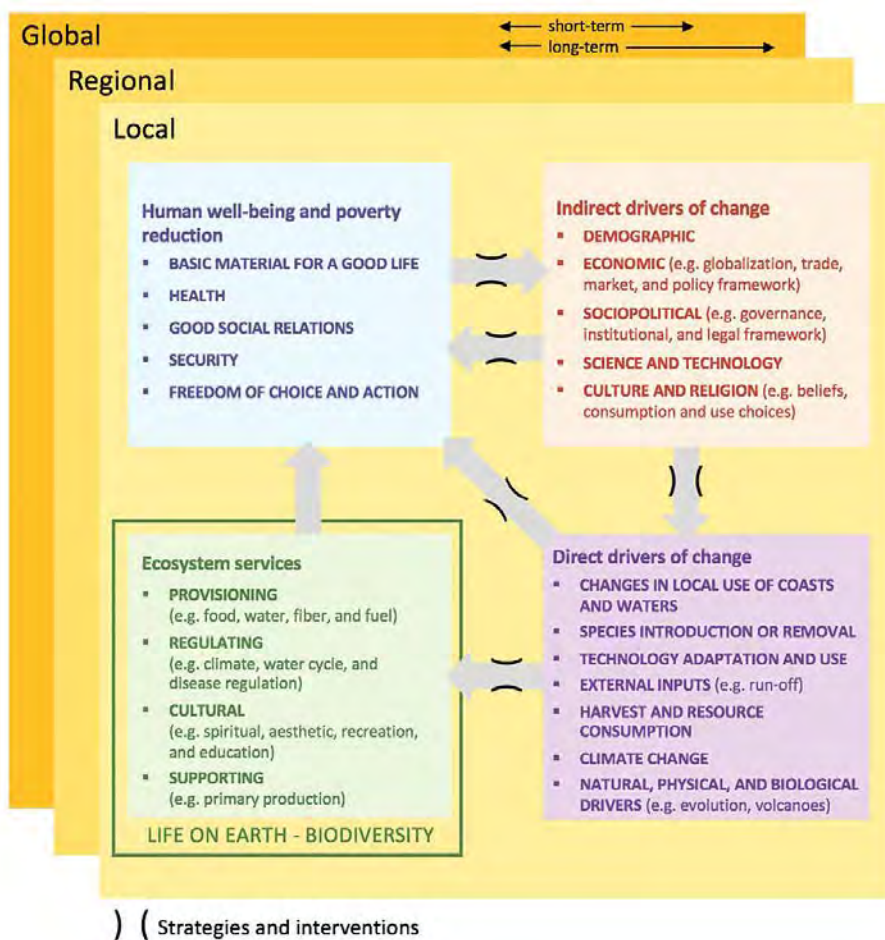


Figure 9.2 The 'macro' Millennium Ecosystem Assessment framework. Adapted from MEA (2005).

For well-being to be achieved a society requires sufficient social, human, natural and manufactured (or economic) capital (MEA, 2003), all of which is derived from or reliant on services provided by the natural world. In contrast, poverty is defined as the "pronounced deprivation of well-being" (MEA, 2003) and occurs when ecosystem services are unavailable or inaccessible. While ecosystem services are essential for deriving well-being, they do not guarantee well-being. Rather, social factors (i.e. societal characteristics, institutions, instruments, organizations, technology, practices and socio-cultural norms) determine whether the well-being potential of ecosystem services is realized and by whom (Fisher et al., 2013); in other words, the process is 'socially mediated'. Critical social factors, that either enable or inhibit one's ability to obtain well-being from ecosystem services, are identified as 'Indirect drivers of change' in the Millennium Ecosystem Assessment's 'macro' framework (Figure 9.2).

Social differentiation is a strong determinant of a group's ability to experience well-being benefits from ecosystem

services as access to services is largely dependent on social status and power (Leach et al., 1999). Controlled through endowments (i.e. ownership of assets) and entitlements (i.e. access to the resources or their services), increased availability of ecosystem services will not increase the well-being of those already living in poverty (i.e. without access to sufficient resources), unless their capacity to access the new services is also increased. Thus, ecosystem services are considered beneficial for poverty prevention, but not poverty reduction (Fisher et al., 2013). Groups with less power and capital also tend to be more directly dependent on ecosystem services than groups with the capacity to purchase traded or manufactured goods, or with the capital assets to avoid the consequences of any decreased functioning of regulating and supporting services (Adger & Kelly, 1999; Leach et al., 1999; Sen, 1981).

Numerous mechanisms translate ecosystem services into human well-being, with the most easily (and commonly) quantified being the contribution of

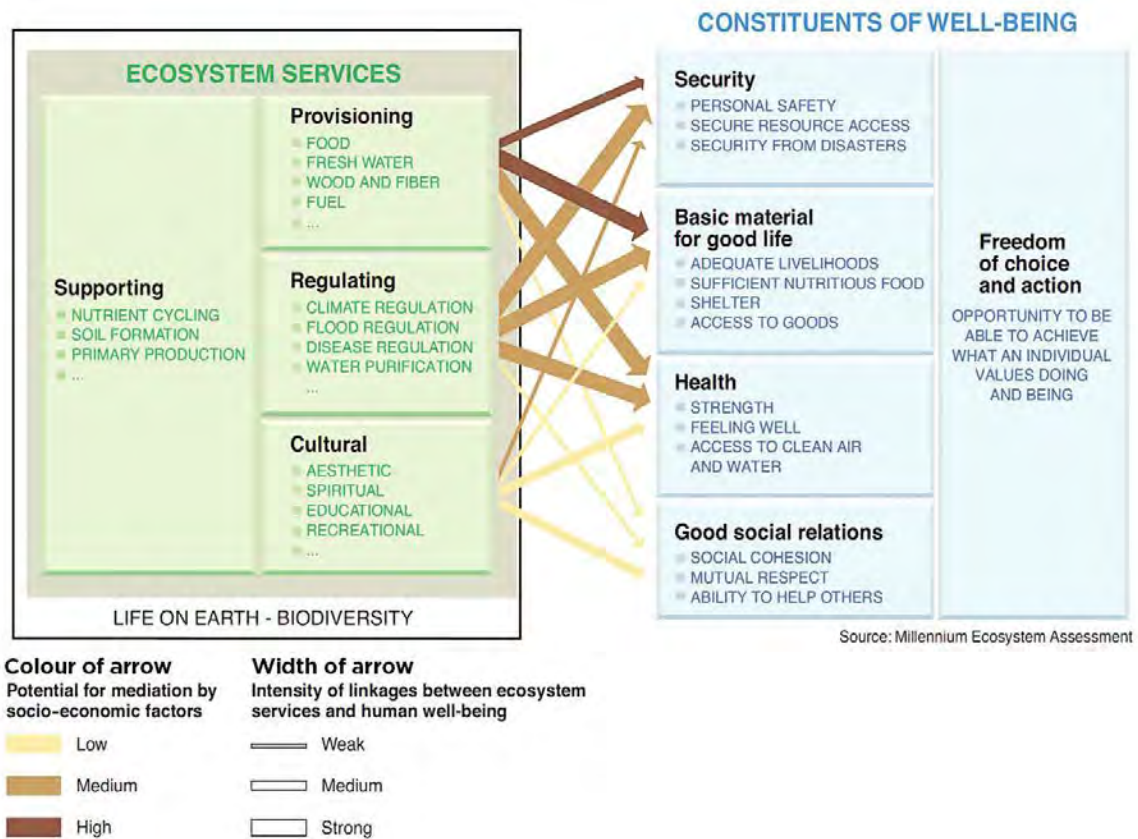


Figure 9.3 The 'micro' Millennium Ecosystem Assessment framework (MEA, 2005).

provisioning services (such as fisheries) to material wellbeing (in the form of income, assets or wealth). Social factors that mediate the relationship between ecosystem services and human wellbeing are also better developed for provisioning services (MEA, 2005a, b). Fisher et al. (2013) note that regulating and supporting services such as the role of coastal and shelf sea and oceanic ecosystems in nutrient cycles, the carbon cycle and oxygen production, derive from ecosystem components and processes that cannot be easily owned or readily controlled and that people cannot be excluded from using, such as the climate system and oceanic circulation. The contribution of these services is driven by complex biogeochemical cycles and large-scale (planetary to mesoscale) forces and their accessibility is not dependent on entitlements. Therefore, the services and their drivers of change can only be effectively governed by high-level actors at a global or transnational scale, through institutions such as the UN Convention on the Law of the Sea, the Paris Agreement of the UN Framework Convention on Climate Change, and the Montreal Protocol on Substances that Deplete the Ozone Layer, and so on. Conversely, in the case of provisioning and cultural services, access can be regulated and denied at national and sub-national scales, through a variety of socio-political controls.

The magnitude and strength of social mediation linkages between ecosystem services categories and components of well-being are represented in the Millennium Ecosystem Assessment's 'micro' framework (Figure 9.3).

9.3.2 Human risk from loss / reduction of ecosystem services

Social factors also play a role in how people experience impacts from natural hazards, such as an absence or reduction of ecosystem services. As illustrated by the Pressure and Release (PAR) model, risk is calculated based on the intensity and frequency of natural hazards and a groups' level of vulnerability to the hazards (Figure 9.4) (Blaikie et al., 1994). Thus, the risk social groups (households, communities, fishing fleets, nations, etc.) are exposed to due to ocean deoxygenation will depend on the degree of hazard experienced (exposure), the degree to which that social group depends upon or benefits from the affected ecosystem services (sensitivity), and their capacity to adapt to the reduction or loss of services (adaptive capacity; Adger, 2006). Vulnerability is a structural and durable social condition established through a 'progression of vulnerability' driven by failures in social systems that

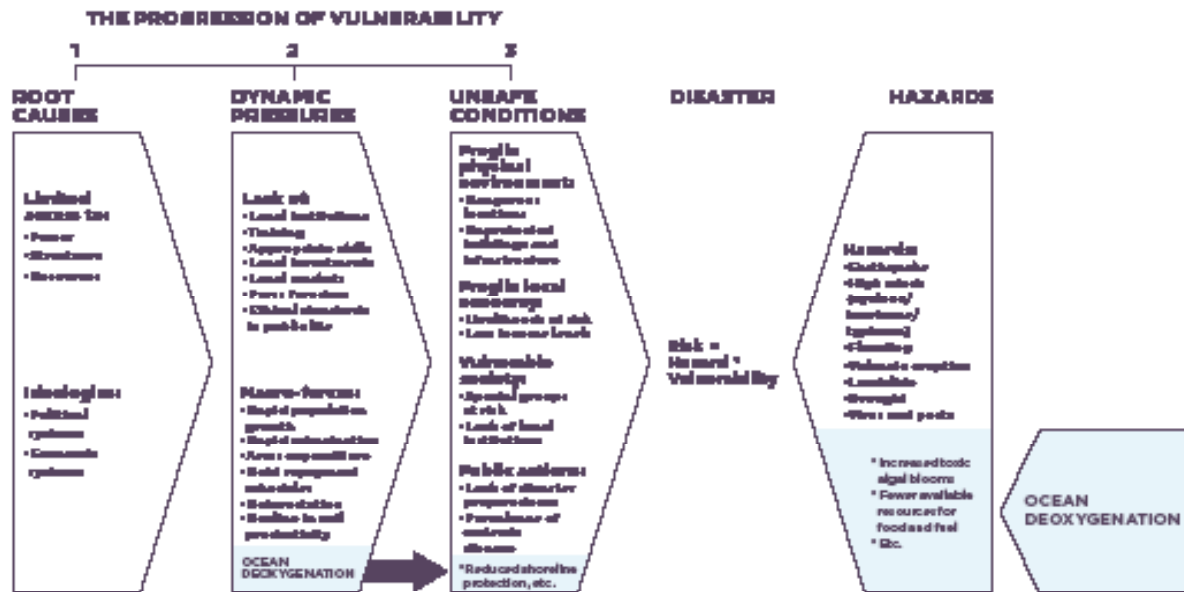


Figure 9.4 Pressure and Release (PAR) model modified to include examples of hazards posed by ocean deoxygenation (shaded in blue). Adapted from Wisner et al. (2004).

ultimately result in ‘unsafe conditions’ leaving people susceptible to natural hazards (Figure 9.4) (Blaikie et al., 1994). This susceptibility is what connects hazardous events to differential levels of risk with impacts that can be disastrous.

Ocean deoxygenation does not itself constitute a hazard, in that reduced ocean oxygen levels do not pose a direct threat to humans, but it contributes to the evolution of risk in two ways (Figure 9.4). First, ocean deoxygenation can drive development of slow-onset hazards via reduction in supporting and provisioning services, such as loss of an important fish stock due to degradation of critical habitat; and second, ocean deoxygenation can contribute to increased human vulnerability to hazards via reduction in regulating ecosystem or cultural services, such as reduced protection from storms due to degraded reefs resulting from coral mortality under low oxygen conditions or reduced adaptive capacity due to loss of community connection to an impacted ecosystem. Thus, as an anthropogenically-catalysed aspect of global environmental change, ocean deoxygenation contributes to human risk by both increasing incidence and magnitude of some hazards and increasing vulnerability of some groups of people.

9.3.3 Responding to changes

People respond to natural hazards through the different, but related, actions of adaptation and mitigation. Adaptation reflects an adjustment of natural or social systems which moderates harm or exploits opportunities

for benefit, while mitigation is a social intervention to lessen the hazard level (Klein et al., 2007). In the context of climate change (one anthropogenic driver of ocean deoxygenation), the word ‘mitigation’ is narrowly defined as actions to reduce greenhouse gas emissions or to increase carbon capture and storage (IPCC, 2001). In that case, the ‘hazard level’ is reduced by a reduction in the concentration of greenhouse gases in the atmosphere. In the context of deoxygenation, mitigation may include measures to reduce eutrophication, which can lead to deoxygenation through the bacterial decomposition of ungrazed phytoplankton blooms that result from excess nutrients in the water.

Actions in either category (adaptation or mitigation) can have consequences for the other: social decisions can lead to synergies or trade-offs between the two activities, and resulting impacts on biophysical processes can, in turn, have consequences for one or both (Klein et al., 2007). A group’s ability to respond to hazards is limited by their capacity to carry out adaptation and mitigation actions, as these actions have associated costs. Thus, the extent to which societies and their social institutions are capable of taking risk-reducing actions will be determined by the amount of human, natural and manufactured capital they are able to access and mobilize. Similarly, communities that gain ecosystem services not previously available, like a fish species newly inhabiting adjacent waters, may or may not have the adaptive capacity to take advantage of these newly available ecosystem services.

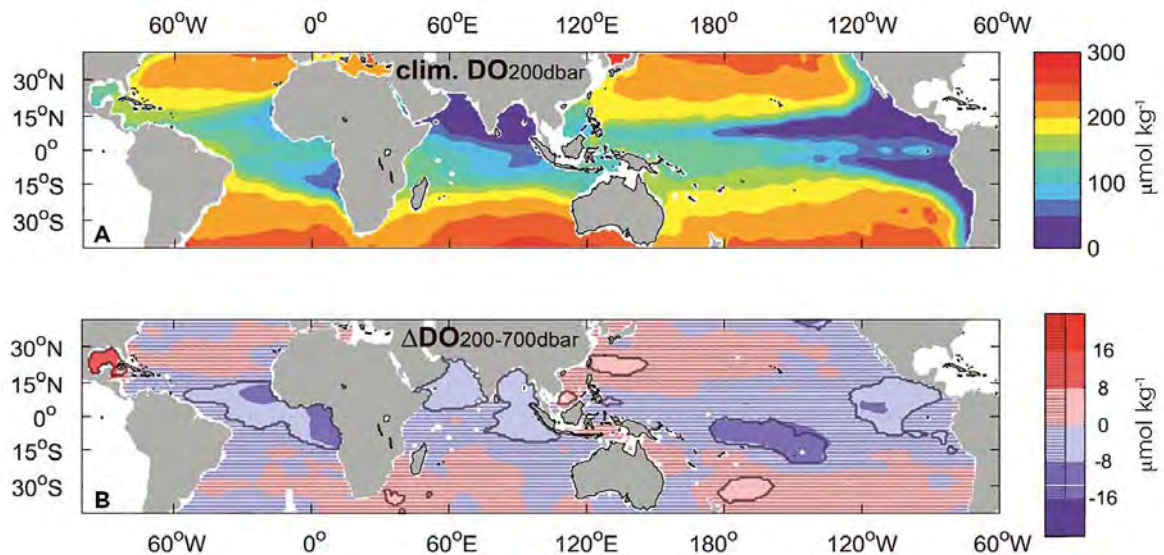


Figure 9.5 (A) Dissolved oxygen levels at 200 dbar at the climatological mean and (B) change in dissolved oxygen levels between 1960-1974 and 1990-2008 (<95% confidence interval in stripes, ≥95% confidence interval without stripes) as averaged from 200 - 700 dbar Adapted from Stramma et al. (2010).

As an example of the role of adaptive capacity, Sumaila et al. (2011) highlight potential monetary costs of climate change adaptation in wild capture and recreational fisheries. As fish distributions change (e.g. populations migrate away from oxygen depleted waters towards more suitable habitat), the functionality of traditional or established fishing grounds are disrupted. Fishers may adapt by travelling further to catch the same amount or even fewer fish, but in the process, accrue greater costs associated with running their boat, and yield smaller profits than under traditional scenarios. If instead, fishers don't have access to vessels capable of travelling further, they may not be able to access the same amount of the resource they could previously. This group has less adaptive capacity and will experience reduced well-being due to loss of income, sustenance, or both. Still instead, a group may choose to take insufficiently seaworthy vessels out to sea to access the resources and, as a result, experience bodily harm or loss of life (e.g. Blythe et al., 2013), thus seeing a reduction of well-being via direct health costs.

9.4 Trends and variability

Effects of ocean deoxygenation on people, economies, and social systems will vary over time and across geographic regions, social groups, and economic sectors due to differences in levels of hazard and vulnerability. However, several trends and sources of variability can be expected based on current knowledge of the processes linking ocean deoxygenation to human well-being.

9.4.1 Magnitude and geographic variation of ocean deoxygenation

Current dissolved oxygen levels vary widely across the world's ocean (from zero to 300 $\mu\text{mol kg}^{-1}$) (Figure 9.5A) (Stramma et al., 2010) and current and predicted rates of oxygen loss range from a decrease of approximately 24 $\mu\text{mol kg}^{-1}$ to an increase of the same magnitude in select geographic regions (Figure 9.5B) (Stramma et al., 2010). Relatively warm equatorial ocean waters and eastern ocean coastal margins with productive upwelling systems are less oxygen rich relative to higher latitude and western ocean basins, and this difference in dissolved oxygen levels is expected to widen in coming decades (Figure 9.5B) (Diaz & Rosenberg, 2008; Middelburg & Levin, 2009; Stramma et al., 2010). Coastal waters see increased incidence of hypoxia due to eutrophication caused by atmospheric deposition as well as run-off from dense urban population centres and agriculture (Figure 9.6) (Breitburg et al., 2018).

On a broad scale, this geographic and biophysical profile of ecosystem effects will result in strong latitudinal variation in ecosystem service impacts. People inhabiting coasts adjacent to waters more affected by ocean deoxygenation will generally experience more exposure to resulting hazards, and thus will be more vulnerable than those who are less exposed. However, due to teleconnections between dissolved oxygen levels and climate regulation as well as distribution patterns of goods, others who are not as proximate to hypoxic waters will also likely experience effects

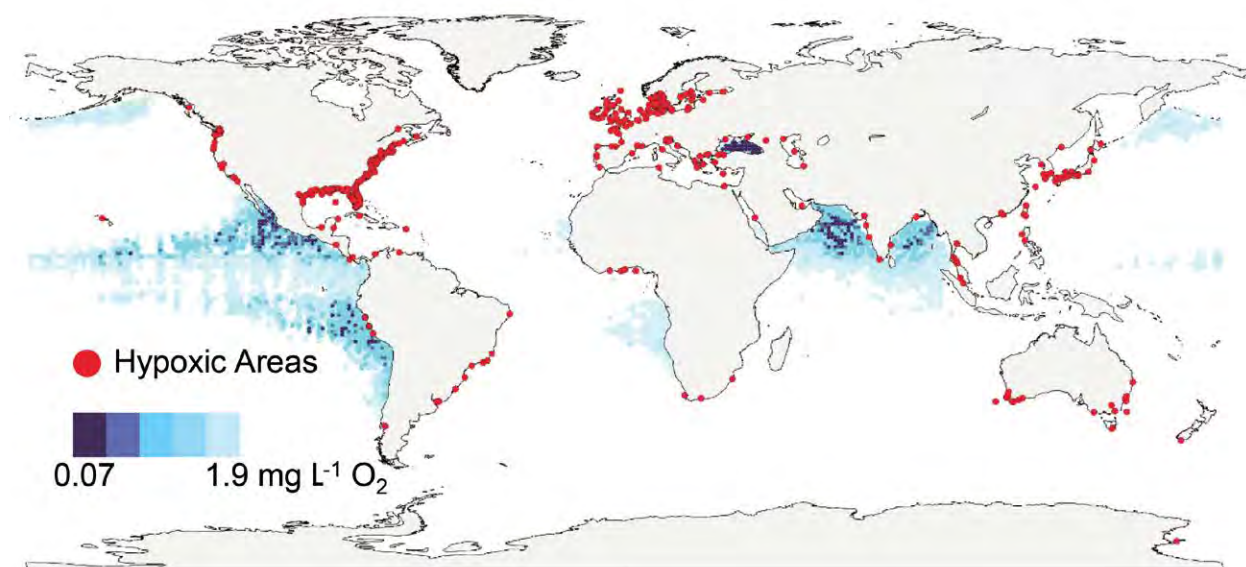


Figure 9.6 Ocean oxygen-minimum zones at 300m depth (blue shaded regions) and coastal hypoxic areas of $< 2 \text{ mg O L}^{-1}$ caused or exacerbated by anthropogenic nutrients (red dots). Figure reproduced with permission from Breitburg et al. (2018) and unpublished data from R. Diaz.

to some degree (Adger et al., 2009; Breitburg et al., 2018). Combined and interacting biogeochemical and ecological processes can result in complex and wide-reaching ripple effects initiated by relatively small areas of hypoxia. Local changes to nutrient-cycling within oxygen minimum zones can be communicated to the wider ocean via circulation (Breitburg et al., 2018) and populations and economic activities far removed from the sea can be impacted by oceanic influences on the global climate system (Allison & Bassett, 2015). These teleconnections link global environmental change, the ocean, and societies (Adger et al., 2009) creating indirect and interacting impact pathways and complicating our ability to isolate impacts of change to one dimension of the larger system.

9.4.2 Temporal and spatial variations

Low oxygen zones can vary in degree of persistence or transience, both spatially and temporally (Breitburg et al., 2018), complicating estimation of impacts over space and time. Several case studies presented here show that ocean deoxygenation can have negligible or even positive effects on ecosystem services in the short-term (e.g. Chesapeake Bay striped bass and Humboldt squid and quahog, respectively), but less favourable or unknown outcomes in the future. There remains a high degree of uncertainty around effects of sustained hypoxia on both the natural and social world (Rabotyagov et al., 2014), making long-term predictions highly challenging. However, researchers highlight that the general trend is toward habitat degradation and

myriad negative impacts of altered ecological systems (e.g. Altieri & Witman, 2006; Breitburg et al., 2018). For example, coral reef researchers have suggested that the long-term effects of hypoxia may be “different from, and more substantial than, those of other disturbances” on reefs because reduced oxygen affects taxa throughout the food web including pathogens, habitat formers, and consumers (Altieri et al., 2017). The rate at which changes occur may also affect the ability of species and human communities or sectors to adapt.

9.4.3 Demographics and social change

Different social groups vary in their vulnerability to hazards in many ways, some of which are predictable. Women and children are generally more vulnerable to losses of ecosystem services due to greater nutrition needs and patterns of impacts of reduced resources reflecting societal norms discriminating against women and children (Otto et al., 2017). Mothers, for example, will forego their own nutrition to provide for their children and instances of ‘famine marriages,’ where “adolescent girls are married off to reduce the number of mouths to feed and/or to generate resources such as cash or cattle” have been documented in Sub-Saharan Africa (Brown, 2012; Marcus & Harper, 2014; Otto et al., 2017).

Groups that are highly reliant on ocean ecosystem services (Figure 9.7) and more exposed to ocean deoxygenation (Figures 9.5 & 9.6) are specifically more vulnerable to reduced DO levels (Dyson & Huppert, 2010). People in lower latitudes are generally more reliant

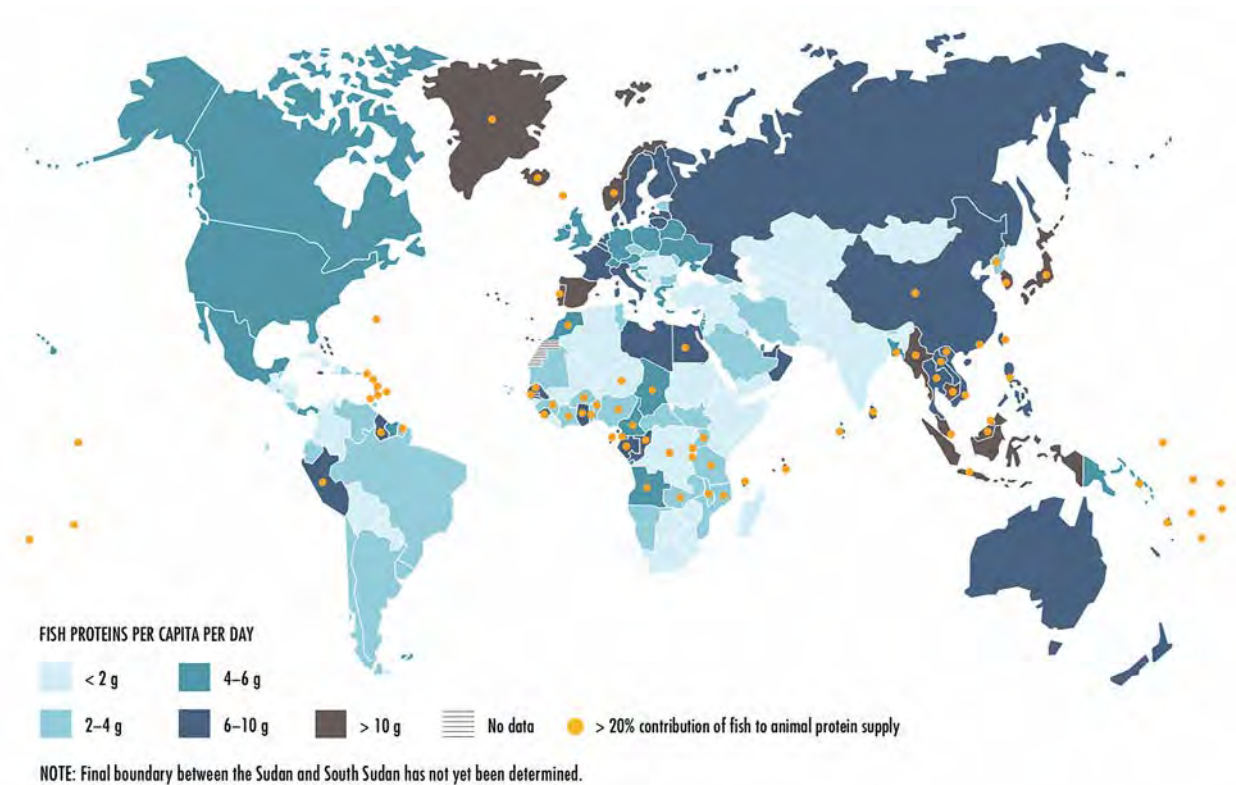


Figure 9.7 Contribution of fish (including wild-caught and farmed fish from marine and freshwater systems) to animal protein supply by country, averaged over 2013–2015 (FAO, 2018).

on access to marine resources for food and livelihoods and experience higher rates of poverty (Figures 9.7 & 9.8). Thus, those in low latitude, low-income developing countries (LIDCs) and in rural coastal areas with less access to credit or wider markets face greater risk from ocean deoxygenation. These groups are more sensitive to loss of marine resources, are more exposed to ocean deoxygenation, and have relatively less adaptive capacity due to systemic and asset-based constraints. Certain regions, such as West Africa, currently experience some of the highest levels of poverty (Figure 9.8), are exposed to low levels of dissolved oxygen (Figures 9.5 & 9.6) and are highly reliant on fish for food (Figure 9.7). Reduced oxygen levels off West Africa are also thought to be lower than current data suggests due to under-sampling (pers. comm. Denise Breitburg). See Chapter 10 for a discussion of the effects of low DO on West African fisheries.

Overall reductions in availability of food resources will lead to increased food prices, which may counteract rent costs of adaptation to change for producers (Sumaila et al., 2011), but persistently high food prices may also result in a global increase in social disruptions (Lagi et al., 2011). The outbreak of violence in Egypt in 2011

is partially attributed by several studies to a food crisis induced by extreme climatic conditions in other regions (Lagi et al., 2011; Sternberg, 2011). Poor households in developing countries typically spend 70–80% of their income on food (as opposed to 10–15% in wealthier country households), so increased prices could have direct effects on health and well-being (Otto et al., 2017). Low income groups in urban areas are recognized as the most vulnerable to the effects of increased food prices, with urban poverty rates in some African cities expected to increase by up to 30% due to climate-related increase in food prices (Otto et al., 2017).

Socio-cultural shifts will affect anthropogenic drivers of ocean deoxygenation and the impact of the stressor on people in an ongoing and dynamic way. Factors such as human population growth, resource use and consumption rates, effects of climate change on the geography of population centres, sanitation and farming practices, and effects of education and income on social processes will influence nutrient discharges and greenhouse gas emissions (Breitburg et al., 2018). Understanding broader social patterns and incorporating them into future models will be essential (Breitburg et al., 2018).

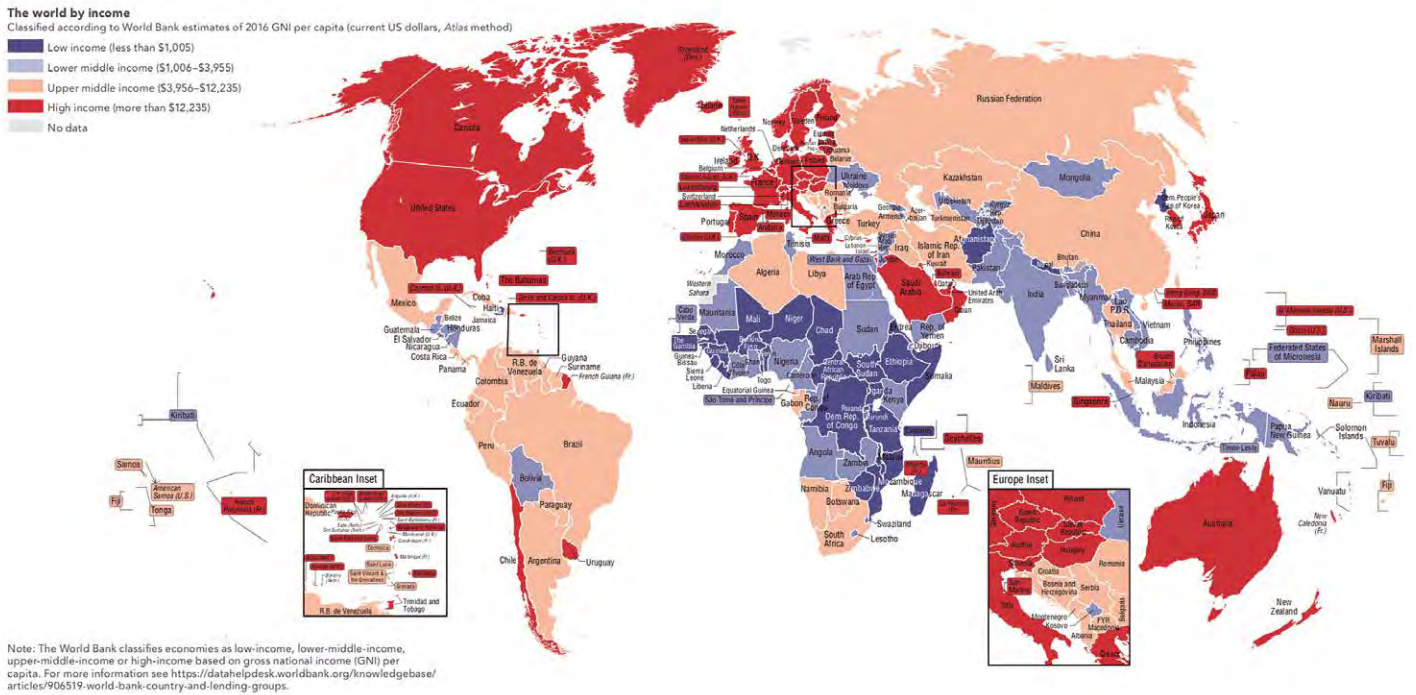


Figure 9.8 Income level by country as an indicator of well-being, vulnerability and adaptive capacity (World Bank, 2017). The World Bank classifies economies into four income groups (low, lower-middle, upper-middle, and high income) using gross national income (GNI) per capita data in U.S. dollars, converted from local currency using the World Bank Atlas method, which is applied to smooth exchange rate fluctuations.

9.4.4 Sensitivity of marine ecosystem subtypes and organisms

Studies have shown non-linear responses to ocean deoxygenation across both marine ecosystem subtypes and species groups. Fish and crustaceans are less tolerant of reduced oxygen levels compared to gastropods and bivalves (Vaquer-Sunyer & Duarte, 2008), so resource use sectors and communities reliant on fish and crustaceans can be expected to see greater impacts on spatial distribution, productivity, and size of stocks (Diaz & Rosenberg, 2011; Stewart et al., 2014). Social groups reliant on gastropods and bivalves may expect to see a range of effects, in the near-term, depending on factors such as the impacts of the suppression of predators on mollusc populations at lower oxygen levels and the physiological optima for different species of molluscs. Examples of improved competitiveness of cephalopods and bivalves can be seen in the Narraganset Bay quahog and Humboldt squid case studies (Sub-sections 9.5.5 & 9.5.6). The effects of low DO on individual organisms are well documented (e.g. Vaquer-Sunyer & Duarte, 2008), so

more specific effects are available for researchers or managers addressing particular species of interest.

Similarly, marine ecosystem subtypes are differentially susceptible to negative effects of ocean deoxygenation. Cooley (2012) noted that coral reefs and wetlands and marshes provide a relatively larger magnitude of ecosystem benefits (in number of service types and relative quantity of each) than other ecosystem subtypes and are also more negatively affected by ocean deoxygenation. Some species of coral have been shown to be more tolerant of reduced oxygen than others, however (Altieri et al., 2017). Mangrove-supported systems provide substantial ecosystem services and the trees are relatively tolerant of ocean deoxygenation (Table 9.2) (Cooley, 2012) while associated organisms may show relatively less tolerance (e.g. Gedan et al., 2017). Kelp forests, seagrass beds, rock and shell reefs, intertidal zones, and lagoons and salt ponds provide a relatively smaller magnitude of ecosystem services (Table 9.2) and are less sensitive to negative impacts of ocean deoxygenation (Cooley, 2012). Despite these observed patterns, particular systems will vary in their

susceptibility to reduced oxygen based on a variety of biophysical factors (Breitburg et al., 2018).

9.4.5 Multiple and interacting stressors

Deoxygenation is mechanistically linked to other ocean stressors, such as warming, acidification, and pollution, which means ecosystems can experience combined or synergistic effects of multiple stressors (Breitburg et al., 2018, 2019 (Chapter 6 this report) Cooley, 2012; Gruber, 2011). The mechanisms of interactions are complex and not entirely understood (Gruber, 2011; Rabotyagov et al., 2014), complicating the task of identifying effects of one or a set of stressors on people. Some general patterns are known, however. Warmer water has reduced capacity to hold dissolved oxygen, so people in areas experiencing warming will also be subject to the effects of deoxygenation. Acidification sometimes exacerbates the effects of low oxygen, but the extent and magnitude of such interactions is not currently estimable (Gobler & Baumann, 2016).

Certain species and ecosystem subtypes have been shown to be more or less affected by synergistic or combined stressors. Several studies suggest that the effects on fish populations of deoxygenation alone can be small to moderate, but when combined with other stressors the combined effect can be large (Chapter 10). For example, Miller et al. (2016) found that acidification increases the sensitivity of two important forage fishes of the genus *Menidia* to hypoxia. Forage fish are important sources of nutrients for people, play important roles in pelagic food web function, and contribute substantially to aquaculture feed and fish meal (Pikitch et al., 2012; Tacon & Metian, 2009). Research on forage fish impacts is nascent, but the potential for human impact is substantial. Wetlands and marshes and coral reefs again provide a relatively large magnitude of ecosystem services (Cooley, 2012) yet are susceptible to interacting negative effects of pollution, ocean acidification, and ocean deoxygenation (Cai et al., 2011; Feely et al., 2010; Howarth et al., 2011) and respond poorly to all three stressors respectively (Riegl et al., 2009).

Similarly, low DO can interact with biological and anthropogenic stressors, by making stocks more susceptible to predation or capture by fisheries via habitat compression or shoaling. For example, Froehlich et al. (2017) showed increased sensitivity of the Hood Canal Dungeness crab fishery to overfishing

when including deoxygenation and other stressors (see 10.6.3). Improved catchability may manifest as increased availability of certain ecosystem services in the near-term, but over the long-term may complicate management and threaten resource-use sustainability.

9.4.6 Ecosystem service categories

Most marine ecosystem services are likely to be negatively affected by reduced dissolved oxygen, although to varying degrees (Table 9.1). Services reliant on living resources are expected to be most negatively impacted and these services generally fall under the categories of provisioning, supporting, and cultural services. Regulating services (air quality, climate, hydrological cycle), transport, fuel and energy, primary production, and food from plants are services thought to be relatively tolerant to ocean deoxygenation (Table 9.1) (Cooley, 2012).

Translation of ecosystem services to human well-being is also likely to vary by category, as the categories are differentially susceptible to social mediation (Figure 9.3). In general, access to certain places is necessary for people to obtain benefits from cultural, provisioning, and, to a lesser degree, supporting services. The potential for access to be mediated by policies and norms, makes benefiting from these service categories more dependent on social factors. On the other hand, controlling access to regulating services is less feasible, so these services are less susceptible to social mediation. Notably, regulating services are the least affected by ocean deoxygenation and access to them is the least dependent on social mediation (Fisher et al., 2013), thus risk due to loss of regulating services is likely to be relatively low generally and more equal across different groups. However, due to existing social factors, some groups may be more exposed or sensitive to changes in regulating services and groups will have more or less capacity to adapt to changes, so a group's vulnerability still plays a role in their level of risk. As a result of these patterns of differential susceptibility and social mediation, ecosystem services that stand to be most affected by ocean deoxygenation are also those that can more readily be taken advantage of by those in power and withheld from those not in power.

9.4.7 Ecological interactions

While ecosystem degradation is commonly understood to lead to reduced biological productivity, ecosystem

service provision, and economic output (Altieri, 2008), ecological community dynamics can lead to increased productivity for some species via altered predator-prey or competitive relationships. One mechanism by which a species can benefit from reduced oxygen conditions is via release from predation. As with natural stress gradients, anthropogenically-induced stressors can create uninhabitable areas for some species, thereby releasing their prey from predation pressure (Altieri, 2008). For the organisms released from predation to experience net benefits, however, they must be tolerant of said stressors themselves (Altieri, 2008). The case of the quahog (*Mercenaria mercenaria*) in Narraganset Bay, Rhode Island and Humboldt squid in the eastern Pacific Ocean provide examples of fisheries which may be benefiting from hypoxia.

Despite these examples of benefits from ocean deoxygenation, altered ecological interactions may instead cause a reduction in prey, increased predation, or otherwise altered dynamics that reduce survivorship of certain species. The complexity of impacts on dynamic food web interactions presents a challenge for predicting effects on people. Less beneficial outcomes from the same hypoxia-induced food web alterations described as 'positive' examples are described in Section 9.5 as well: namely, hake in the eastern Pacific Ocean (increased predation by Humboldt squid), and softshell clams and blue mussels in Narraganset Bay (decreased competitive ability). Similarly, Altieri (2008) cautions that a focus on positive outcomes from hypoxia could distract from the reality of continued environmental degradation.

9.4.8 Multiple scales and feedbacks

In many cases, the process of continued ocean deoxygenation may be subject to both social and ecological positive feedbacks at a variety of geopolitical

scales, further complicating predictions of human impacts, but also providing important insights into the dynamics of anticipated changes. For example, urbanization may both lead to and be driven by reduced dissolved oxygen levels. Rapid growth of urban centres is associated with environmental degradation, including eutrophication-driven ocean deoxygenation (Moore et al., 2003) and the availability of more resources and job opportunities in cities is a major part of the draw to urban areas (Jiang & O'Neill, 2017). Urbanization is projected to continue under all societal development scenarios analysed (Jiang & O'Neill, 2017) and a reduction of available ocean ecosystem services in rural coastal areas could contribute to the continued trend of cityward movement and further ocean deoxygenation in those areas. Similarly, in semi-enclosed systems, such as the Baltic Sea, enhanced nitrogen fixation in response to deoxygenation has led to undesirable cyanobacteria blooms which then contribute to continued deoxygenation (Conley et al., 2009). These blooms can also be toxic and directly negatively affect people and ecosystems.

Long-term effects at spatial scales of ecosystem service use and stewardship will depend on a wide variety of biophysical and social factors, including and beyond the trends discussed here: extent and synergy of multiple stressors, multi-directional ecological interactions and cascading effects within food webs, multi-directional impact pathways between natural and social systems, vulnerability of communities and groups, trends in root causes and dynamic pressures on vulnerability, and socio-political and economic dynamics from local to global scales.

9.5 Case studies

Six case studies are presented in which the effects of ocean deoxygenation on ecosystem services have



Figure 9.9 (A) Blue crab, (B) striped bass, and (C) Atlantic summer flounder are important commercial fishery stocks in the Chesapeake Bay. © blue crab - wpop [CC BY-SA 3.0 (<http://creativecommons.org/licenses/by-sa/3.0/>)]; striped bass - FishWatch (see Gallery) [Public domain]; Atlantic summer flounder - <https://www.capecod.com/newscenter/new-stock-assessments-released-for-summer-flounder-atlantic-striped-bass/>.

been assessed for particular systems. The impacts have been valued in monetary units in all but the last two cases, which attribute impacts to low DO, but do not quantify them. Most cases (four) focus on valuing the loss of provisioning services due to hypoxia, primarily related to fisheries, three consider mitigation options (Baltic Sea, North Carolina, and Gulf of Mexico wetlands), two account for adaptation strategies (Chesapeake Bay and North Carolina), and one considers human well-being impacts holistically (rather than valuing a particular ecosystem service) as well as existence values (Baltic Sea).

The cases presented here provide examples of the trends presented thus far, including: effects of differential sensitivity to ocean deoxygenation across species types (Humboldt squid and Pacific hake, and Narraganset Bay quahog), the importance of understanding adaptive capacity of affected human communities as well as temporal variation in outcomes (Chesapeake Bay striped bass and Narraganset Bay quahog), the importance of understanding social dynamics in determining not only the nature of the impacts, but who experiences them (Baltic Sea, North Carolina, and Gulf of Mexico wetlands), the complicating role of interacting stressors (Baltic Sea, Gulf of Mexico wetlands), and the high value of services provided by several marine ecosystems (Baltic Sea, Chesapeake Bay, Gulf of Mexico). Additional case studies that consider impacts of low DO on fisheries are described in Chapter 10.

9.5.1 Chesapeake Bay and nearby coastal bays

Studies from the Chesapeake Bay and other nearby bays on the U.S. east coast have examined potential monetary losses in commercial and recreational fisheries by using economic models to make simplified assumptions about biological responses to low dissolved oxygen. The Chesapeake Bay is a large coastal estuary on the east coast of the United States that experiences low DO levels year-round due to eutrophication (Higgins et al., 2011). Dissolved oxygen ranges between 0 and 12 mg L⁻¹, with substantial temporal and spatial variation (Breitburg, 1992) and fish stocks can be low (or absent) where DO is low. Affected species include the commercially important blue crab (*Callinectes sapidus*), striped bass (*Morone saxatilis*), and Atlantic summer flounder (*Paralichthys dentatus*) with potential for human welfare losses due to further water quality loss demonstrated in all cases (Figure 9.9)

(Lipton & Hicks, 2003; Massey et al., 2006; Mistiaen et al., 2003).

Incorporating fishing effort and variable DO levels into two harvest production models, Mistiaen et al. (2003) assessed the potential effects of further reduced water quality on harvest efficiency of blue crabs in the Patuxent, Chester, and Choptank tributaries. Their simulations suggest that a decline in average mid-channel bottom dissolved oxygen in the Patuxent River to 4 mg L⁻¹ would result in a 49% decline in harvest and revenue with the same amount of fishing effort. Based on the market price from 2000 of US\$1.00 per pound they estimated reduced catch would result in US\$228,000 of lost earnings (from a total fishery value of US\$465,306) if the crabbers fished in the same areas with the same effort. However, the authors noted that this would be the upper bound of losses under the assumption that fishermen would likely adjust their fishing behaviour in the case of such a decline in water quality. Furthermore, the authors suggested that the crabs that escaped harvest in the assessed fisheries could move to other harvest areas, effectively redistributing the resource to other crabbers, or could be considered part of the reproducing stock, thus the areas of reduced water quality may act as a refuge. Incorporating fisher behaviour and the ultimate outcome for escaped crabs (i.e. crab stock dynamics) into future models would improve understanding of long-term impacts of reduced oxygen levels.

Similarly, Lipton and Hicks (2003) estimated potential losses for the striped bass recreational fishery in the Patuxent River using Poisson catch rate and random utility models. They estimate that if waters are allowed to deteriorate so that they do not exceed 5 mg L⁻¹, the recreational fishery will see an annual loss of more than US\$100,000 in net present value. If waters dip below and do not exceed 3 mg L⁻¹, annual losses would reach US\$195,000, and anoxic conditions would result in annual losses around US\$300,000. The latter outcome is considered unlikely, however, by current water quality models. These modest estimated total losses reflect that short-term welfare effects would be mitigated by the anglers' ability to adapt by focusing fishing effort on less-degraded areas nearby. Should water quality never exceed 3 mg L⁻¹ bay-wide, however, annual losses would be substantially larger around US\$145 million net present value. This outcome is not occurring now or projected to occur in the future, but highlights the importance of alternative healthy fishing grounds. The authors also noted that their study addresses

a small piece of the puzzle as they analyse only one economically-important fishery in the area and they do not incorporate reproduction effects or the population's long-term health.

In contrast, Massey et al. (2006) considered both long-term effects on reduced survival and reproduction as well as short-term effects on species crowding and abundance to examine potential gains in the recreational Atlantic summer flounder fishery with increased DO levels. Linking a bioeconomic model to a recreation demand model, they estimated that a 25% increase in dissolved oxygen in all bays and estuaries throughout the range of the species would increase catch rates by 20% and result in total annual angler benefits of approximately US\$630,000 within the study area and exceeding US\$80 million across the range of the species (Massey et al., 2006).

The studies presented here use economic models to examine potential impacts of changes in DO levels on economic earnings of fishermen in a handful of fisheries. They do not comprehensively consider the range of ecosystem services provided by Chesapeake Bay, its tributaries, and nearby coastal waters, nor do they go the next step to consider impacts on human well-being. Non-use and existence values of the blue crab, striped bass, and Atlantic flounder stocks and fisheries have not been incorporated in the analysis, nor has the affected community's vulnerability or resulting level of risk been considered, with exception of the adaptive capacity of recreational striped bass anglers discussed above.

9.5.2 Baltic Sea

The Baltic Sea is home to the world's largest anthropogenically-induced hypoxic zone (Diaz & Rosenberg, 2008). Cod fisheries have seen impacts from eutrophication and the associated hypoxic zone (described in Chapter 10.6.4) and a transdisciplinary research effort has assessed human well-being impacts of the degraded Baltic Sea in the surrounding countries. Turner et al. (1999) studied user preferences to establish benefits of a 50% reduction of nitrogen and phosphorous inputs, estimating an annual economic benefit of around US\$10 billion (or SEK70 billion). Their analysis considers potential increases in the Baltic by considering potential improvements in ecosystem services including beach recreation, existence and option values of preserving species and their habitats, and benefits from preserving and restoring wetlands. The authors acknowledge that

the exact dollar amount is imprecise and note that the sheer magnitude is telling of potentially large benefits.

Assessing the Baltic drainage basin at a regional level, Turner et al. (1999) identified numerous sources of nutrient loading and several social drivers of eutrophication and hypoxia (including air and water pollution externalities, groundwater depletion, overfishing, poor land use policies, and market price interventions). The authors explored the potential for international agreements amongst bordering countries and found that most countries would see a net gain from pollutant reduction. Their model identified that pollution reduction concentrated on areas of high nutrient loads would be environmentally and economically optimal, as opposed to a uniform abatement strategy. Countries containing sub-drainage basins with larger proportionate impacts are also the countries that stand to benefit most from nutrient reduction. Their results suggest that reducing nitrogen and phosphorous loads concurrently via improvement of existing sewage effluent treatment, coastal wetland creation and restoration, and adjustments to agricultural practices would be highly effective. Targeting areas of sub-standard treatment would be more effective than improving already acceptable, if imperfect, treatment facilities.

This study was concerned with potential for coordinated international action, thus its scope was regional in scale and further differentiation of costs and benefits to the level of sector, community, or group was not included in the analysis. The scale of analysis was appropriate for informing policy at the regional level and, based on Turner et al.'s (1999) analysis, Gren (2001) evaluated four policies aimed at reducing nitrogen loading in the Baltic Sea. Her analysis suggested that coordinated actions across countries would be substantially more effective than independent actions by individual countries.



Figure 9.10 Brown shrimp (*Farfantepenaeus aztecus*) is one of the largest fisheries in the U.S. © Smithsonian Environmental Research Center [CC BY 2.0].

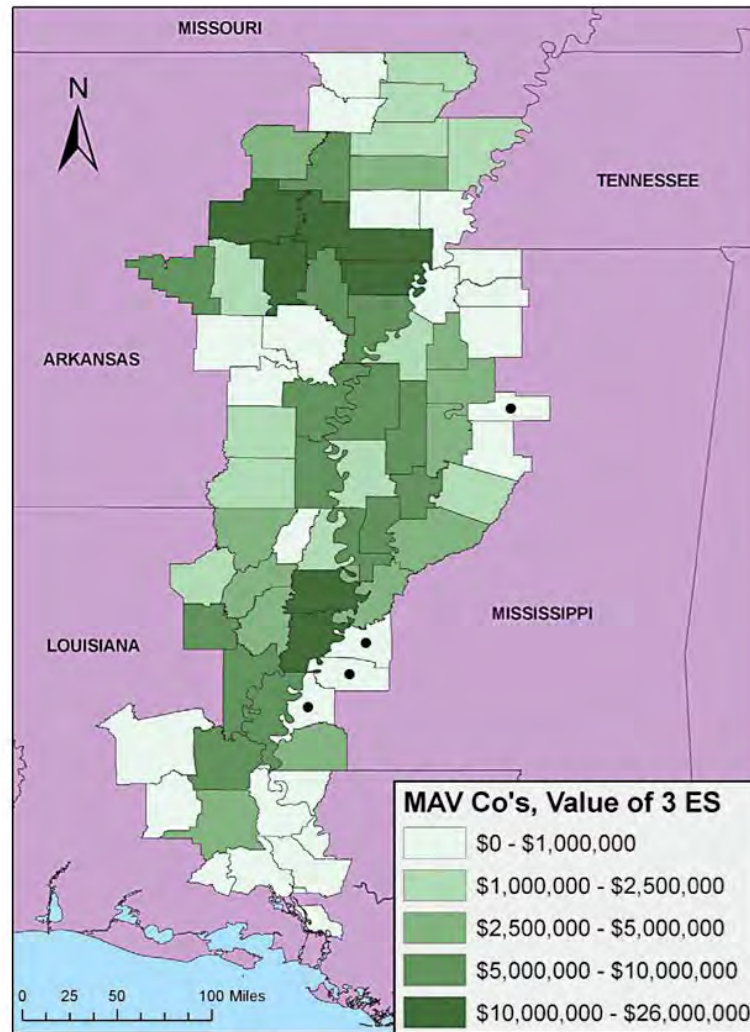


Figure 9.11 Mississippi Alluvial Valley (MAV) counties by annual aggregate social value of the three bundled ecosystem services – greenhouse gas mitigation, nitrogen mitigation, and waterfowl recreation - generated by restored wetlands on Wetlands Reserve Program land (dot indicates insufficient data to construct agricultural baseline for county). Reproduced with permission from Jenkins et al. (2010).

These two studies highlight the utility of interdisciplinary examinations of social-ecological systems at a scale appropriate for management. Ocean deoxygenation is expected to continue in the Baltic Sea under all but the most aggressive nutrient-reduction plans (Meier et al., 2011), making careful assessment of impacts and mitigation options crucial for taking effective action.

9.5.3 North Carolina brown shrimp and blue crab

Several studies in North Carolina have provided insights into the combined effects of hypoxia and social dynamics on fishery sector profits as well as optimal fishery functioning. Huang et al. (2010) estimated an annual loss of US\$1.27 million from catch losses during the period 1999-2005 in the Neuse River and Pamlico Sound Estuary brown shrimp (*Farfantepenaeus*

aztecus) fishery (Figure 9.10). An important contribution of this study was that their model accounted for lagged effects of hypoxia reflecting cumulative exposure. Much of the economic consequences resulted from effects of hypoxia on juvenile shrimp prior to arrival at the fishing grounds. Model results found that losses in Pamlico Sound in perpetuity would amount to US\$27,560,000 in lost revenue. Recouping these lost rents would pay for only a fraction of the costs of mitigating hypoxia in the Sound in perpetuity, estimated to be between US\$155,000,000 and US\$266,000,000 by Schwabe et al. (2001). The authors suggest that the range of ecosystem services provided by the Sound would need to be assessed to justify policy actions to reduce nutrient inputs. By incorporating shrimpers' behaviour and demand for shrimp into the model, Huang et al. (2012) were able to estimate producer and consumer surplus losses and found that all losses accrued to

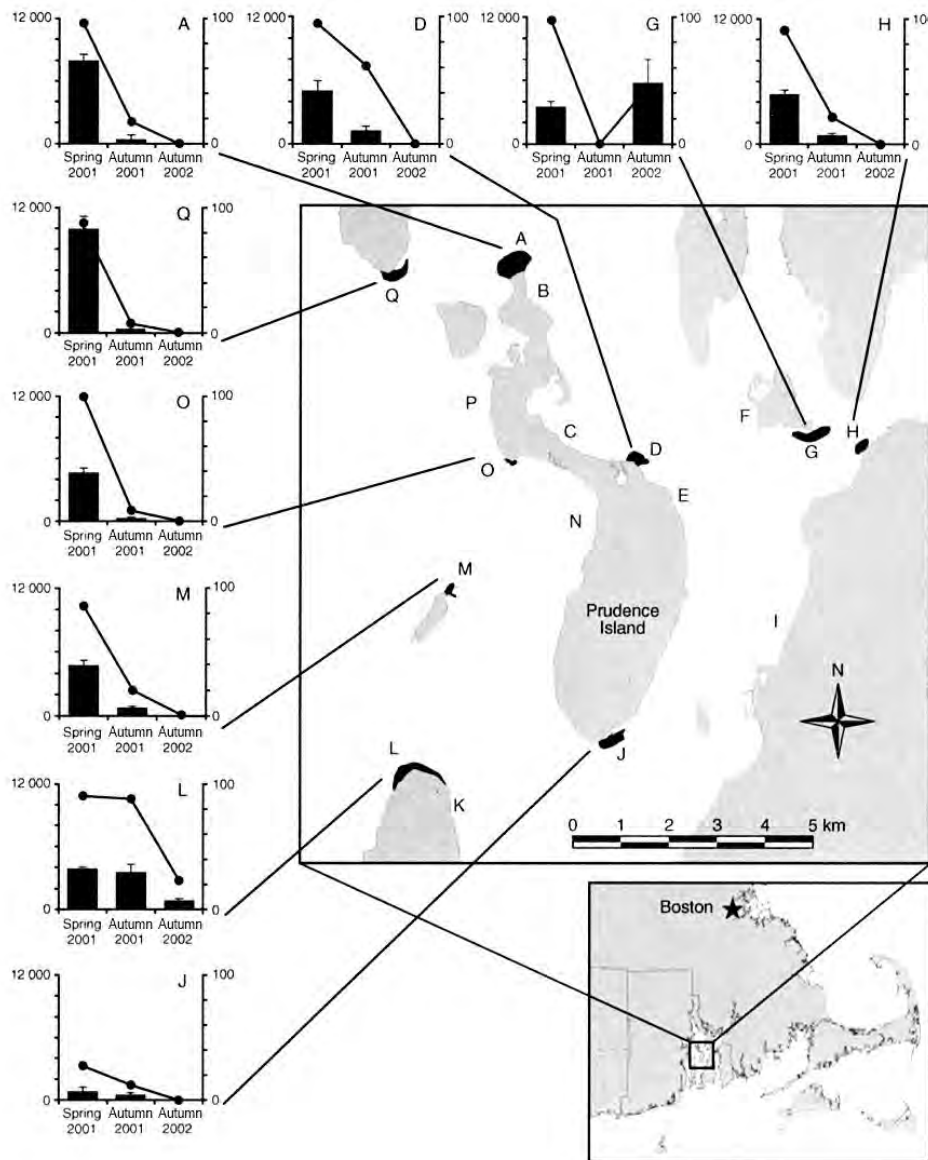


Figure 9.12 Declines in blue mussel density (histograms, mean + SE, count m^{-2}) on the left-hand axis and percentage cover (lines) on the right-hand axis during three sampling periods (before, during, and after the hypoxic event). Study sites: A. Providence Point; B. Bear Cove; C. Potter's Cove; D. Mount Tom Rock; E. Homestead Point; F. Hog Island West; G. Hog Island East; H. Marker 6A; I. Portsmouth Abbey; J. T-Wharf; K. Conanicut Point East; L. Conanicut Point West; M. Hope and Despair Islands; N. Home Beach; O. Pine Hill Point; P. Rossi Farm Backside; Q. Warwick Point. Figure and description reproduced with permission from Altieri and Witman (2006).

producers. In a separate study, Huang and Smith (2011) used a bioeconomic model to find that under hypoxic conditions, optimal harvest occurred earlier in the season.

Similarly, Smith (2007) used a bioeconomic model of the Neuse River Watershed blue crab fishery to reflect both biophysical components of the system, such as spatial dynamics of hypoxia and the relationship between hypoxia and population dynamics, as well as social components in the form of different management regimes and regional market dynamics. He estimated total benefits of a 30% reduction in nitrogen and

associated reduction in hypoxic conditions to range between US\$1 million and US\$7 million annually, with the magnitude of benefits depending on management regime.

These studies demonstrate the value of integrated assessments that consider both social and biophysical processes as well as consider differential impacts on groups reliant on particular ecosystem services. The studies are limited to provisioning services accessed through fisheries and do not consider cultural, supporting, or regulating services or non-fishery provisioning services. Thus, the estimates of fisheries

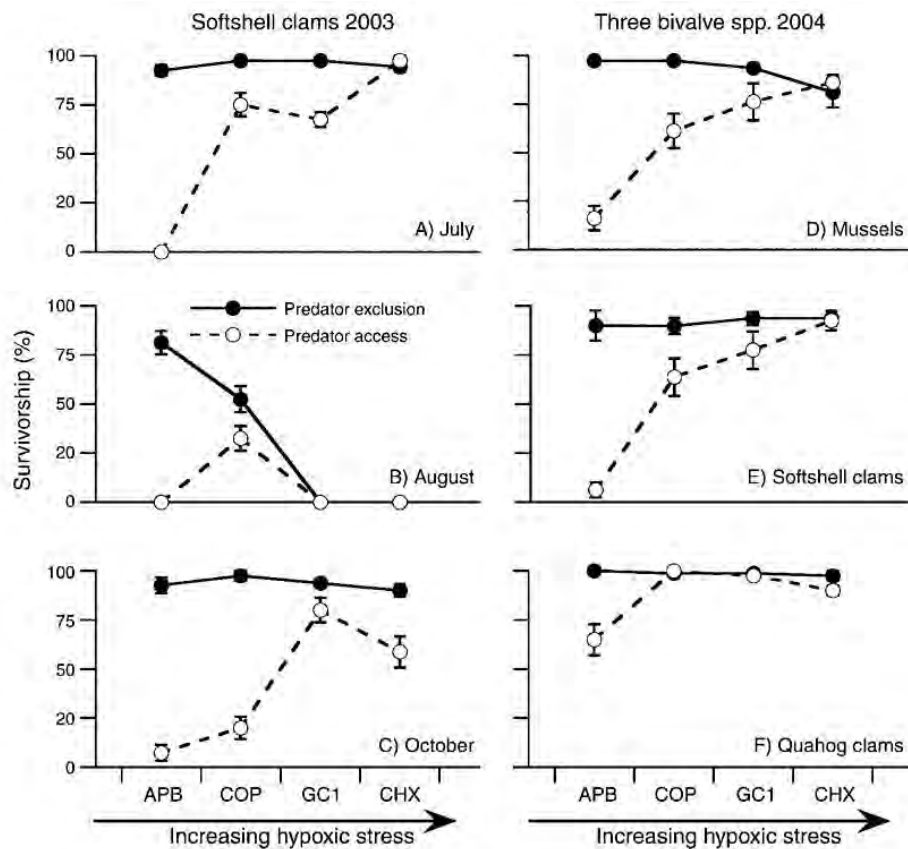


Figure 9.13 Bivalve survivorship along the hypoxic gradient at four hypoxic sites in Narragansett Bay, Rhode Island, USA in predator-exclusion (solid circles) and predator-access (open circles) treatments. There was temporal and spatial variation in net survivorship of softshell clams, exhibiting the interacting hypoxia-driven effects of predator release and physiological stress (A-C). All three species exhibited decreased predation with increasing hypoxic stress (D-F). Differences in survivorship between treatments were assessed with two-way ANOVA. Data were arcsine square-root transformed to meet ANOVA assumptions of normality. Data are survivorship (mean \pm SE) in 10 replicates. Sites on the x-axis are in order of increasing hypoxic stress: APB = Arnold Point Bay, CPO = Conimicut Point, GC1 = Greenwich Cove (navigational marker number 1), and CHX = Chepiwanoxet Point. Figure and description reproduced with permission from Altieri (2008).

gains and losses reflect only partial human impacts of hypoxia levels within the system.

9.5.4 Gulf of Mexico wetlands

Effects of ocean deoxygenation on Atlantic croaker and shrimp fisheries in the Gulf of Mexico are discussed in Chapter 10, but other studies have evaluated the benefits of ocean deoxygenation mitigation more generally. As the largest floodplain in the U.S., nutrient loading from the Mississippi Alluvial Valley (MAV), is considered a principal driver of the “dead zone” in the Gulf (Goolsby & Battaglin, 2001). Wetland restoration presents an opportunity for hypoxia mitigation by increasing the ecosystem’s provision of pollution and waste control (a regulating service) through denitrification (removal of nitrate) and nitrogen sequestration (Jenkins et al., 2010). In addition to wetland restoration contributions to nitrogen mitigation, Jenkins et al. (2010) evaluated potential social welfare benefits of greenhouse gas

mitigation and waterfowl recreation. Despite upfront costs of wetland restoration and reclamation of lands previously converted to agriculture, the estimated social value received from restored wetlands surpasses restoration costs within one year. The study estimates a social welfare value of US\$1,435 to US\$1,486 ha⁻¹ yr⁻¹ with annual MAV-level benefits of approximately US\$300 million. Most of the value (75%) is supplied by 21 of the 67 counties (Figure 9.11) and the authors note that expanded public programmes or novel ecosystem service markets would be necessary to deliver payments to landowners in order for restoration to be economically rational for that user group. For taxpayers who are not directly invested in agriculture on eligible restoration lands, restoration has a social value well above agricultural use and is economically rational.

The authors note that other services that did not have clear monetary value at the time of publication were not included, suggesting their estimate of social value of

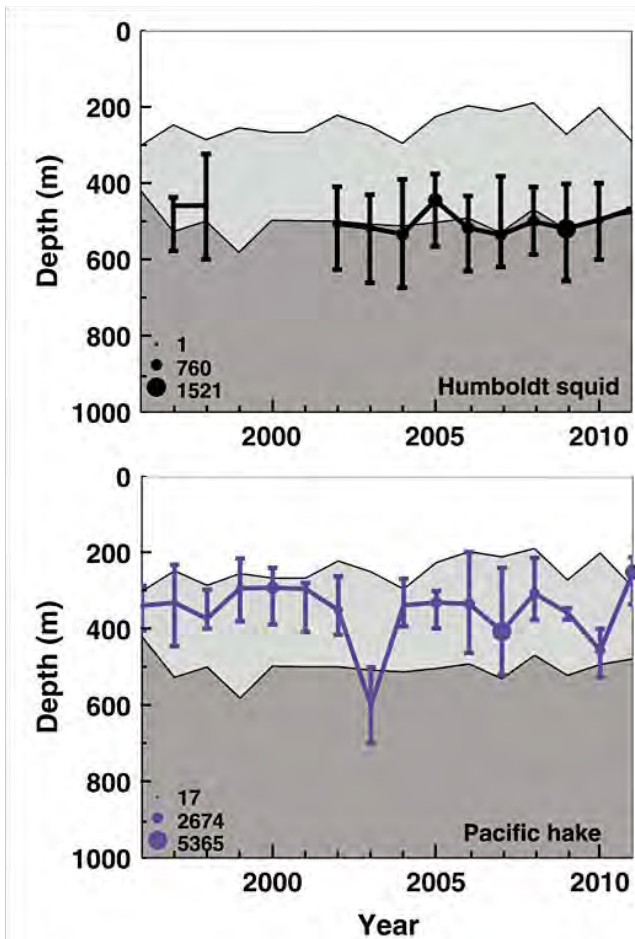


Figure 9.14 Annual depth distributions and abundance of Humboldt squid and Pacific hake in relation to hypoxia. Light grey illustrates the mean depth-range of the oxygen limited zone (OLZ; between 0.5 and 1.5 ml L⁻¹ dissolved oxygen concentration); darker grey indicates the mean depth range of the oxygen minimum zone (OMZ; <0.5 ml L⁻¹ dissolved oxygen). Circles show relative encounter rates for each species, with actual values indicated. Adapted from Stewart et al. (2014).

restoration is on the conservative side. While nitrogen mitigation accounted for the majority of benefits construed from wetland restoration, inclusion of other ecosystem services highlights the interconnection of biogeophysical processes and the necessity of considering the suite of interacting stressors and mechanisms in considering impacts of large-scale environmental change, such as ocean deoxygenation, on people.

9.5.5 Narraganset Bay quahog and blue mussels

Hypoxia in Narraganset Bay, Rhode Island, USA is chronic and has played a central role in shaping ecosystem dynamics and services within the semi-enclosed system. Altieri and Witman (2006) examined impacts of a severe hypoxic event in the summer of

2001 and found that it led to local extinction of blue mussels, a foundational species in the Bay (Figure 9.12). With mass mortality of blue mussels, the species, bay-wide filtration capacity was reduced by >75% and was still further reduced a year later. Their analysis also found that blue mussel density had a bottom-up effect on predator abundance with their presence enhancing four of seven predator populations, including sea stars (*Asterias forbesi*), rock crabs (*Cancer irroratus*), spider crabs (*Libinia emarginata*), and drills (*Urosalpinx cinerea* / *Eupleura caudate*), the abundance of those other species fell when mussels succumbed to hypoxia. In contrast, quahogs (*Mercenaria mercenaria*), another bivalve species, benefited from the new low DO conditions (Altieri, 2008). Following the loss of blue mussels and other harvested bivalve species due to declines in dissolved O₂ concentration (Altieri, 2008; Altieri & Witman, 2006; Desbonnet & Lee, 1991; Good et al., 2003; Oviatt et al., 2003), quahogs are currently the most important fishery within Narraganset Bay (DeAlteris et al., 2000). The fishery is now one of the largest quahog clam fisheries in the United States (Desbonnet & Lee, 1991).

Using the “chronically hypoxic” bay’s seasonal fluctuation in dissolved oxygen levels for *in situ* experiments, Altieri (2008) found that certain levels of hypoxia released quahog, softshell clams (*Mya arenaria*), and blue mussels (*Mytilus edulis*) from predation (Figure 9.13). Common predators of bivalves, such as sea stars, fish, and crustaceans, are highly sensitive to hypoxia and tend to move away from oxygen-depleted waters (Altieri & Witman, 2006; Bell & Eggleston, 2005; Lenihan et al., 2001; Pihl et al., 1991) or stay and become lethargic with reduced predation behaviour (Baden et al., 1990; Bell et al., 2003; Breitburg, 1992; Grantham et al., 2004). However, at still lower levels of dissolved oxygen, gains from reduced predation were counteracted by reduced survival of both the softshell clams and blue mussels (Figure 9.13). Quahog, known as “facultative anaerobes” (Hochachka & Somero, 2002), are highly tolerant to reduced oxygen conditions and were able to survive under the most hypoxic conditions observed (Altieri, 2008). Altieri (2008) noted that, as the most important fishery in the Bay, the success of quahog under hypoxic conditions serves to benefit the community and industry and should be considered in planning for adaptation to sustained hypoxic conditions. He adds, however, that it will be important to consider the dissolved oxygen content threshold of quahog in long-term adaptation strategies.

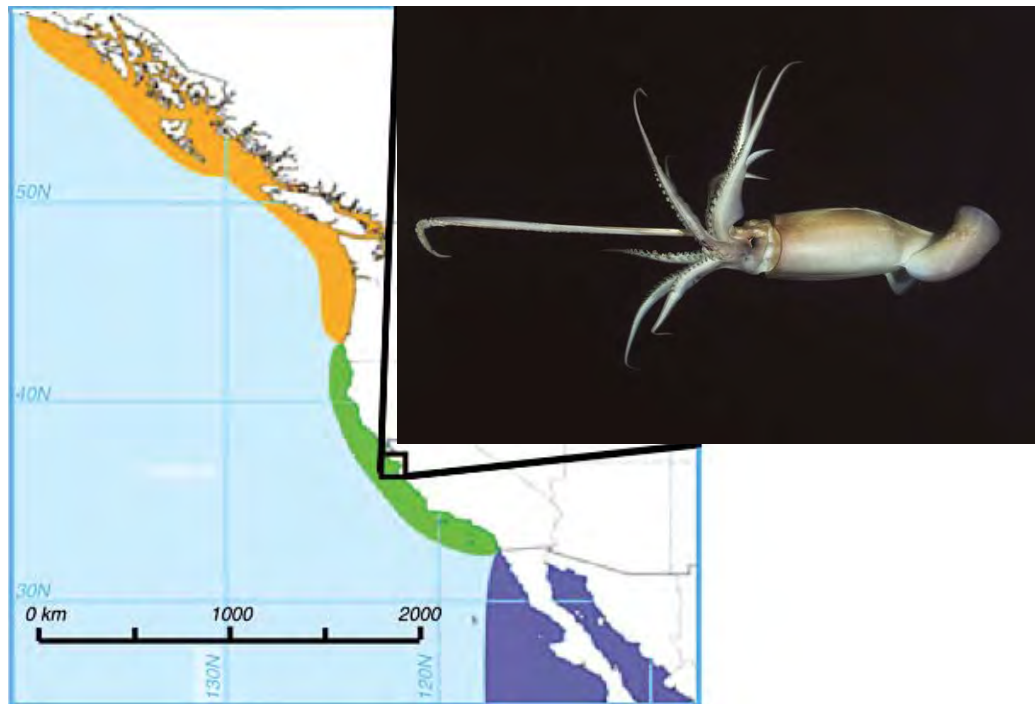


Figure 9.15 Map of Humboldt squid range expansion in the north-eastern Pacific Ocean. Humboldt squid likely came to the Gulf of California and Mexico in the 1970s (blue: Gilly, 2005), were first observed in California and Southern Oregon in 1997/1998 (green: Percy, 2002; Zeidberg & Robison, 2007), and further north in 2004-2005 (orange: e.g. Brodeur et al., 2006; Wing, 2006). Adapted from Stewart et al. (2014). Humboldt squid © WaterFrame / Alamy stock photo.

9.5.6 Humboldt squid and Pacific hake

The Humboldt squid (*Dosidicus gigas*) and Pacific hake (*Merluccius productus*) are two commercially important species in the eastern Pacific Ocean thought to be impacted by ocean deoxygenation in different, but interrelated ways. Humboldt squid are cephalopods with relatively high tolerance to low oxygen levels (Figure 9.14) (Stewart et al., 2014), while hake, a pelagic fish in the same taxonomic order as cod and haddock (Gadiformes), are less tolerant of low oxygen conditions (Figure 9.14). Hake is the largest fishery by volume on the continental U.S. and Canada (Thomas et al., 2011) as well as a prey species of Humboldt squid.

Previously not found in north-eastern Pacific waters, Humboldt squid have expanded their range by increasing the distance of their seasonal migration (Figure 9.15) to access prey species whose distribution patterns have changed as a result of shoaling of oxygen minimum zones (Gilly et al., 2013; Stewart et al., 2014). Squid range expansion has consequently had negative impacts on several commercially-important species via increased predation (Field et al., 2007, 2013). Hake, in particular, have seen increased predation by Humboldt squid in both the north-eastern Pacific California Current system (Zeidberg & Robison, 2007) and the Humboldt

(or Peru) Current system (Alarcón-Muñoz et al., 2008; Arancibia & Neira, 2008). In addition, increased presence of the predators is disrupting hake schooling structures in the California Current (Holmes et al., 2008) and presents challenges for hake management through increased uncertainty of hake stock estimates due to interfering with acoustic methods used to monitor hake numbers and set national quotas (Holmes et al., 2008; Stewart & Hamel, 2010; Thomas et al., 2011). Additional effects of the OMZ on Peruvian fisheries are discussed in Chapter 10.

As a result of environmental and ecological changes (partially driven by reduced dissolved oxygen and shoaling of oxygen minimum zones), the eastern Pacific Humboldt squid fishery has been the largest invertebrate fishery in the world in most years since 2004 (Gilly et al., 2013; Stewart et al., 2014). Global catch has increased from 19,000 t in the 1980s (Rodhouse et al., 2016) to 1.16 million t in 2014 (FAO, 2016) with most of the catch coming from the Peru Current (Stewart et al., 2014). During this period, the hake fishery saw reduced catch, with Chilean total allowable catch (TAC) reduced by more than half from 40,000 t in 2013, to 15,000 - 19,000 t between in 2014 - 2015 (Plotnek et al., 2016). While the hake fishery losses have not been directly tied to increased squid predation, it appears to be a plausible

explanation given the Humboldt squid's opportunistic predation behaviour, high turnover rates, and high consumption rates (Field et al., 2007). Further fisheries impacts are considered likely as Humboldt squid prey include several of the largest fisheries by volume on the U.S. West Coast (Field et al., 2007).

Understanding human well-being impacts resulting from the known or hypothesized changes to provisioning service availability in these two fisheries requires examination of the role each species plays in local, regional, and global markets as well as the ability of communities and relevant groups and sectors to adapt. For example, in Chile, both hake and Humboldt squid are targeted by industrial and artisanal fishing fleets. Distribution of the fishery types varies along the coastline, so geographic regions will be differentially impacted by the growth of the squid fishery and decline of the hake fishery. Specifically, squid fisheries predominate in urban coastal *caletas* (Aburto et al., 2013), which may stand to benefit more from the species' expansion, in the near-term, relative to rural coastal *caletas* that do not generally have developed squid fisheries. The relatively slow rate

of change in Humboldt squid distribution may have facilitated adaptation, indicated by the relatively high number (2350) of artisanal fishing boats targeting squid in recent years (Rodhouse et al., 2016) compared to those targeting hake (approx. 400; Plotnek et al., 2016), despite the squid fishery's more recent establishment.

The Humboldt squid case study provides another example of a fishery that has seen improved performance due to ecological interactions being altered by ocean deoxygenation, likely at the cost of hake fishery performance. While expansion of hypoxic zones did not directly benefit Humboldt squid, the effects of reduced oxygen on their prey populations ultimately benefited the squid, highlighting the power of altered ecological interactions in determining the ultimate impacts of ocean deoxygenation on people. This case further highlights the potential for both positive and negative effects of ocean deoxygenation on people via changes to ecosystem service availability, as well as the potential for uneven distribution of impacts across groups due to existing socio-economic structures.

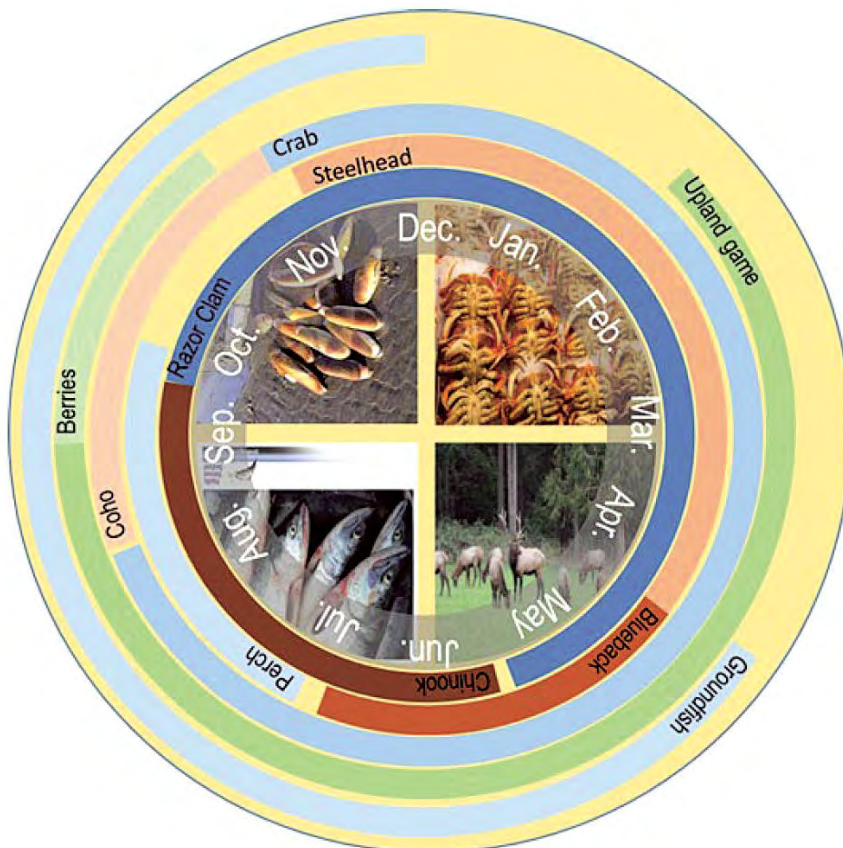


Figure 9.16 Seasonal cycle of the Quinault Indian Nation's harvested food resources. The cycle highlights the reliance on marine resources harvested for subsistence and commercial use and is based on interview data. Reproduced with permission from Crosman et al. (2019).

9.6 Impact pathways

As exemplified by the case studies presented above, assessment of ocean deoxygenation's impacts on people are predominantly focused on valuing specific ecosystem services that are more easily assigned monetary value and are situated in relatively small, bounded systems in more capitalized regions. However, ocean deoxygenation affects people via a variety of complex pathways as shown in trend and case studies described here. Despite challenges, even impossibilities, of calculating the monetary value of such impacts, current knowledge can be used to construct impact pathways to inform adaptation and mitigation policies and actions.

Here we present cases that illustrate two key challenges to comprehensive and quantitative analysis of ocean deoxygenation impacts on human well-being: (a) appropriate inclusion of services that are not readily quantified, such as cultural services (e.g. fish harvest in Native American culture, though this applies to all social-ecological systems), and (b) high risk situations in which numerous interacting stressors and social factors are creating critical and daunting social-ecological problems (e.g. coral reefs). These particularly challenging systems require relatively more research capacity to be appropriately examined.

9.6.1 Native American harvest

For coastal Native American tribes in the Pacific Northwest (PNW) and Alaska, traditional foods such as salmon, clams and crabs represent more than sustenance; they are revered as spiritually fulfilling and central to well-being (Lynn et al., 2013). Traditional foods are central in tribal life through harvest and associated acts (such as preparing, storing, bartering, selling, and consuming the foods) as well as in other facets of life essential for creating and maintaining healthy communities, such as education, ceremonies, and community events (Crosman et al., 2019; Donatuto et al., 2011). For example, Crosman et al. (2019) describe the Quinault Nation's concept of 'clam hunger' as "a deeply felt physical and emotional craving for a traditional food, the harvest of which connects tribal members with traditional places and the eating and sharing of which connects them to their childhoods, their families, and their ancestors" (Figure 9.16). These marine resources that Native American tribes rely on are subject to multiple stressors, including ocean deoxygenation (e.g. Crosman et al., 2019). The upwelling-prone eastern Pacific Ocean boundary current waters adjacent to tribal lands are currently experiencing reduced DO levels and projections predict further reductions (Figures 9.5 & 9.6). With fish and crustaceans particularly vulnerable to negative physiological impacts of ocean

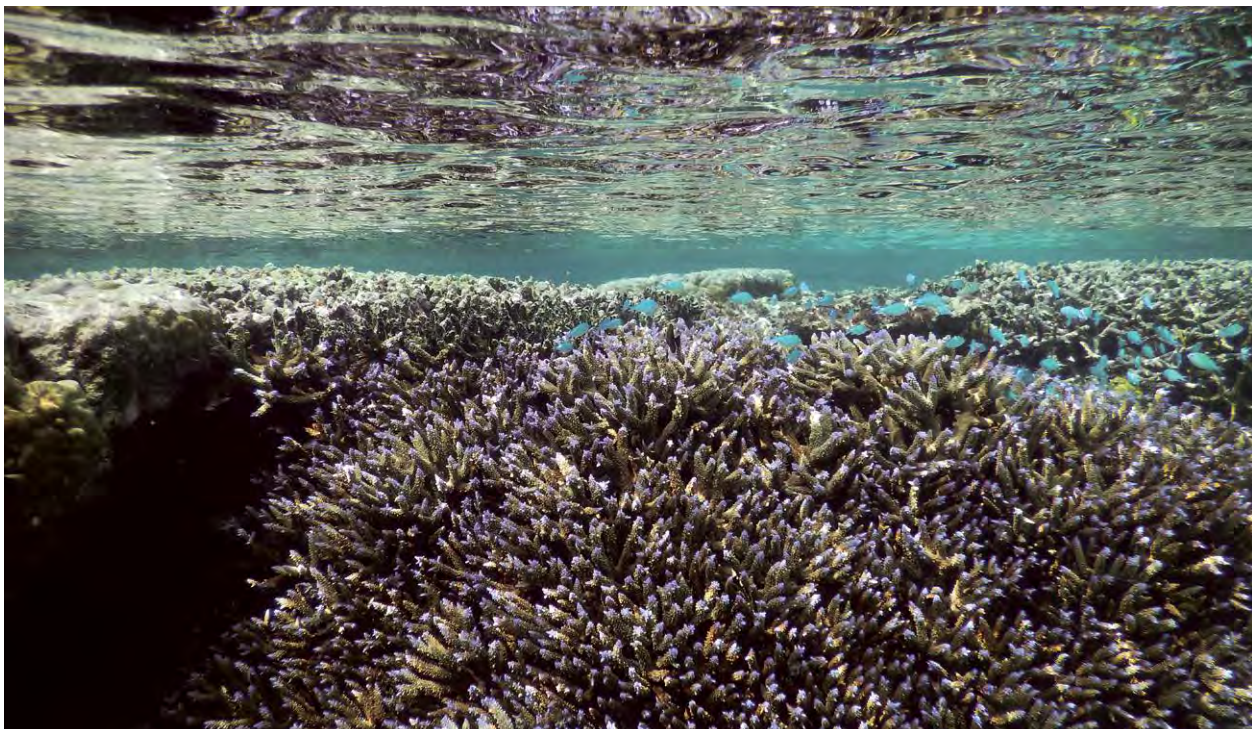


Figure 9.17 Coral reefs provide important ecosystem services, including shoreline protection and provision of nursery habitat for many species. © Rickard Törnblad [CC BY-SA 4.0 (<https://creativecommons.org/licenses/by-sa/4.0/>)].

deoxygenation, and bivalves to a lesser degree (Chan et al., 2008; Vaquer-Sunyer & Duarte, 2011), reduced fitness of important species is likely to lead to changes in availability and movement patterns of different species. For example Dungeness crab in Hood Canal are an important tribal fishery and hypoxia has been shown to increase catch variability and lower minimum catch returns (Froehlich et al., 2017; Chapter 10). As a result, non-lethal environmental forcing from hypoxia threatens the fishery's ability to continue to provide a range of ecosystem services by increasing its sensitivity to overfishing and other pressures.

Not only are the tribes sensitive and exposed to the hazards presented by ocean deoxygenation, their capacity for adaptation or mitigation actions is limited by political and economic exclusion brought about by historical dispossession and alienation from both culture and nature. Tribal access to resources is strongly influenced by the legal and regulatory relationship with the U.S. federal government (Whyte, 2013) and, in particular, restriction of tribal harvest activities to reservations or “usual and accustomed” areas (Silvern, 1999) prevents tribes from employing traditional responses to resource shifts, such as harvesting different species or in different geographic areas (Berkes & Jolly, 2002). Historical place attachments and economic challenges common to indigenous communities in the U.S. (Cornell & Kalt, 1998) further constrain tribal populations' adaptive capacity.

While the nuanced and geo-temporally-relevant impacts of ocean deoxygenation on marine species important to PNW and Alaska Native Americans are not entirely understood, it can be reasonably hypothesized that Native Americans are, and will continue to be, affected by low DO-driven reductions in availability of the ecosystem goods and services they rely on for food, cultural practice, and spiritual wellbeing.

9.6.2 Coral mortality

As a final example and another exercise in transitive reasoning, here we connect deoxygenation-induced coral mortality to potential effects on people. There are no studies yet that directly connect ocean deoxygenation-induced coral mortality to human well-being impacts, however, potential impact pathways can be inferred from existing knowledge. It is well-established that corals provide a wide range of ecosystem services, including shoreline protection, important nursery grounds for

many species harvested commercially, recreationally and in the aquarium trade (Agardy et al., 2011), all cultural services, such as tourism, recreation, education, and aesthetic and spiritual values (e.g. Barbier et al., 2011) and a variety of other services across all four categories (see Table 9.2; Figure 9.17) (MEA, 2005a). Millions of people are highly dependent on the goods and services provided by coral reefs, primarily in developing countries, where there is an especially high reliance on reefs for food provision (Figure 9.7) (FAO, 2018; Teh et al., 2013). It is also established that ocean deoxygenation leads to the decline of corals, though mechanisms of impact and recovery are understudied and not well-understood (Altieri et al., 2017). Studies suggest that coral reefs are one of the ecosystem subtypes most susceptible to multiple and interacting biogeochemical stressors of ocean warming, pollution, and ocean deoxygenation (Altieri et al., 2017; Cooley, 2012; Nelson & Altieri, 2019). Ocean deoxygenation may be particularly harmful for coral reefs over the long-term and compared to other reef disturbances, because hypoxia impacts a wide range of taxa including consumers, habitat formers, and pathogens (Altieri et al., 2017). It also mediates many important processes on the reefs and so interacts with climate change and ocean acidification (Nelson & Altieri, 2019).

Applying transitive reasoning, ocean deoxygenation-induced decline of corals could lead to a decrease in or loss of the services listed above and thus create hazards for reef-dependent and reef-associated human communities. Coral reef social-ecological systems may face some of the highest levels of hazard and risk from ocean deoxygenation due to relatively high sensitivity of the natural system to interacting and multiple stressors (Nelson & Altieri, 2019) and relatively high vulnerability (high sensitivity and low adaptive capacity) of associated human populations. Coral reef social-ecological systems are further disadvantaged by the lack of research addressing the role of ocean deoxygenation in coral reefs and a dearth of historical data on oxygen concentration on reefs due to traditional data collection protocols in reef systems (Altieri et al., 2017). Despite appearing to play a major role in coral mortality, recent research suggests that low-oxygen events on reefs are likely under-reported, in part because the effects of hypoxia may be confused with other factors (Altieri et al., 2017; Nelson & Altieri, 2019). The lack of research and management capacity in affected areas reflects the crux of the problem when high levels of hazard meet low levels of adaptive capacity.

Table 9.3 Select examples of potential impact pathways of ocean deoxygenation (OD) on human well-being assembled using transitive logic to link knowledge from disparate disciplines.

ES Category	Biophysical process, resource, or habitat	(A) Effect(s) of OD on biophysical process, resource, or habitat	(B) Select ecosystem service(s) affected	(C) Potential effect(s) on human well-being
Provisioning	Fish	Decrease in biomass (Breitburg, 2002)	Food, income (Agardy et al., 2011)	A reduction in fish body size can lead to a reduction in food providence and income; fishers will need to catch more small fish to equal the same pay and food provision as catching fewer larger fish. (Díaz & Rosenberg, 2011)
	Fish	Decrease in abundance, survival and availability (Diaz et al., 2013)	Food, income (Agardy et al., 2011)	Fewer fish and lower fish availability may result in lower income for fishers, less food available for communities, and more conflict over limited resources. (Dubik et al., 2018; Smith et al., 2017)
	Fish	Constrains and compresses fish habitat (Hughes et al., 2015; IPCC, 2014)	Food, income (Agardy et al., 2011)	Shrinking of fish habitat reduces the suitable area for fishers to fish and could put further economic strain on them by inducing the need to travel further or switch gears to catch the same type and amount of fish as previously. (Díaz & Rosenberg, 2011; Dubik et al., 2018; Pecl et al., 2017)
	Fish	Habitat expansion (Stewart et al., 2014)	Food, income (Agardy et al., 2011)	Habitat expansion can provide new fishing opportunities as species move into new areas and become a newly available resource for fishers. (Pecl et al., 2017)
	Coral reefs	Coral bleaching and mass mortality (Altieri et al., 2017)	Shoreline protection (Agardy et al., 2011)	Coral mortality will result in a weakening and/or loss of shoreline protection (Gattuso et al., 2015)
Cultural	Fish	Decrease in survival, availability and abundance (Chan et al., 2008)	Spiritual (Lynn et al., 2013)	Indigenous groups who rely on shellfish and finfish harvest for cultural and spiritual well-being are more negatively affected by declines in availability of culturally important species. (Lynn et al., 2013)
	Fish	Decrease in fish catch (Lipton & Hicks, 2003)	Recreation	Decrease in recreational fish catch results in economic losses for those who profit from that fishery and loss of cultural services. (Lipton & Hicks, 2003)
	Coral reefs	Coral bleaching and mass mortality (Altieri et al., 2017)	Education and recreation (Agardy et al., 2011)	Coral die-offs result in an absence or reduction of educational, recreational and research opportunities, and people who make a livelihood from these activities will be more negatively affected. (Gattuso et al., 2015; Mora et al., 2013)
Supporting	Coral reefs	Coral bleaching and mass mortality (Altieri et al., 2017)	Nursery and essential fish habitat (Agardy et al., 2011)	Declines in nursery and essential fish habitat (supporting services) may result in fewer fish available as resources for fisheries, tourism, recreation, and other provisioning and cultural services.
	Biodiversity	Decrease in fish species richness (Hughes et al., 2015; Pecl et al., 2017)	Invasion/perturbation resistance, Recovery from fish collapse, Recreation, Waste removal (microbial diversity), Habitat protection (Palumbi et al., 2009)	Reduced resilience to invasive species and fishery collapse; loss of recreation potential, waste removal and habitat protection.
Regulating	Oxygen Minimum Zones (OMZs)	Increased carbon sequestration in OMZs (Cavan et al., 2017)	Carbon sequestration	Increased carbon storage in the ocean could potentially counteract effects of greenhouse gas emission on people to some degree, though this mechanism of change is understudied at present.

The transitive method of thinking can be applied to better understand other impacts of ocean deoxygenation on people that follow pathways yet to be holistically researched, but for which reliable knowledge exists (scientific, indigenous, or otherwise) about each string of arguments; further examples of such cases are given in Table 9.3.

9.7 Continued ocean deoxygenation: anthropogenic hazards with human solutions

Effects of ocean deoxygenation on people remain understudied and inherently challenging to assess. In particular, non-use and existence value as well as cultural services are underdeveloped in the ecosystem services literature (Fisher et al., 2013; Rabotyagov et al., 2014) and, indeed, within the context of ocean deoxygenation. Spiritual, therapeutic, and aesthetic values of ecosystems are difficult to quantify and, thus, challenging to incorporate into the empirical framework of ecosystem services. Even the more readily assessed welfare losses associated with ocean deoxygenation have only been addressed by a relatively small number of studies and examinations of effects on humans are limited by gaps in knowledge of the biophysical mechanisms and impacts of reduced dissolved oxygen levels (Rabotyagov et al., 2014).

Despite the lack of extensive research on the topic, current knowledge based in both the natural and social sciences, as well as the humanities, offers useful insights into what can be expected from continued ocean deoxygenation. Reductions in dissolved oxygen are expected to disrupt functioning of ecosystems which support a range of services that human communities, groups, and economic sectors currently rely on for well-being. Documented and anticipated biophysical impacts are generally negative, including habitat degradation and decreased fitness and survival of species, emigration of species from certain areas, and loss of critical habitats. People reliant on certain species and in certain regions may benefit from reduced DO levels, if only temporarily, and generally in association with losses to other species. Coral reefs and wetlands and marshes are most susceptible to negative effects of ocean deoxygenation and are considered to provide the largest magnitude of ecosystem services. Low latitude, coastal urban and rural populations, and poor households in developing countries are most vulnerable to the impacts of ocean deoxygenation. These represent

systems of priority focus and regions and communities where they overlap are uniquely at risk, such as coastal communities in West Africa and low income developing countries (LIDCs).

Social factors will play a critical role in how biophysical changes are experienced by different groups and communities. A group's social role and characteristics will determine their level of vulnerability to ocean-deoxygenation-induced or -exacerbated hazards and changes based on their ability to adapt to, mitigate for, and possibly take advantage of altered ecosystem services. Owing to the variability of biophysical effects and disparate capacities of social groups to adapt to and mitigate for environmental changes, effects of reduced DO levels on different communities will be highly variable with outcomes generally exacerbating existing inequalities and reinforcing social-ecological poverty traps (Cinner et al., 2018). Any resulting benefits will largely accrue to those in power who have greater capacity to take advantage of new opportunities, while those in positions of less power will generally have less access to newly available or increased ecosystem services. Similarly, negative impacts will disproportionately affect those with less power, who are more reliant on ecosystem services, more vulnerable to hazards, and have less adaptive capacity to respond to changes. Conversely, those in power, will experience hazards to a lesser degree due to their reduced vulnerability and greater adaptive capacity.

Improved understanding of nuanced impact pathways of ocean deoxygenation to human well-being outcomes will be of critical importance for effective planning in response to ocean deoxygenation and other large-scale environmental changes going forward. Anticipating both long- and short-term biophysical and social changes under continued ocean deoxygenation is both essential and challenging. Further studies should endeavour to better understand the nature of non-linear responses of both natural and social systems to slow-onset hazards driven by ocean deoxygenation as well as biogeochemical interactions with other stressors. Analyses of ecosystem services should consider the entire range of service types (e.g. Ash et al., 2010; Landsberg et al., 2012), even where not quantifiable, in order to provide the depth and accuracy of information needed for proper planning. Transdisciplinary approaches to assessing systems holistically present promising means for achieving nuanced and policy-relevant knowledge of complex and dynamic

social-ecological system dynamics. Adaptation plans should include consideration of species and habitats that are relatively tolerant of hypoxia in order to bolster their utility in providing ecosystem services. However, attention should remain on these near-term benefits as indicators of overall habitat degradation (Altieri, 2008).

The ultimate consequences of reduced oxygen levels in the ocean will result from complex interactions between natural and social systems, yet the opportunity to minimize negative impacts lies squarely within the social system alone. Efforts to reduce human vulnerability, increase adaptive capacity, mediate conversion of ecosystem services into human well-being, and mitigate for impacts of ocean deoxygenation on ocean systems must all come from actions of people and social institutions and maintain a focus on equity. An effective way for society to reduce the impacts of any environmental change, including deoxygenation, is to reduce the vulnerability of at risk groups and individuals by targeting ultimate and proximate causes of sensitivity, exposure, and capacity to adapt to hazards. In preparing to mitigate for and adapt to impacts of ocean deoxygenation, attention should be paid to the central role that social institutions play in mediating access to ecosystem services and the inherent inequities in the ways in which humans experience natural hazards.

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“Coral reefs, wetlands and marshes, and fish and crustaceans are most susceptible to negative effects of ocean deoxygenation, so people reliant on these systems will be particularly at risk of negative impacts.”

Chapter 9 authors

“The extent of the deoxygenation effects on fisheries is anticipated to increase because the areas of the ocean that will show increasing deoxygenation overlap with the coastal and oceanic regions that support high fisheries production.”

Chapter 10 authors

Impacts of ocean deoxygenation on fisheries

10

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Summary

- Fisheries (commercial, artisan, recreational harvest) are an ecosystem service that provide employment and nutrition in the global food system. Worldwide production of capture fisheries has levelled off, while demand continues to increase. Over-harvesting and effects on habitats and the food web switches fisheries from an ecosystem service to a stressor.
- Deoxygenation is anticipated to expand over the next decades, and can affect fisheries through negative effects on growth, survival, and reproduction affecting biomass, and movement of fish affecting their availability to harvest. The extent of the deoxygenation effects on fisheries is anticipated to increase because the areas of the ocean that will show increasing deoxygenation overlap with the coastal and oceanic regions that support high fisheries production.
- Quantifying the effects of deoxygenation on fisheries is complicated by the effects of co-varying environmental factors and other stressors that also affect the population dynamics of the species of interest, and because the dynamics of oxygen and fisheries (fishers and vessels) are highly site-dependent. Global climate change involves simultaneous changes in temperature, acidity, and oxygen, as well as effects caused by other stressors such as sea-level rise.

- Isolating a direct hypoxia effect on fisheries landings using a correlation-based analysis of landings and nitrogen loadings across coastal ecosystems was difficult, but trophic efficiency (landings per unit nitrogen loading) was lower in systems with extensive hypoxia.
- Eight case studies show the various ways deoxygenation affects fisheries. Examples include low oxygen effects on the target fish population itself through reduced recruitment and population abundance and examples of spatial distribution effects on the fish and crustaceans resulting in changes in the dynamics of fishing vessels. Analyses range from circumstantial evidence based on field data to extensive data and modelling.
- Modelling analyses demonstrate that in those situations when hypoxia alone may have small to moderate population-level effects, the effects can become large or amplified when hypoxia is combined with other stressors.
- A prevalent effect of deoxygenation documented in the case studies was changes in fishing locations in response to fine-scale distribution changes of the target species due to hypoxia that then affects the catchability and bio-economics of fishing. Catchabilities are relied upon for effective fisheries management and not including the effects of deoxygenation on catchability can result in ill-informed management analyses and incorrect harvesting advice.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen concentrations in habitats presently used by fish that support fisheries will result in species-specific reductions in growth, survival, and reproduction of individuals. When sufficient numbers are affected, there will be effects at the population level.	<ul style="list-style-type: none"> • Reduced fishable biomass. • Poor quality of fish (e.g. skinny) in the catch.
Increasing areas of the ocean will experience lower oxygen concentrations that will cause organisms to avoid lethal areas, and in some cases, cause individuals to aggregate around the hypoxia areas or shift their spatial distributions.	<ul style="list-style-type: none"> • Fishing activities will be affected economically (higher costs) by vessels requiring longer trips, and spending less time fishing because they spend more time motoring to access the fishing grounds. • In some situations, fish will become easier to catch (aggregation closer to shore) and more available to local fishers. • In both cases, deoxygenation will affect management (likely being riskier than thought) that relies on relating catch to population abundance (catchability) because catches will no longer adhere to the underlying assumptions about catchability used in stock assessments.
Increasing deoxygenation is occurring worldwide, especially in coastal areas that also provide much of the world's commercial and subsistence fisheries catch.	<ul style="list-style-type: none"> • With the catch of wild fish approaching maximum sustainable levels, the need for accurate management advice is critical. • Management needs to account for the effects of deoxygenation in its stock assessments and deliberations.

10.1 Introduction

Fisheries involve the harvest of individuals from populations or stocks. Fisheries include harvested invertebrates (e.g. shrimp), finfish, sharks, and rays; the terms fish and fisheries are used here to refer to all of these. Fisheries vary in their scale from highly localized activities involving small boats that provide fish for a local community to large vessels and fleets that operate trans-oceanic and enter their catches into world-wide markets. Fisheries also include recreational activities, which are fishing activities that do not serve as a primary source of nutrition and whose catch is not generally sold or otherwise traded (FAO, 2012) (Figure 10.1).

Fisheries play a vital role in the global food system and in nutrition (or food) security and are therefore considered an ecosystem service (Daily et al., 1997; Holmlund & Hammer, 1999). In situations of persistent over-harvesting, or fishing affecting critical habitat, or removals altering the food web and ecosystem function, a fishery becomes a stressor (Chapman, 2017; Worm et al., 2009). Proper management of a fishery involves considering the biology of the species, economic aspects of the harvesting, how the species fits into the broader ecosystem, and consideration of the well-being of the human communities that rely on the catch (Marshall et al., 2018). Fisheries are a source of nutrition for many people, ranging from the primary source in some developing countries and for some local communities to a supplemental, but still important, source in other places (Béné et al., 2015). Insufficient protein in many developing nations leads to human health issues (Golden et al., 2016).

Deoxygenation is anticipated to increase over the coming decades (Chapter 4; Breitburg et al., 2018; Keeling et al., 2010). We consider three types of deoxygenation that affect marine ecosystems: (1) coastal hypoxia (Rabalais et al., 2014), and oxygen minimum zones (OMZs) in

both (2) upwelling and (3) open-ocean systems (Levin, 2018). Upwelling systems are also coastal but their low oxygen is driven by the upward nearshore influxes of low oxygen waters, while coastal hypoxia is fuelled by eutrophication (e.g. nutrients coming in through rivers and land runoff). Low dissolved oxygen affects the habitat quantity and quality for many species of interest, and can have both direct (e.g. reduced growth, spatial displacement) and indirect effects (e.g. slowed growth from low oxygen causing reduced prey) on individuals. Direct and indirect effects can affect a sufficient number of individuals to then influence the abundance, mean size, tissue composition (quality as food), and locations (e.g. displacement due to avoidance) at levels that would affect the catch of fisheries (i.e. population or stock level) or the behaviour or economics of the fishers.

In this chapter, we first summarize the status of fisheries worldwide and discuss possible effects of deoxygenation on fisheries dynamics. Second, the complications arising from oxygen concentrations being correlated with other environmental variables, such as water temperature, and that the species of interest are often actively managed that affects their abundance are discussed. We then present the evidence for deoxygenation effects on fisheries using available correlation-based analyses and using a suite of case studies. Finally, we discuss the implications of deoxygenation on the management of fisheries.

10.2 Current status of fisheries

Annual catches world-wide have levelled off at about 90 million MT, suggesting many stocks are fully exploited and some are over-exploited (Figure 10.2; FAO, 2016). The percentage of fish stocks within biologically sustainable levels has declined from 90% in 1974 to 68% in 2013, and the percentage of stocks fished at unsustainable levels increased rapidly from 10% in 1974 to 26% in 1989 and then at a slower rate to 31% in



Figure 10.1 (A) Artisanal fishing boats Senegal © Juan Vilata / Alamy stock photo (B) Pelagic trawlers tied up in Peterhead harbour, Scotland © Keith Lloyd Davenport / Alamy stock photo (C) Sea angling off rocks at North, Scotland © John M Baxter.

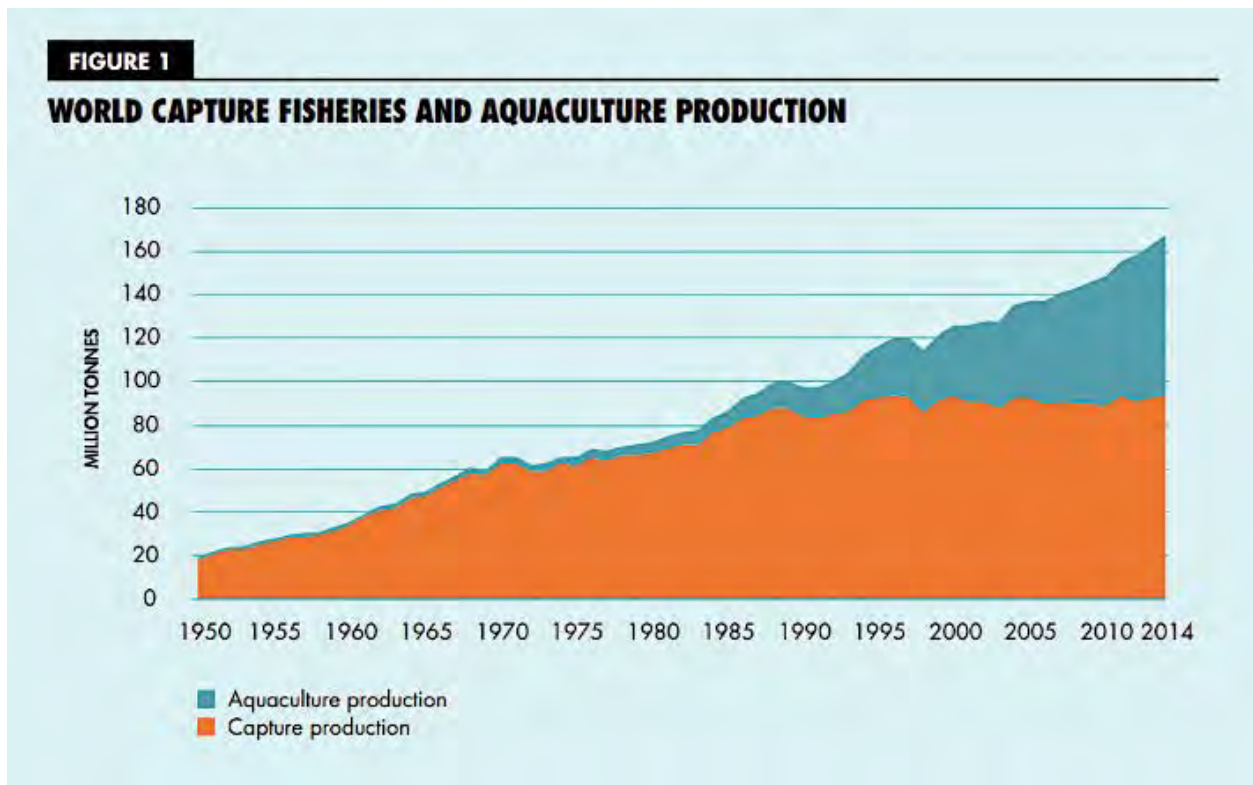


Figure 10.2 Worldwide fisheries and aquaculture production for 1950 to 2014 (FAO, 2016).

2013 (FAO, 2016). The terms overfishing and overfished are rooted in the classical view of a single species management approach and relate to the spawning biomass and fishing rate at maximum sustainable yield (MSY) (Hilborn & Stokes, 2010; Murawski, 2000; Ulltang, 2002). Sound management results in stock biomass being at the biomass associated with MSY, which is often substantially below the biomass that would occur without any fishing. In general, when the current spawning stock size is below the stock size at MSY (i.e. allowing for more stock would increase yield), the stock is considered overfished. Overfishing (as distinct from overfished) occurs when the current fishing rate is above the fishing rate at MSY. In both cases, there can be “safety factors” included to adjust the targets of biomass and fishing at MSY; sometimes referred to as part of the precautionary approach (Darcy & Matlock, 1999; FAO, 1996; Restrepo & Powers, 1999).

The degree of the over-exploitation of fisheries worldwide, and therefore the degree of success of current management practices, is an ongoing debate (Branch et al., 2011; Pauly et al., 2002; Worm et al., 2009). Fisheries management has been challenged in its ability on how to achieve an equitable and sustainable balance between the upper limits imposed by fish production in nature and the ever-increasing demand.

This has led to scrutiny of the status of fisheries stocks worldwide and to debates about the current status of the populations supporting the fisheries and about the effectiveness of fisheries management itself. Some have suggested that additional long-term yield is possible (albeit with large reductions of fishing pressure in the short-term) with better management and effective stock rebuilding efforts (Ye et al., 2013). Regardless, there is no doubt that there is a low likelihood of expanded global yields from capture fisheries, while the demand for fish products will continue to rise into the future (Bell et al., 2016). Rice and Garcia (2011) estimated that an additional 75 million MT will be needed to provide 20% of the protein requirements for the human population expected in 2050. Aquaculture is expected to increase its contribution to worldwide fish harvests, but even with a significant contribution from aquaculture, capture fisheries will continue to be pushed to their limits (FAO, 2016).

Effective management of fisheries is absolutely critical to ensure optimal use of the resource in terms of sustainable harvesting and ensuring ecosystem health and human well-being. Allowing for too much harvest will endanger fisheries yields and ecosystem health in the future. An overly cautious approach, such as greatly reducing harvests to purposely under-exploit many stocks, is also

non-optimal because of the heavy and growing reliance on fisheries for nutrition. With this current status of near-maximum harvesting by fisheries and the urgent need for management to be highly effective, it is critical for us to understand and quantify the effects of stressors such as deoxygenation on fish populations and the dynamics of fisheries.

10.3 Possible deoxygenation effects on fisheries

The effects of low dissolved oxygen on individual organisms are well studied and documented (e.g. Vaquer-Sunyer & Duarte, 2008). Effects on growth, survival, reproduction, and movement are of primary interest to assessing possible effects on fisheries. These effects on individuals and in localized areas can lead to responses at the population and food web levels (Pörtner & Peck, 2010; Rose et al., 2009), which in turn, can change the harvestable stock abundance, body sizes and quality of the tissues of harvested individuals, and where harvestable individuals are vulnerable and feasible to be caught (Breitburg et al., 2009a; Townhill et al., 2017).

Many population processes in fish, such as survival rate, maturity, and fecundity, are size-dependent; thus, effects on growth can lead to changes in population abundance and other attributes that affect fisheries (Rose et al., 2001). Available prey and growth can also affect the composition of the tissues of individuals, which affects their nutritional value and price (e.g. tuna – Carroll et al., 2001; Wessells, 2002). Movement typically also increases with size or age, and a common response of mobile individuals to low DO is for individuals to move away to avoid exposure to very low DO concentrations that could be lethal (Zhang et al., 2009). Movement also results in individuals experiencing different environmental, habitat, and food web (prey and predators) conditions than they would have if they had not avoided the low DO, and this, in turn, affects the growth, survival, and reproduction (fecundity, maturity) of these individuals (Breitburg, 2002; Ekau et al., 2010). Deoxygenation can therefore affect fisheries in two ways: effects on individual fish that result in population changes that affect catch, and effects on the fishers' behaviour and vessel dynamics (e.g. which species to target and where to fish) that affect fishing location and pressure and thus catch. Low DO can reduce growth, survival, and reproduction, of individual fish and thus the abundance of the fishable stock itself (Townhill

et al., 2017). Smaller individuals and altered spatial distributions due to avoidance movement can affect the dynamics of the fishing vessels and the economics of the fishery (e.g. Huang et al., 2012; Langseth et al., 2014).

A key consideration determining potential effects of deoxygenation on fisheries is whether enough individuals are exposed and sufficiently affected to result in meaningful changes in the fishable stock. This moves the analysis from effects on individuals to the effects seen at the population level. Such scaling-up of individual effects to the population level is a common requirement for assessing the ecological effects of many stressors (e.g. Barnthouse et al., 2008; Pastorok et al., 2001) because it puts the effects of the stressor on an ecologically- and publically-relevant scale and, for fisheries, the same biological level (i.e. population) at which management operates (Barnthouse et al., 2008; Hilborn & Walters, 2013).

Documenting and quantifying the effects of deoxygenation on fisheries is necessarily site-specific. This is because the spatial and temporal dynamics of low DO are site-specific depending on local conditions such as bathymetry, nutrient inputs, and biota. Fisheries also are highly site-specific depending on access to the fishable stocks, location of ports, types of vessels used, and because most fisheries are managed locally or regionally. We therefore use case studies to illustrate how deoxygenation affects fisheries.

10.4 Multiple stressors and managed populations

A challenge in the study of deoxygenation effects is to separate oxygen effects from the concomitant changes in other simultaneously changing stressors (Chapman, 2017). Oxygen, temperature, and ocean acidity are all changing, and they interact and affect each other (Bopp et al., 2013; Gruber, 2011). Warmer temperatures and higher acidity are associated with lower dissolved oxygen. Other simultaneous changes will be sea-level rise (and its possible direct or indirect effects on oxygen) and uncertain changes in nutrient loadings that drive hypoxia in coastal ecosystems. Nutrient loadings and low oxygen act in opposite ways on fish: increasing nutrient loadings can positively affect fish stocks (more prey), while the concomitant increase in hypoxia can negatively affect fish stocks (Breitburg et al., 2009a, b). Examination of the role of a single stressor (deoxygenation) when

multiple stressors are varying is challenging (Chapter 6) but also a common situation in the analysis of coastal and marine ecosystems. One result is that the power to isolate the effects of an individual stressor become lower even though the effects of that stressor may be present (Rose et al., 2017c). The effects of the stressor of interest can simply be undetected or inseparable amongst the mix of multiple stressors that co-vary to some degree or because the stressor of interest is important only under certain conditions and has secondary effects under other conditions (e.g. hypoxia effects may be especially important in years of high nutrient loadings and warm summers).

Several modelling studies demonstrated that the effects of deoxygenation alone on fish populations can be small to moderate but, when combined with other stressors, the combined effect can be large. For example, Ainsworth et al. (2011) used Ecosim for five ecosystems in the North-east Pacific and showed that the average change in landings caused by projected climate change factors (primary production, zooplankton size structure, oxygen, and acidification) were individually less than 7% but when combined resulted in a 20% reduction. When range shifts were added to the effects, landings were predicted to be reduced by 77%. Cheung et al. (2016) used coupled physical and ecological models that covered the major large marine ecosystems worldwide and showed that the maximum catch potential (a proxy of MSY) was most sensitive to changes in net primary production and temperature and generally moderately sensitive to deoxygenation alone (low DO assumed to cause reduced productivity). When all effects were combined, they concluded negative impacts would dramatically increase if warming above 1.5 to 2 °C occurred. De Mutsert et al. (2016) used the Ecospace model configured for the Gulf of Mexico and concluded the positive effects of increased nutrient loadings outweighed the negative effects of more hypoxia, although some species showed predicted decreases in their total biomass and projected landings under higher nutrients. Finally, Froehlich et al. (2017) showed increased sensitivity of the Dungeness crab fishery to overfishing when deoxygenation was included with a mix of other stressors (see 10.6.3).

Examining stressor effects on fisheries is also challenging because fisheries are often managed for stability (constrained inter-annual variability in long-term biomass) so that detecting the effects of stressors on the population and catch can be masked by

good management practices. Providing fishers with relatively accurate expectations of future yields enables them to plan, at least in the near term. Management actions occur in response to changes in population dynamics. Thus, a signal of a low oxygen effect would not be in the population abundance itself (which is difficult to measure) but rather in the lowering of the allowable catch that was dictated by management as their response to the lowered population abundance. Detecting a deoxygenation effect in catch can also be difficult because catch reflects how the fishers and fleets respond to other factors, such as fishing effort, price, costs, profitability, dynamics of other species that could be fished, and general environmental conditions. Thus, harvest levels fluctuate due to many factors, not just as a result of the effects due to deoxygenation. Linking deoxygenation effects to fisheries often relies on modelling to separate oxygen effects from the effects of other stressors and management actions.

10.5 Correlation-based analyses

Studies that have utilized cross-system comparisons, considering whole ecosystems and total fisheries landings, have provided two views of the relationship between eutrophication, hypoxia, and fisheries. Analyses and conceptual models by Caddy (1993, 2000) and de Leiva Moreno et al. (2000) suggested that very high nutrient loads resulted in general system degradation, including hypoxia (Caddy, 1993, 2000) or very high chlorophyll-a levels (de Leiva Moreno, 2000), and were associated with reduced fisheries landings and increases in the ratio of planktivore to demersal species (P/D ratio) in the catch. They suggested that hypoxia reduced the availability and quality of the demersal habitat resulting in a decline in demersal species, and in some cases, an increase in pelagic species that benefited from reduced predation, increased food, or reduced competition. In contrast, Nixon and Buckley (2002) examined quantitative relationships among nitrogen loads, primary production, and fisheries landings, and found a positive relationship between nitrogen loads, primary production, and fisheries landings across a very wide range of ecosystems. These analyses did not explicitly consider hypoxia, but do not indicate catch declines in systems where hypoxia would be expected to be problematic.

Cross-system comparisons that have explicitly considered the spatial extent of hypoxia generally support Nixon's model of increasing landings (sum of

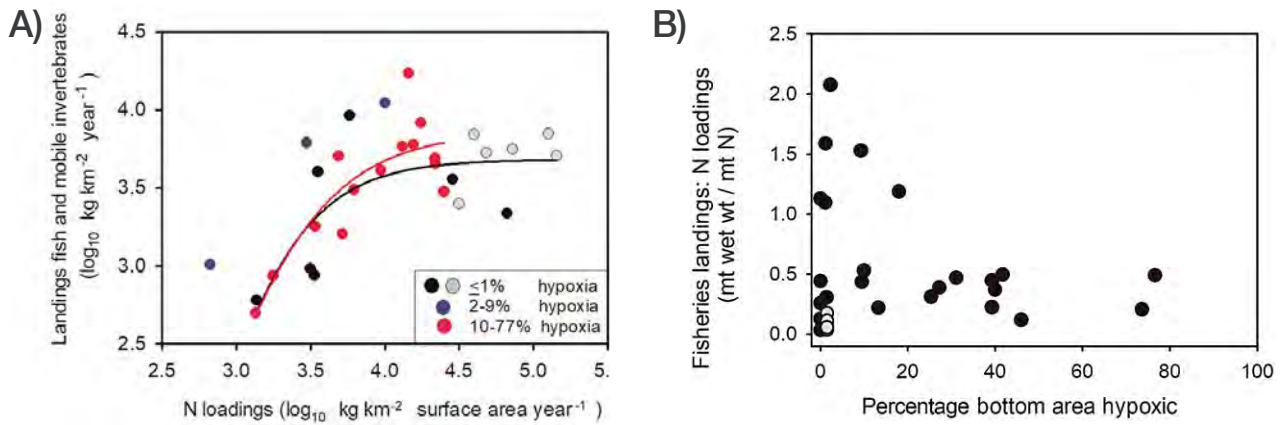


Figure 10.3 Relationship between fisheries landings, nitrogen loadings and hypoxia in estuaries and semi-enclosed seas. (A) fisheries landings versus nitrogen loadings to the basin and (B) landings per unit of nitrogen loadings versus spatial extent of hypoxia (as percentage of total bottom area). (A) shows that the relationship between nitrogen loadings and fishery landings is similar for systems with <1% of the bottom area hypoxic (black regression line; $R^2 = 0.55$) and systems where hypoxic waters can cover as much as with 10–77% of the bottom (red regression line; $R^2 = 0.73$). Both categories are fitted with 4 parameter sigmoid functions. The points in panel (A) are colour coded for the percentage of bottom that is hypoxic. (B) shows a decrease in trophic efficiency (decreasing landings per unit nitrogen) under high hypoxia conditions. Both panels plot small Australian systems in grey. (modified from Breitburg et al., 2009b). Note that landings reflect fishing effort and regulations as well as system production, and that aquaculture production was excluded.

finfish, decapods, and cephalopods) with increasing nitrogen loads (Breitburg et al., 2009 a, b; Hondorp et al., 2010). These analyses included a suite of estuaries, coastal, and semi-enclosed seas that varied sufficiently in physical characteristics that nitrogen loads, and the spatial extent of hypoxia were not significantly correlated to each other, allowing effects of nutrients and hypoxia to be statistically separated. In these analyses, the spatial extent of hypoxia did not affect the relationship between nitrogen loads and total landings (Breitburg et al., 2009b) (Figure 10.3A). Instead, the primary effect of hypoxia was to reduce the efficiency of the transfer from nutrients to secondary production, resulting in a decline in the ratio of fisheries landings to nitrogen loadings with an increasing percentage of bottom area hypoxia (Figure 10.3B). In contrast to predictions from earlier cross-system studies, further analyses of these systems found a negative relationship between total nitrogen load and the P/D ratio in landings (Hondorp et al., 2010). The maximum spatial extent of hypoxia was, nonetheless, positively related to the P/D ratio in this dataset. However, this relationship was largely driven by low landings of pelagics in estuaries where purse seining is not practised or is restricted, and low landings of benthic/demersal species in the Black Sea—a semi-enclosed sea with a deep hypoxic and anoxic basin that covers nearly 80% of its bottom area.

These cross-system analyses do not preclude the possibility that landings of individual species decline, shift in geographic location, or lead to changes in fisher behaviour. Rather the results of cross-system

comparisons suggest the importance of compensatory mechanisms related to fish and fisher behaviour, enhanced fish production, and fisheries practices and regulations that sustain total landings across a broad range of spatial and temporal patterns of hypoxia.

10.6 Case studies

Eight case studies are presented where deoxygenation effects on fisheries have been suggested based on empirical data or have been clearly documented with data or modelling (Table 10.1). These examples involve various combinations of deoxygenation effects on different fisheries types located in ecosystems impacted by coastal hypoxia and OMZs. The exact effects and role of deoxygenation versus other co-varying factors are not always clearly known. However, all of the case studies have at least some evidence or supporting information that deoxygenation played a role. These include several case studies with very strong evidence, mostly because of extensive data and analyses specifically designed to assess deoxygenation effects (i.e. croaker and shrimp in Gulf of Mexico, Dungeness crab in Hood Canal, cod in Baltic Sea). We also include several case studies with suggestive but not always conclusive evidence because they also illustrated features like possible impacts on a major fishery (i.e. anchovy in Peru EEZ), artisanal and traditional fisheries (i.e. Indian oil sardine, white grouper in coastal North-west Africa), and a highly migratory top predator (i.e. billfishes in the eastern tropical Atlantic). Many are model-based because of the challenges of using field data only to detect and isolate the effects

of low oxygen amongst the many factors affecting fish population and fisheries dynamics.

There are multiple examples of analyses examining the effects of global climate change on fisheries that include changes in oxygen as one of the drivers of the response (e.g. Ainsworth et al., 2011; Cheung et al., 2016). However, the role of oxygen changes was not the major focus and so deoxygenation effects were often limited in the analysis and their effects were not

always cleanly isolated from the other drivers, such as temperature. This made it difficult to quantify the role of deoxygenation itself in influencing the predicted effects on fish and fisheries. We therefore selected case studies that focus on deoxygenation effects (Table 10.1), with the knowledge that other case studies, including global change analyses, include deoxygenation but not in a simple way that permits us to say what role oxygen changes played.

Table 10.1 Summary of the characteristics of the eight case studies described in this chapter.

System	Species	Deoxygenation	Fisheries	Oxygen Effects	Fisheries and Management
Gulf of Mexico	Atlantic croaker	Nutrient-driven coastal shelf hypoxia	Past and now limited for use as bait fish	Trade-off between nutrient loadings affecting food (growth) and hypoxia (growth, mortality, reproduction) in opposite directions	An example 25% nutrient reduction would result in sufficient reduction in hypoxia to offset the lowered food effect and likely benefit the population
Gulf of Mexico	Shrimp	Nutrient-driven coastal shelf hypoxia	Major trawl fishery	Growth, mortality, and spatial displacement effects on fleet dynamics and price	Price changes showed decrease in availability of large-sized shrimp
Hood Canal	Dungeness crab	Fjord with nutrient loading	Recreational and commercial	Catchability decreases with shallower depth of hypoxia	Hypoxia magnified the negative effects of other stressors (e.g. illegal harvest) thereby affecting management advice by increasing the sensitivity of the population to overfishing
Baltic Sea	Cod	Nutrient-driven estuarine hypoxia	Major multi-national fishery	Oxygen and salinity determine the effective volume of reproductive habitat; decreased body condition related to hypoxia	While the details are debated, hypoxia has a clear negative effect on recruitment; the negative effects of hypoxia on body condition may also contribute to the lowered cod population
Peruvian EEZ	Anchovy, sardine, jack mackerel, giant squid, demersal species	OMZ	Anchovy is a major biomass contributor to worldwide fisheries	Spatial distribution shifts among pelagic species that leads to effects on the anchovy population; upwelling acts opposite to the effects of hypoxia (more food with worse hypoxia); fishing fleet dynamics	Under small extent/deep hypoxia and intrusion of oceanic waters, sardine, jack mackerel, and predatory species come closer to the coast (more vulnerable and higher catches) and may heavily forage on anchovy (lowered abundance). Warm SST, high primary production, and shallow oxycline allowed anchovy schools to be onshore and vessels to fish near the coast. Opposite conditions resulted in deep and dispersed anchovy that caused fishers to spend more time in transit and searching
Southwest Coast of India	Indian oil sardine	Upwelling and nutrient inputs	Multi-national commercial and local traditional fisheries	Low oxygen into spawning areas	Low oxygen affecting spawning and recruitment as well as the availability of fish to capture
Coastal West Africa	White grouper or "thiof"	Deep and shallow water OMZ	Commercial and artisanal	Exposure of adults to low oxygen, likely causing mortality	White grouper is overexploited and critical to human welfare and economic activities
Eastern Tropical Pacific	Billfishes	Oceanic OMZ	Commercial	Shallowness of low oxygen affects habitat	Increases vulnerability to harvest and confounds estimation of catchabilities in stock assessment

10.6.1 Atlantic croaker in Gulf of Mexico

Atlantic croaker (*Micropogonias undulatus*) in the Gulf of Mexico supported a fishery in the 1950s (about 55,000 MT) and there is a small inshore fishery for croaker as bait fish (including as bycatch from shrimping) for recreational harvesting of other species (VanderKooy, 2017). The Gulf of Mexico exhibits annual summertime hypoxia that started in the 1950s and has slowly but steadily increased in volume since then, with significant interannual variation due to fluctuating nutrient loadings dependent on Mississippi River flows in the spring (Scavia et al., 2017). Croaker is a dominant demersal forage fish in coastal Louisiana (Monk et al., 2015). Rose et al. (2017a, b) simulated the population-level response of croaker to changes in nutrient loadings, which affected both food availability and the extent of hypoxia. While croaker do not presently support a large fishery in the Gulf of Mexico, the croaker analysis is included as a case study because the modelling did project effects at the population-level (relevant scale for fisheries) and included a quantitative tradeoff between the counteracting effects of nutrient loadings affecting food availability and affecting hypoxia (i.e. higher

nutrients can mean more food (positive) but also more hypoxia (negative)).

Model simulations were for 140-years with an average year of seasonally-varying temperatures repeated every year, DO randomly selected each year from one of three years (mild, intermediate, or severe,) and chlorophyll concentrations dependent on the hypoxia year type (higher chlorophyll with more severe hypoxia years since both occur with high nutrient loadings). While the simulated individual croakers were good at avoiding DO less than 2.0 mg L^{-1} , which is considered hypoxia and stressful to aquatic life in many systems, some mortality due to exposure to less than 2.0 mg L^{-1} occurred. More importantly, relatively large growth and fecundity effects occurred on some individuals because those effects occurred at DO above levels that triggered avoidance (i.e. 2.0 to 4.0 mg L^{-1}).

Simulations to examine the tradeoff of how a 25% reduction in nutrient loading negatively affects croaker through reduced food versus positively affects croaker through less hypoxia were undertaken. The simulations used were: (1) unadjusted hypoxia and chlorophyll concentrations (i.e. representing present-day or baseline

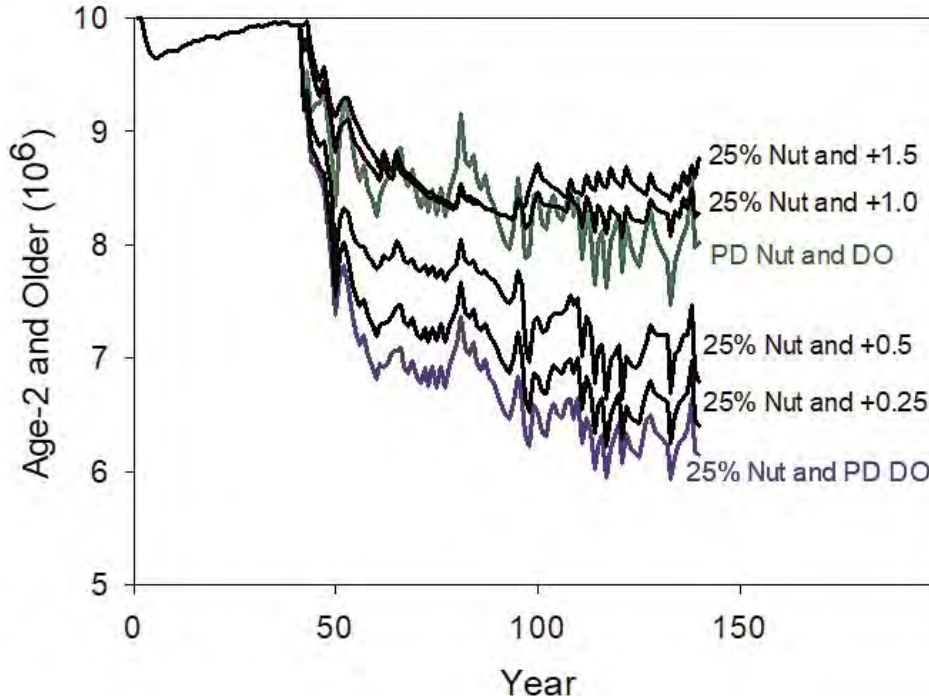


Figure 10.4 Simulated annual age-2 and older croaker abundance for present-day (PD) nutrient loadings (nut) and hypoxia (green), reduced food (25% Nutrients) and present day hypoxia (blue), and reduced food and dissolved oxygen (DO) adjusted by adding $+0.25$, 0.5 , 1.0 , and 1.5 mg L^{-1} to the hourly values. Reduced food was due to the 25% reduction in nutrient loadings. The decrease in population from green to blue is due to the reduced food resulting from reduced nutrient loadings. The progressively higher population abundances from $+0.25$ to $+1.5$ is the effect of improving oxygen (reducing hypoxia). Note the y-axis starts at 5×10^6 . Source Rose et al. (2017b).



Figure 10.5 (A) Shrimp trawler operating in the Gulf of Mexico © Tosh Brown / Alamy stock photo (B) Brown shrimp catch from Gulf of Mexico © Inga Spence / Alamy stock photo (C) White shrimp catch © Frank Bienewald / Alamy stock photo.

conditions), (2) unadjusted hypoxia but reduced food for croaker expected with a 25% reduction in nutrients (lowered chlorophyll due to reduced nutrients), and (3) reduced food and DO manually increased by adding 0.25, 0.5, 1.0, and 1.5 mg L⁻¹ to every hour's value. The first simulation is considered baseline and representative of current conditions. The second simulation is hypothetical – prediction of croaker abundance with reduced food under present-day hypoxia and serves as a measure of the deficit in abundance caused by reduced nutrients leading to lowered food. The third set of simulations then start with the second simulation (reduced food) and adds known concentrations of DO to see how much DO would have to increase to offset the deficit caused by reduced food. A review of the statistical models used to predict summer hypoxia area from nutrient loadings showed that a reduction in hypoxia equivalent to a 0.5 mg L⁻¹ addition was reasonable to expect under a 25% reduction in nutrient loadings but that the larger increase of 1.0 mg L⁻¹ was unlikely to be achieved.

The addition of 0.5 to 1.0 mg L⁻¹ of oxygen offset the negative effects of lowered food that would result from a 25% reduction in nutrient loadings (25% Nut and +0.5 and +1.0 lines bracket the green line in Figure 10.4). Other models show that it is feasible that a 25% reduction in nutrients would result in a 0.5 to 1.0 mg L⁻¹ increase in DO. Thus, reduced nutrient loadings would not reduce, and may increase, the croaker population abundance. Moving towards an integrated modelling approach that can simultaneously look at how reduced nutrient loadings affect croaker food availability and hypoxia is now underway.

10.6.2 Shrimp in the Gulf of Mexico

The Gulf of Mexico shrimp fishery is a bottom trawl fishery that operates in estuarine and coastal shelf waters from southern Florida to the Texas-Mexico border. The fishery primarily targets two penaeid shrimp

species: brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*) (Figure 10.5). As recently as 2000, brown shrimp generated the highest revenue of any US single-species fishery. Brown shrimp, like a number of other demersal species, avoid low oxygen water on the Louisiana shelf and aggregate at high densities near the edges (< 5 km) of the hypoxic zone (Craig, 2012; Craig & Crowder, 2005; Craig et al., 2005). Increased susceptibility to the Gulf shrimp trawl fishery, which peaks during the summer when hypoxia is most severe, is a potential indirect effect of hypoxia-induced aggregation of the shrimp (Purcell et al., 2017). If shrimpers are able to locate these high-density aggregations of shrimp, then catchability, or the harvest efficiency of a given unit of shrimping effort, could increase.

Huang et al. (2010), in an analysis of the North Carolina shrimp trawl fishery and oxygen conditions in the Neuse-Pamlico estuarine system, determined that hypoxia had reduced catch by about 10-15% with an annual value loss of US\$1.25 million relative to pristine (normoxic) conditions. The Neuse-Pamlico system supports harvest within its waters and also contributes shrimp to the Pamlico Sound where much of the state-wide harvest comes from. This economic loss was much reduced in subsequent analyses that allowed the fishers to dynamically respond to the changing economic (e.g. price) incentives (Huang et al., 2012). Here, we focus on spatial bio-economic models of the brown shrimp fishery in the Gulf of Mexico that included the same researchers (Smith et al., 2014, 2017).

Smith et al. (2017) analysed 20 years of monthly brown shrimp price data in the Gulf of Mexico and found that the severity of hypoxia measured by the spatial extent of low DO water was related to short-run deviations from long-run prices. More severe hypoxia caused short-run increases in the price of large shrimp relative to small shrimp. Based on model estimates, about a 1000 km² increase in the spatial extent of hypoxia (a 6% increase

from the long-term mean) triggers a 1% increase in the relative price of large brown shrimp. The interpretation is that in years when hypoxia is severe, there are more, small brown shrimp caught due to some combination of increased aggregation of smaller shrimp early in the season, impaired growth, and reduced survival that had a larger effect on the abundance of large shrimp than on small shrimp. As a result, there are fewer large shrimp available to be harvested later in the season. Severe hypoxia thus results in increased catch when shrimp are smaller (and of lower monetary value) and reduced catch of the more valuable larger shrimp later in the season. The smaller sized shrimp captured earlier in the season, with their lower prices, make up most of the harvest and thus severe hypoxia imposed an economic cost on the fishery. This effect was not detectable in the catch data itself because the fleet is highly mobile and integrates catches across hypoxic and non-hypoxic areas. Price data could be used because the shrimp markets are highly integrated and the relative prices of different sized shrimp in the Gulf of Mexico have been remarkably consistent over time. These analyses demonstrate that hypoxia can have important (albeit complex) economic effects on fisheries that would be very difficult to detect in traditional fisheries data.

10.6.3 Dungeness crab in Hood Canal

The Dungeness crab (*Metacarcinus* or *Cancer magister*) is one of the most valued and heavily exploited species on the west coast of North America (Figure 10.6), with some estimates that 90% or more of the legal-sized males are harvested by stationary traps during the fishing season (Armstrong et al., 2003, 2010; Gotshall, 1978; Pauley et al., 1986; Smith & Jamieson, 1991). Both recreational (open-access) and commercial (limited entry) fishing are regulated by a quota system with additional restrictions on the size and sex of crab that can be harvested during certain seasons (Armstrong et al., 2003).

Hood Canal (110 km) is a seasonally hypoxic, fjordic estuary in Puget Sound, Washington State, USA (Figure 10.7), where hundreds of thousands of Dungeness crab are landed by recreational and tribal fisheries every year (Washington Department of Fish and Wildlife (WDFW) unpublished data). The narrow sill at the mouth of the estuary and the deep bathymetry (maximum depth ca. 200 m) reduce tidal and exchange rates (turnover ≥ 1 year) that set up the deoxygenated conditions that expand through the water column over the summer

months, particularly in the southern reaches (Cope & Roberts, 2013; Newton et al., 2007; Warner et al., 2001). Oxygen conditions appear to be worsening, in part, due to climate change and nutrient loading (Cope & Roberts, 2013; Fagergren et al., 2004; Newton et al., 1995, 2007). Importantly, Dungeness crabs – even with their relatively high tolerance to hypoxia (Bernatis et al., 2007; Froehlich et al., 2015) – appear to shoal, similar to other demersal species, into shallower depths in order to avoid the lower, deoxygenated extremes (Froehlich et al., 2014) (Figure 10.8).

A management strategy evaluation (MSE) was performed to examine the indirect effects of hypoxia on the performance of management practices and the long-term sustainability of the Hood Canal Dungeness crab fisheries. Based on an age-structured population and fishery model of the system, the MSE revealed that hypoxia effects can erode the effectiveness of the management system when other fishing-related pressures are included (Froehlich et al., 2017). Hypoxia was included by specifying that catchability increased with decreasing minimum hypoxic depth (higher catchability when hypoxia is near the surface). Simulations showed that changes in catchability due to hypoxia alone did not significantly reduce catch or crab abundance ('base-case' scenario in Figure 10.9C and F with all other pressures at zero). However, the effects of other stressors associated with fishing, including increased fishing effort, illegal crabbing, incidental mortality of captured non-harvested crabs (i.e. bycatch or discards), and impaired reproduction ability due to fishing were all magnified by hypoxia-induced behavioural shifts that affected catchability. This is seen in Figure 10.9 by the black lines increasingly lower than the grey lines for the population (10.9A



Figure 10.6 Dungeness crabs for sale at Seattle's Pike Place market © The Old Major / Shutterstock.com.



Figure 10.7 Hood Canal, Seabeck, Washington looking towards the Olympic Mountains © Don Paulson / Alamy stock photo.

and B) and landings (10.9D and E) as other stressors (illegal crabbing, incidental mortality) were increased in intensity, and by black bars being lower than grey bars for impaired reproduction (10.9C and F) that only had two levels (off and on) of intensity. In addition to the effects on average population abundance and legal catch, the presence of hypoxia also affected the year-to-year variability of catch. The presence of hypoxia resulted in patterns of significantly higher catch variability and lower minimum catch returns (Froehlich et al., 2017). Thus, non-lethal environmental forcing from hypoxia increased the sensitivity of the fishery to other pressures and increased its susceptibility to overfishing.

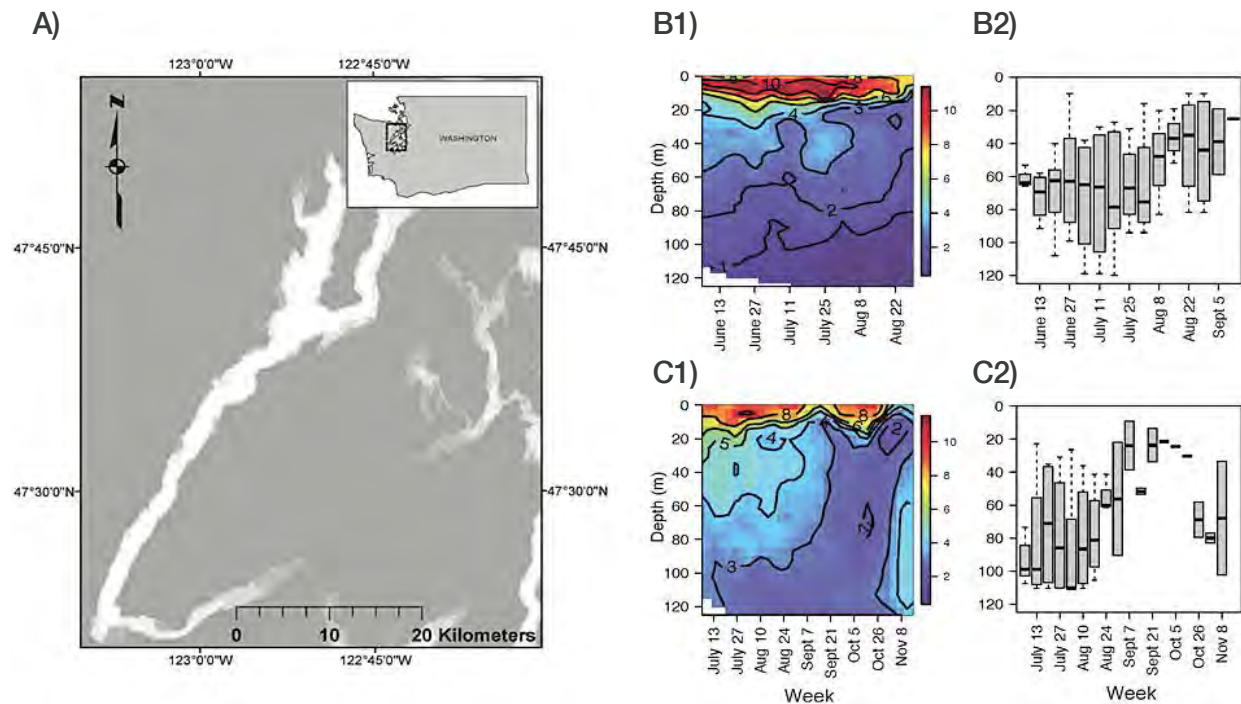


Figure 10.8 A) Hood canal; B1) and C1) Interpolated dissolved oxygen (DO, mg L⁻¹) in Hood canal and B2) and C2) maximum depth (metres) ranges of acoustically-tagged Dungeness crab for (B) July to August in 2010 and (C) July to November in 2009 (from Froehlich et al., 2014). Note low DO concentrations are shown in darker blue colours. Comparison of oxygen with depths of crabs shows that crabs move towards the surface to avoid shoaling low oxygen.

10.6.4 Cod in Baltic Sea

The biomass of fish in the Baltic is dominated by three species: cod (*Gadus morhua*), herring (*Clupea harengus*), and sprat (*Sprattus sprattus*) (Ojaveer et al., 2010). Total marine fisheries landings for the nine coastal countries bordering the Baltic Sea was conservatively estimated as 41.3 to 53.5 million tonnes for the period between 1950 and 2007 (Zeller et al., 2010, 2011). When the cod population size was high, large amounts of cod were landed in the northern areas of the Baltic Sea, while landings shifted to the southern region when population size was low (Bartolino et al., 2017).

The Baltic Sea is the largest anthropogenically-induced hypoxic area in the world (Conley et al., 2009). The dramatic increase in hypoxia area in the Baltic Sea over the last 115 years is primarily linked to increased inputs of nutrients from land, although increased respiration due to warmer temperatures during the last two decades has also contributed (Figure 10.10A). Reducing anthropogenic nutrient inputs is a major policy goal for restoring good environmental status of coastal marine ecosystems. However, it is unclear to what extent reducing nutrients would also lower fish production and thus fisheries yield (MacKenzie et al., 2007). The strongest factor influencing the biodiversity of benthic communities is the increased prevalence of

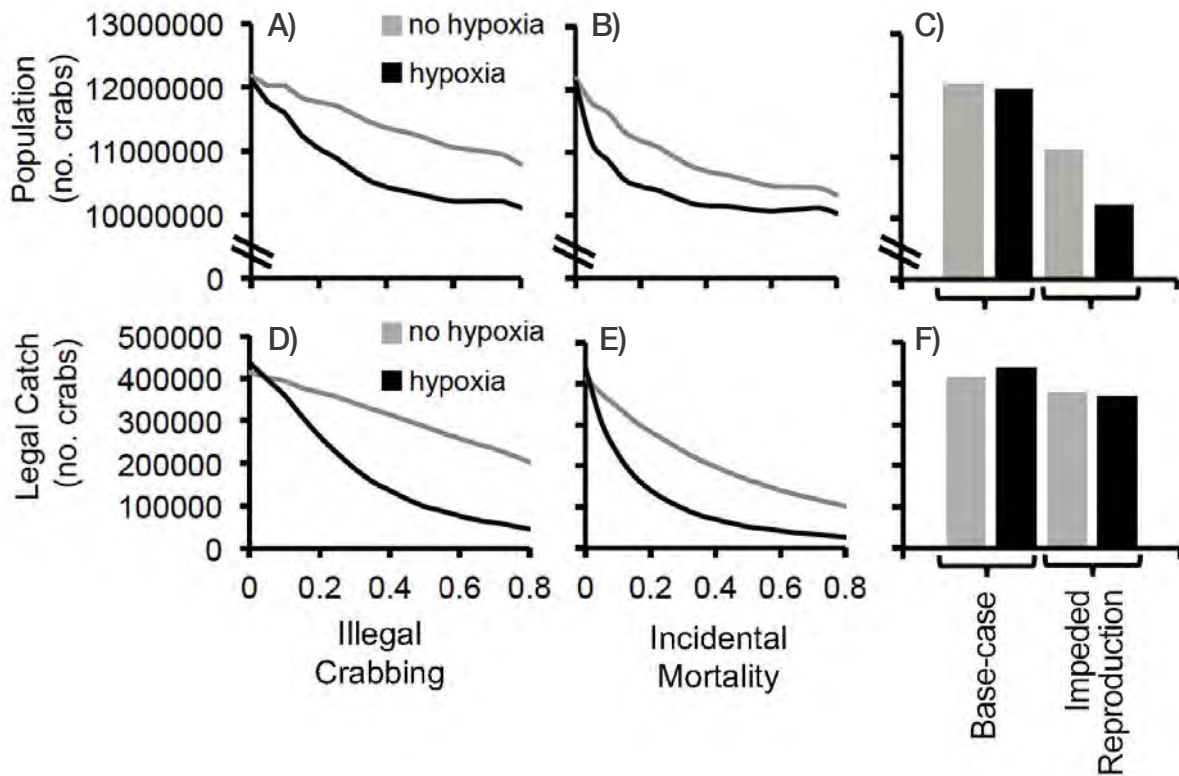


Figure 10.9 Simulated equilibrium (average over 50 years) population abundance (A-C) and catch (D-F) of Dungeness crab in Hood Canal under high fishing effort (20,000 pots/week) and increasing levels of three stressors (illegal crabbing incidental mortality, and impeded reproduction). Mean values are shown for no hypoxia effects (grey) and with hypoxia effects (black). Panels (A) and (D) show the mean values for increasing intensity of illegal crabbing. Panels (B) and (E) show the predictions for increasing intensity of incidental mortality. Panels (C) and (F) show the predicted abundance and catch for the base-case (all stressors set to zero) and for the third stressor of impeded reproduction that only had two intensities (off or on). The effect of hypoxia alone is small (grey and black bars similar in Base-case) but hypoxia effects amplify the negative effects of the other stressors (black lines and bars below grey lines and bars). Source: Froehlich et al. (2017).

oxygen-depleted bottom water, which has resulted in habitat loss and the elimination of benthic macrofauna over vast areas (Figure 10.10B) and severely disrupted benthic food webs (Conley et al., 2009).

Cod in the Baltic Sea live in an estuarine environment whose salinity and oxygen conditions impose physiological stresses on spawning success including egg fertilization and survival (Hinrichsen et al., 2016). Earlier field and laboratory studies have shown that spawning success and egg survival is greatly reduced at salinities less than 11 and oxygen content less than 2 ml L⁻¹. Reproductive habitat, estimated as the volume of the water column conducive for successful reproduction based on salinity and oxygen, has been quantified by numerous authors (e.g. Bartolino et al., 2017; Eero et al., 2015; MacKenzie et al., 2000) and has been shown to be a key driver of cod recruitment success (e.g. Jarre-Teichmann et al., 2000; Koster et al., 2005; Margonski et al., 2010). The mean and variance of the reproductive volume time series changed after 1983, due primarily

to a reduction in the frequency of large reproductive volume years (Carstensen et al., 2014). As a result, the mean and range of reproduction volume has declined, reducing egg survival and resulting in lower cod recruitment. Reproductive volume, and similar measures of reproductive habitat, were used to affect cod recruitment in an Ecosim model and was important in enabling the Ecosim model to better fit to stock biomasses estimated from stock assessments (Harvey et al., 2003). Hansson et al. (2007) used a version of the same model and showed, among other things, that cod catch would increase if the reproductive volume was increased as estimated under an oligotrophic Baltic Sea (i.e. as expected by reduced nutrient loadings); however, if primary production (food) was also reduced, catch of cod showed a net decrease. They also showed that in some oligotrophic conditions, lowering fishing intensity results in higher biomasses of key stocks and higher cod catches. This suggests that fisheries management targets need to be adjusted based on the productivity of the ecosystem.

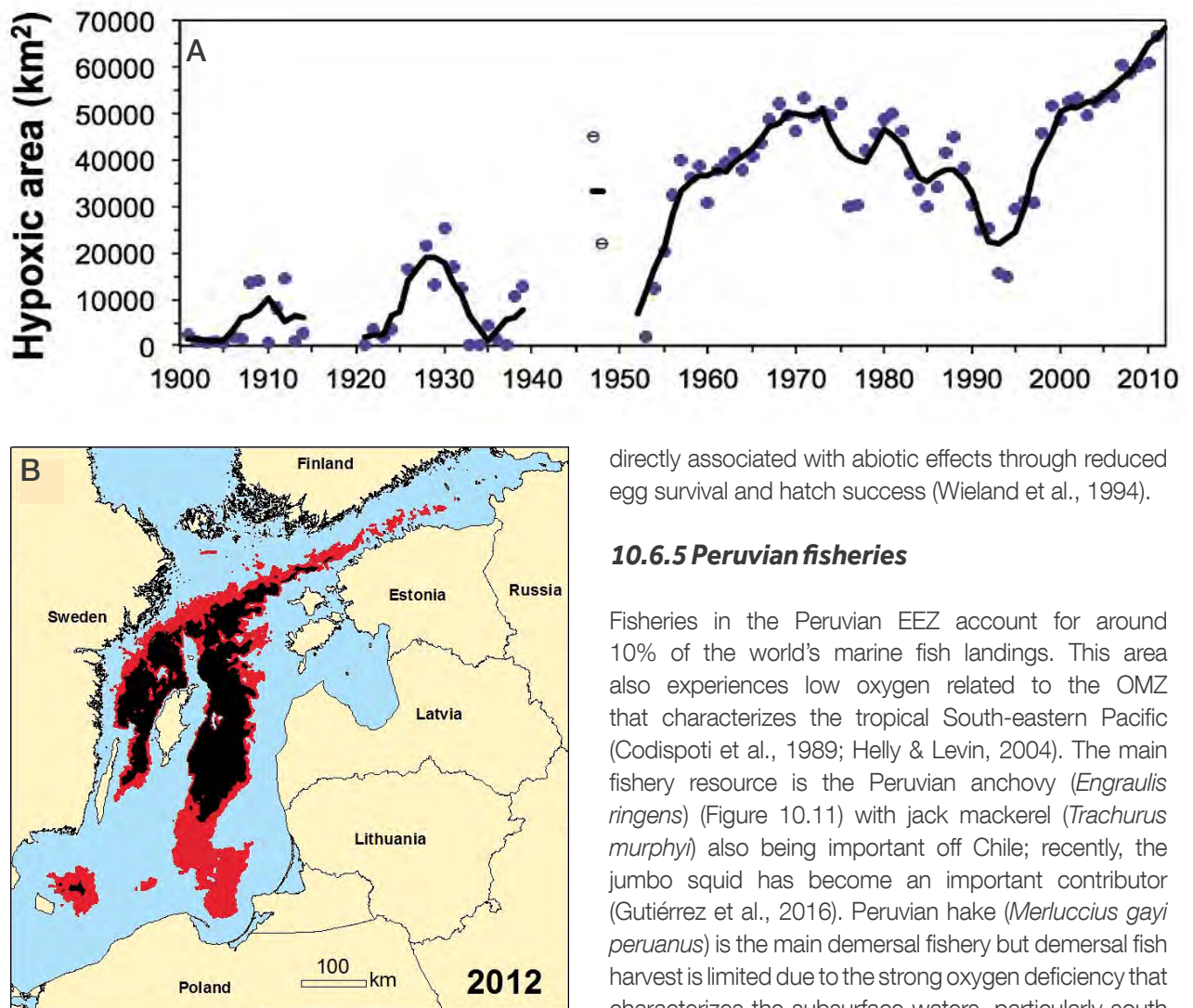


Figure 10.10 (A) Annual average hypoxic area with oxygen concentrations $<2 \text{ mg L}^{-1}$ in the Baltic Proper (redrawn from Carstensen et al., 2014). (B) Red are hypoxic areas with oxygen concentrations $<2 \text{ mg L}^{-1}$ and black areas are anoxic $<0 \text{ mg L}^{-1}$ in the Baltic Sea (from Carstensen et al., 2014). The increasing hypoxic area is primarily due to increased nutrient loadings. The spatial extent of the hypoxia causes widespread habitat loss and mortality of the benthos and distribution of the benthic food web.

In addition to low oxygen affecting reproductive success, the increasing areal extent of hypoxic waters was also related to a decrease in the condition of cod, leading to a major decline in condition over the last 10 - 20 years (Casini et al., 2016; Limburg & Casini, 2018). Fish condition was quantified by the weight compared to length cubed of individuals and indicates degree of girth or how streamlined a fish is; “fatter” fish are considered healthier. The effects of such a decline on population dynamics are presently unclear, but low condition cod in other regions usually produce fewer eggs and eggs of lower quality (e.g. lipid content, developmental ability). Consequently, it is possible that hypoxia may be having effects on Baltic cod populations in addition to those

directly associated with abiotic effects through reduced egg survival and hatch success (Wieland et al., 1994).

10.6.5 Peruvian fisheries

Fisheries in the Peruvian EEZ account for around 10% of the world's marine fish landings. This area also experiences low oxygen related to the OMZ that characterizes the tropical South-eastern Pacific (Codispoti et al., 1989; Helly & Levin, 2004). The main fishery resource is the Peruvian anchovy (*Engraulis ringens*) (Figure 10.11) with jack mackerel (*Trachurus murphyi*) also being important off Chile; recently, the jumbo squid has become an important contributor (Gutiérrez et al., 2016). Peruvian hake (*Merluccius gayi peruanus*) is the main demersal fishery but demersal fish harvest is limited due to the strong oxygen deficiency that characterizes the subsurface waters, particularly south of 7°S (Bertrand et al., 2011). It has been proposed that one factor that contributes to the exceptional pelagic fish productivity is that low oxygen compresses the epipelagic habitat in the region and that compression results in a highly efficient trophic transfer of the high rates of upwelled nutrients to the upper food web levels (Bertrand et al., 2011).

The relatively higher tolerance to hypoxia of the Peruvian anchovy is evidenced by its more coastal distribution than other pelagic species. Onshore surface oxygen content can decrease to 40% saturation, with the oxycline being located shallower ($\sim 30 \text{ m}$) than offshore ($\sim 100 \text{ m}$) (Bertrand et al., 2011). By contrast, the distribution of sardine, jack mackerel, and the giant squid (Alegre et al., 2015; Bertrand et al., 2016) are restricted to offshore, more oxygenated waters. Recent studies of coastal sediment records have revealed significant natural variability of abundance indicators of the main fish populations at multidecadal to millennial



Figure 10.11 Peruvian fishermen unloading their catch of Peruvian anchovy © Mark Bowler – MBSI / Alamy stock photo.

time-scales (Gutiérrez et al., 2009; Salvatelli et al., 2017). Periods of higher overall abundances coincide with enhanced coastal upwelling and productivity, but also increased oxygen deficiency (less DO) in the water column. From the late 1970s to the early 1990s, warmer conditions developed off the Peruvian coast and coastal upwelling was reduced, along with the positive phase of the Pacific Decadal Oscillation (Alheit & Niqun, 2004; Chavez et al., 2003; Purca et al., 2010). At the same time, highly oxygenated surface waters (saturation >80%) approached onshore and the oxycline was deepened (Bertrand et al., 2011). These changes allowed the increase of the populations of sardine, jack mackerel, and other predatory species nearer to the coast, where anchovies were negatively impacted due to the increased predation, and lower macro-zooplankton abundances (prey) were triggered by the environmental changes (Ayón et al., 2008; Bertrand et al., 2011). The higher availability of sardine and jack mackerel was reflected in the increase of their fisheries (Bertrand et al., 2011, 2016). The habitat compression of the pelagic, anchovy-dominated system by the shallow oxycline enhanced prey accessibility to predatory birds and fishers (Barbraud et al., 2017; Joo et al., 2014; Passuni et al., 2016).

Joo et al. (2014) identified four scenarios from the analyses of concomitant satellite, acoustic survey, and extensive Vessel Monitoring System data for the

2000 – 2009 period off Peru. The favourable scenarios for the fishing activity were characterized by relatively high SST, high primary production, and a shallow oxycline. In these scenarios, relatively more time was spent on fishing rather than on cruising, and in cases when anchovy patches were located closer to the coast, the vessels did not need to go as far in order to catch fish. In contrast, the unfavourable scenarios were characterized by relatively low SST, low primary production, and a deep oxycline. Under these conditions, anchovy was scarce, concentrated in very few spots, and the schools were deep. Fishermen went far from the coast and made fishing trips that lasted longer; more time was spent cruising and relatively less time searching and fishing, resulting in a non-efficient activity budget.

10.6.6 South-west coast of India

The coastal shallow waters of south-west coast of the Indian sub-continent experience low oxygen conditions of varying intensities during upwelling. Observations of the dissolved oxygen levels in the coastal waters along the south-west coast have clearly indicated the occurrence of short spells of low oxygen conditions (<1.0 ml L⁻¹) (Johannessen et al., 1987; Murty & Vishnudatta, 1976; Pillai et al., 2000; Ramamritham & Jayaraman, 1960; Rao et al., 1973).

The Indian oil sardine (*Sardinella longiceps*) supports a commercial fishery in India, Iran, Oman, Pakistan, United Arab Emirates and Yemen (FAO, 2017). India has been the major contributor in all the six decades (1956 to 2015) and, among the 10 maritime Indian states, the major contribution of sardine landings is from Kerala where sardines have been the major target species for thousands of traditional fishers (Nair & Chidambaram, 1951; Shyam et al., 2015) (Figure 10.12). The major sardine habitat and fishing areas are the coastal waters with depths from 5 to about 30 m. This region is influenced by upwelling and also by river runoff during the monsoon (Johannessen et al., 1987; Longhurst & Wooster, 1990; Madhupratap et al., 1994). Historically, sardine would abandon its coastal habitat for several years and these lean periods negatively affected the economy of the coastal communities (ICAR, 1971; Nair & Chidambaram, 1951). The fishery for oil sardine typically starts in June to July with the entry of spawners that were spawned during the previous year. Spawning then occurs during June to September, and adults and large shoals of juveniles spawned earlier in the same year are vulnerable to harvest within the 30 m depth zone. The fishery for oil sardine has shown wide fluctuations on seasonal, annual, and decadal scales (Pillai et al., 2003) and has experienced recent (1994 and 2015 - 2016) dramatic drops in landings (Figure 10.13).

Low oxygen waters usually spread into the coastal fishing area during or soon after the monsoon season. Negative effects can also occur pre-monsoon when intense upwelling occurs during early and low oxygen conditions prevent sardines from moving towards their preferred nearshore coastal waters for spawning. This upwelling the low oxygen pre-monsoon effect can be seen in the fishery in the following year (Kripa et al., 2015). Recruitment can be affected when the low oxygen occurs very close to the shore (5 to 20 m depth zone) during late or post-monsoon, and this affects catch in the same year. Length frequency studies and observations on gonad maturity and spawning have clearly shown that spawning of sardine occurs with the onset of monsoon and recruitment to the fishery starts by August (Antony Raja, 1964, 1969). Kripa et al. (2015, 2018) noted that the two rapid declines in landings (Figure 10.13) were coincident with low oxygen conditions in the shallow waters during late or post-monsoon. Correlation analysis between monthly catch rates of different size classes of Indian oil sardine and environmental data, which included the 2015 - 2016 decline, showed that low oxygen waters, especially inshore, had both positive and negative relationships with catch rates, suggesting low DO has effects both on spawning success and early life stage abundance (recruitment) as well as on the availability of fish to capture (Kripa et al., 2018).



Figure 10.12 A catch of Indian oil sardines being spread out to dry in the sun © Minden Pictures / Alamy stock photo.

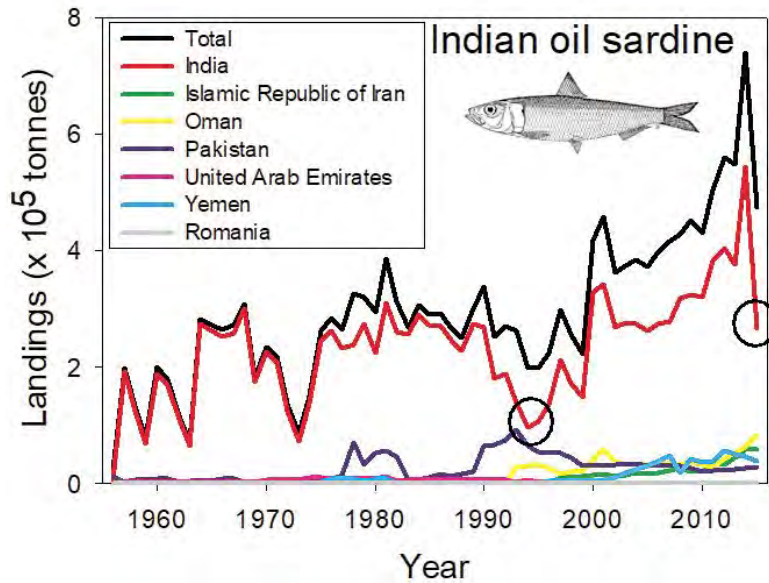


Figure 10.13 Annual landings ($\times 10^5$ tonnes) of Indian oil sardine by country and total for 1956 to 2015. Note the rapid drops in Indian and total landings in 1994 and 2015-2016 (circles).

10.6.7 North-west African fisheries

Fishing is a major socio-economic consideration for coastal countries in West Africa, as it represents more than US\$1.5 billion in fish annually legally captured, employs over 3 million individuals in the West African industry, and generates substantial export revenues (World Bank, 2009). For example, the fisheries sector in Senegal report a catch of over 350,000 tons that provides 70% of the protein intake, employs about

600,000 people, and contributes 37% of the total export revenues. The North-west African upwelling area is known to be the richest fishing ground in West Africa (Aristegui et al., 2009; Cury & Roy, 1988) and sustains a large variety of demersal and pelagic commercial fish species (Cury & Roy, 1989; Demarcq & Faure, 2000; Guénette et al., 2001; Ribeiro et al., 2004). The North-west upwelling is dynamically linked to the OMZ that is part of the Eastern Tropical North Atlantic (ETNA), which is composed of a deep OMZ at about 400 m depth

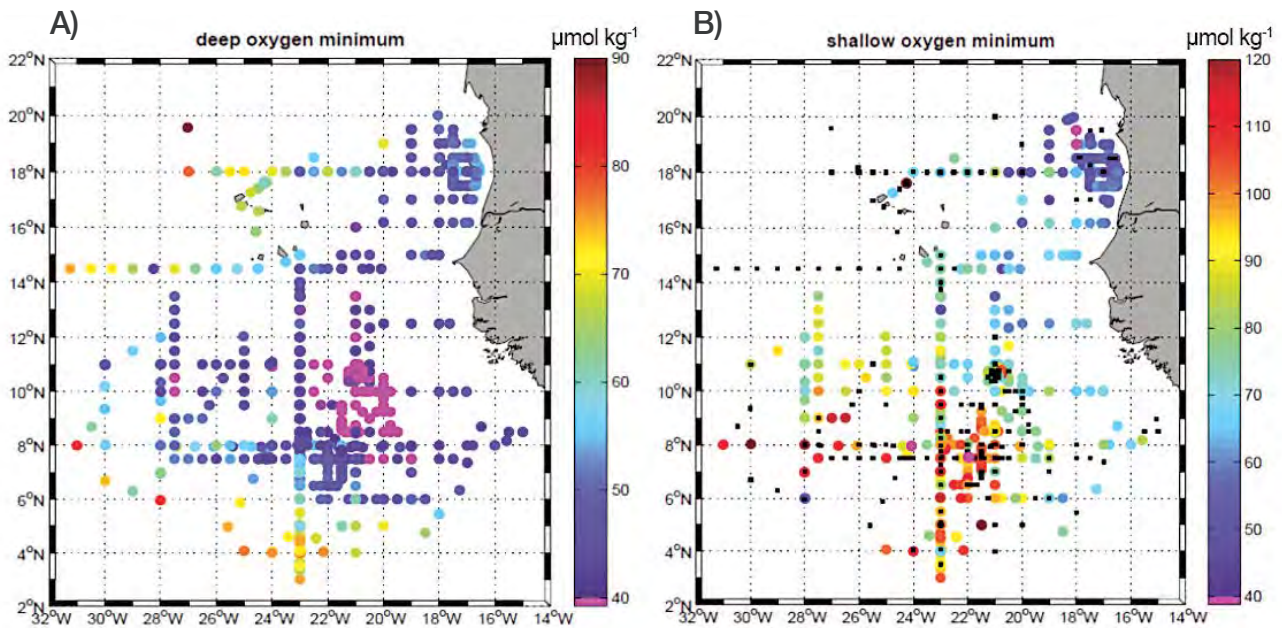


Figure 10.14 Oxygen concentrations illustrating the (A) deep oxygen minimum (>200 m depth) and (B) shallow oxygen minimum (<200 m depth) zones in the Eastern Tropical North Atlantic (source: Brandt et al., 2015). The data are CTD station data during 2006-2013. Purple dots show locations with oxygen less than $40 \mu\text{mol kg}^{-1}$ and black dots in (B) show vertical profiles without a shallow oxygen minimum (i.e. minimum occurred at the lower boundary of 200 m).



Figure 10.15 White grouper *Epinephelus aeneus* © Paulo Oliveira / Alamy stock photo.

offshore and a shallow OMZ at about 100 m depth (Figure 10.14; Brandt et al., 2010, 2015).

In this West Africa coastal region, unusually high mortality rates of demersal Serranidae were observed in the late 1980s, mainly for the most important commercial fish *Epinephelus aeneus* (white grouper) locally known as “thiof” (Figure 10.15). Commercial catches from industrial, and mostly artisanal, fisheries decreased from about 4000t in 1987 to less than 1000t by 2007 (Figure 10.16, Ndiaye et al., 2013). The mortality of the “thiof” was related to low bottom DO concentration (Caveriviere & Toure, 1990). While the evidence is not conclusive, similar episodes of high Serranidae mortality with their abdomen distended have been reported along the Senegalese coast by local fishers and investigators of the Senegalese National Research Center in Oceanography (CRODT). The Senegalese-Mauritanian sub-region is the only one within the North-west African upwelling

with hypoxic conditions (Karstensen et al., 2008). The “thiof” stock harvested by the Senegalese is considered over-exploited (Ndiaye et al., 2013; Thiao et al., 2012), and given its importance to the welfare and economics of the area, determining the role of deoxygenation on the population is critical.

10.6.8 Tropical pelagic billfishes

The OMZs in the eastern tropical Pacific and Atlantic oceans overlaps with where valuable commercial fisheries for tunas and billfishes, and recreational and bycatch fisheries for sailfish and blue marlin occur. Harvested tunas and billfishes include swordfish, skipjack tuna, and yellowfin tuna (Figure 10.17). These fishes require oxygen-rich environments and typically have high hypoxic thresholds (3.5 mg L^{-1}) below which they experience respiratory distress. Furthermore, billfishes prefer the warmest water available that typically occurs at the surface (Hoolihan et al., 2011). Suitable physical habitat for tropical pelagic fishes becomes compressed into a narrow surface mixed layer while the cold, hypoxic water below limits vertical distribution and diving behaviour (Prince & Goodyear, 2006; Prince et al., 2010; Stramma et al., 2011). The amount of the surface ocean layer (measured as depth) that is above 3.5 mg L^{-1} has been decreasing at a rate of one metre per year in the tropical North-east Atlantic, resulting in a loss of 15% of the volume of the usable vertical habitat in the upper 200 m for billfishes in this region since the 1960s. Habitat compression is evident from depth distributions of blue marlin (Figure 10.18) and sailfish monitored with

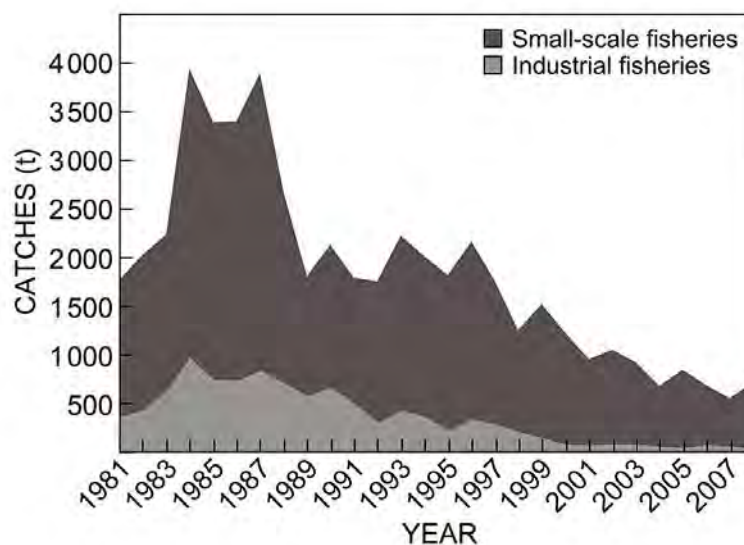


Figure 10.16 Total annual landings of *Epinephelus aeneus* by small-scale and industrial fisheries in Senegal between 1981 and 2008. (Source: Ndiaye et al., 2010).



Figure 10.17 Yellowfin tuna *Thunnus albacares* © David Fleetham / Alamy stock photo.

pop-up satellite archival tags. Comparisons of tagged fish between the Western North Atlantic (WNA), which lacks a vast OMZ, with fish tagged in the Eastern Tropical Pacific (ETP), which has one of the most extensive OMZs in the world, show striking differences in vertical habitat use (Prince & Goodyear, 2006). While the fish primarily occupy the upper 50 m of the water column in both oceans, Atlantic billfishes spent 25-35% of their time below 50 m while Pacific billfishes only spent 1-5% of their time below 50 m. Sailfish and blue marlin also spent more time in surface waters in the Eastern Tropical Atlantic (ETA) than the WNA, suggesting the OMZ in the ETA region, like that in the ETP, compresses available habitat to near surface waters as well (Prince et al., 2010).

The shallowing depth of suitable surface habitat has been hypothesized to increase the vulnerability of pelagic predators to surface fishing gear, such as longlines and purse seines (Prince & Goodyear, 2006; Prince et al., 2010; Section 8.2). Many billfish and related stocks are considered overfished, mostly due to bycatch mortality from fisheries targeting swordfish and tunas, suggesting expansion of OMZs could potentially exacerbate overfishing for these and related species. High catch rates in habitat-compressed areas can lead to overly optimistic estimates of population status and potentially biased management advice from stock assessment models. If catch data used to develop abundance indices are simply pooled for samples inside and outside of OMZ regions, then estimates of catchability will be biased (Prince et al., 2010). Increases in catchability due to habitat compression that are not accounted for in stock assessment models will often lead to overestimates of harvestable biomass and underestimates of fishing mortality, so that management advice based on these models may be less conservative than intended.

10.7 Management implications

Deoxygenation has complicated effects on fish populations and fisheries that can be difficult to isolate and quantify. Deoxygenation in all ecosystems often occurs with changes in other environmental conditions. When deoxygenation occurs in coastal systems influenced by riverine inputs, there are the competing effects of more food occurring with greater hypoxia (both are fuelled by nutrient loadings). This view of a food versus hypoxia tradeoff presumes that the increase in food quantity can at least partially compensate for the habitat lost to hypoxia, reduced food quality, and other negative effects of eutrophication, such as plankton community shifts and harmful algal blooms (Cloern, 2001; Rabalais et al., 2009). Under global climate change, warming and increased acidification is expected to co-vary with worsening hypoxia (Gruber, 2011).

Fish populations are often managed for sustainable yield and certain population sizes, and so management can reduce allowable catch to compensate for a lowered population resulting in no decline in the population itself but rather a lowered catch. Thus, data on population abundance trends can disguise a deoxygenation effect. Multiple stressors and managed fisheries make isolation of the effects of deoxygenation difficult; however, our difficulties in quantifying deoxygenation effects does not mean that the effects are necessarily small or unimportant. Most analyses that attempted to isolate the effects of hypoxia determined that deoxygenation itself has small to moderate effects on fish populations and food webs (like many of the other factors looked at one-at-a-time), but when hypoxia is combined with the other co-varying factors, large effects are predicted (e.g. Ainsworth et al., 2011).

The various case studies illustrate the complicated effects of deoxygenation on fisheries (Table 10.1); under continued and likely accelerating deoxygenation, these effects will intensify at the same time that demand for fish for nutrition will rise. We described effects on the populations themselves that then affected the fisheries. These included low oxygen dynamics affecting croaker recruitment and abundance in the Gulf of Mexico, cod recruitment and adult condition in the Baltic Sea, and possibly white croaker or “thiof” mortality in West Africa, and the sudden drop in landings of Indian oil sardine off the south-west coast of India. Other case studies showed how hypoxia affected the spatial distributions of the population that then determined the availability of



Figure 10.18 Blue marlin *Makaira nigricans* © Waterframe / Alamy stock photo.

individuals to harvest and had cascading effects through the fishery. Habitat compression led to changes in the availability of billfishes to harvest in the Eastern Tropical Pacific. The key fisheries species in the Peruvian EEZ illustrated a multi-species response to low oxygen; overlap of sardine and jack mackerel can affect predation pressure on anchovy and the availability of all three species to harvest. Prices of brown shrimp in the fishery in the Gulf of Mexico showed the effects of hypoxia causing a lessening of large shrimp relative to smaller shrimp. From a management viewpoint, the Dungeness crab in Hood Canal case study demonstrated how hypoxia can negatively affect fisheries management performance (e.g. sensitivity to overfishing), especially when hypoxia is combined with other stressors.

Fisheries management is under intense scrutiny about whether it is sufficiently effective, adequately protective of the resource (sustainability), and equitable. There is also great pressure to move towards an ecosystem-based fisheries management approach (Essington et al., 2016). Deoxygenation is part of the mix of stressors that, when combined, have population-level effects on abundance and spatial distributions that affect the fisheries. There are multiple examples of hypoxia affecting the catchability of the fish. Altered catchability can have profound effects on how abundance indices

from monitoring data are interpreted and the accuracy of the population dynamics models that underlie stock assessment. Almost all management analyses rely on indices derived from field data (catch, fishery-independent) at some level. Most fisheries management analyses are not detailed in space and so the effects of deoxygenation, which are localized within the spatial area used for management, are difficult to quantify and incorporate into the analyses. The effects of hypoxia on catchability are therefore not considered, which can result in misleading management advice. This applies to data-limited and well-studied species, and to artisanal and commercial and recreational fisheries.

The effects of deoxygenation on fisheries can, at times, be difficult to truly isolate and quantify, but nevertheless are important. Effects manifest themselves through the dynamics of the populations and the fishery, and often co-vary with other environmental variables. Furthermore, oxygen and fisheries dynamics are both dependent on local conditions, making most analyses complicated and dependent on extensive data and modelling to account for the site-specific conditions.

Further understanding and incorporating the role of deoxygenation on fisheries can increase the effectiveness of management by providing better information on

the temporal and spatial dynamics of the populations and how fisheries respond. This will enable proper interpretation of population fluctuations (e.g. growth, recruitment), the vulnerability of individuals to harvest (e.g. catchability), and population indices derived from monitoring data that are used to determine stock status and trends and also used to tune assessment models. There is little room for management miscalculations and offering misguided advice; too many people depend on effective management of fisheries to ensure sustainable harvests and healthy ecosystems.

10.8 References

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What can we do? Adaptation and solutions to declining ocean oxygen

11

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Summary

- The oxygen content of the open ocean and coastal waters has declined since the middle of the 20th century, and is expected to decline further during the 21st century as a result of climate change and increased nutrient discharges. Consequences of this ocean oxygen decline include decreases in biodiversity, shifts in species distributions, displacement or reduction in fisheries resources, and changes in biogeochemical cycling.
- Fossil fuel combustion and agriculture contribute to both global warming and over-enrichment of waters with nutrients. Sewage – biomass in untreated sewage and nitrogen and phosphorus in both treated and untreated sewage effluent – is also a major contributor to oxygen depletion in coastal waters.
- Nutrient reduction strategies that have been most effective have utilized legal requirements, set specific targets, and have employed monitoring to detect problems and responses to management strategies. A range of potential solutions to nutrient reduction exists and can be tailored to local needs and economies.
- Reducing the rate of oxygen decline in the global ocean, and minimizing the contribution of climate change to deoxygenation of coastal waters, requires a dramatic climate mitigation effort, primarily through global reduction in greenhouse gas emissions due to human activities. Restoring oxygen lost over the past century on less than millennial time scales will likely also require reducing atmospheric greenhouse gas concentrations to levels lower than the present, through active greenhouse gas removal.
- Continued and enhanced efforts to quantify trends in deoxygenation and project future oxygen conditions, to understand deoxygenation effects on biological, biogeochemical and ecological processes, and to incorporate deoxygenation in development of fisheries and other management strategies are needed.
- Governance at scales ranging from local jurisdictions to international bodies such as the United Nations plays important roles in identifying the problem of deoxygenation, and in mitigation and adaptation efforts to reduce deoxygenation and its negative consequences.

- Solutions to ocean deoxygenation, and development of adaptation strategies in its presence, depend on sound and sufficient science. The international scope of scientific collaboration on this issue is notable; scientific working and expert groups can help facilitate communication among different stakeholders, and support decision makers to take measures required to stem increasing deoxygenation at local, regional and global scales. Further progress is needed, however, in the science of ocean deoxygenation, especially to improve predictions of future conditions and impacts on human welfare.

11.1 Introduction

Declining oxygen in the world's ocean, including its coastal waters, is one of the starkest examples of degradation of ocean ecosystems caused by human activities (Breitburg et al., 2018) (Figure 11.1). Since the middle of the 20th century, the open ocean has lost an estimated billion metric tons of oxygen, and the volume of water in which oxygen is completely lacking¹ has increased 4 fold (Schmidtko et al., 2017). Much of this oxygen loss is attributable to global warming through its effects on oxygen solubility, stratification, ocean circulation and respiration rates (IPCC, 2019; Oschlies et al., 2018). Over a similar period of time, more than 500 estuaries, semi-enclosed seas and other coastal water bodies have reported first instances or expanded areas of dissolved oxygen concentrations at or less than 2 mg L⁻¹ or 63 µmol L⁻¹ (hypoxia) as a result of an over-supply of nutrients from agriculture, aquaculture, human sewage and the combustion of fossil fuels (Breitburg et al., 2018; Diaz & Rosenberg, 2008; Isensee et al., 2015). Inaccessibility of information, and lack of monitoring, has likely led to an undercount of such systems, particularly in developing nations. Numerical models project that continued warming and increasing human populations will increase the severity of the problem of oxygen decline in both the open ocean and coastal waters (e.g. Cocco et al., 2013).

Severely oxygen-depleted waters, and those in which oxygen is completely lacking, represent habitat that is unusable by most multicellular marine organisms that are important to marine food webs and fisheries. Instead, these areas host rich microbial communities that alter biogeochemical cycles, increasing production of toxic compounds and greenhouse gases, and reducing the supply of biologically available nitrogen in regions of the ocean where nutrients can be in short supply. Even

less severely oxygen-depleted waters alter distributions, growth rates and disease in marine organisms. The combined effects of oxygen decline with those of other anthropogenic stressors — warming, acidification and population-level and food web-effects of fisheries, for example — can be more severe than effects of oxygen decline alone. Oxygen is fundamental to multicellular life and to many microbes, and when in short supply, it can greatly alter the functioning of marine ecosystems, with the potential to negatively affect human wellbeing.

How do we move forward, given the magnitude of the problem of ocean oxygen decline? The first step is to raise awareness of the issue among policy-makers and within civil society. Increasing awareness and understanding of ocean² oxygen decline is a major goal of this report, as well as of several other recent publications (e.g. Breitburg et al., 2018; GO₂NE, 2018; Isensee et al., 2015; Levin & Breitburg, 2015; Limburg et al., 2017). Although the problem of low oxygen caused by nutrients and sewage in coastal waters has been recognized for over a century, progress in correcting the problem has generally been slow except where solutions also address issues that create a direct threat to human health (e.g. discharge of raw sewage into waterways). The magnitude of the effect of global warming on ocean oxygen content is only recently becoming understood (Levin, 2018). It is important to raise the profile of oxygen decline within the larger conversation on the effects that increasing greenhouse gas (GHG) emissions are having on the global ocean. Improved understanding of the economic consequences of oxygen decline, lost ecosystem services and effects on human well-being may contribute to this effort.

In the remainder of this chapter, we discuss the way forward — the steps and strategies needed, as well as opportunities to stem the loss of ocean oxygen, and especially in nutrient-enriched coastal waters, to

¹ The designation of an area as 'anoxic' or 'completely lacking in oxygen' is based on detection limits of instrumentation used to measure oxygen and the presence of biogeochemical processes that are inhibited by oxygen. As instrumentation improves, we are finding that some areas classified as anoxic contain nanomolar concentrations of oxygen, but these are levels that are too low to support most multicellular organisms and many microbes.

² We use the term 'ocean' or 'global ocean' to include the open ocean, and coastal water bodies such as semi-enclosed seas, estuaries, and similar systems. 'Open ocean' refers to areas where the influence of local watershed processes is secondary or undetectable.

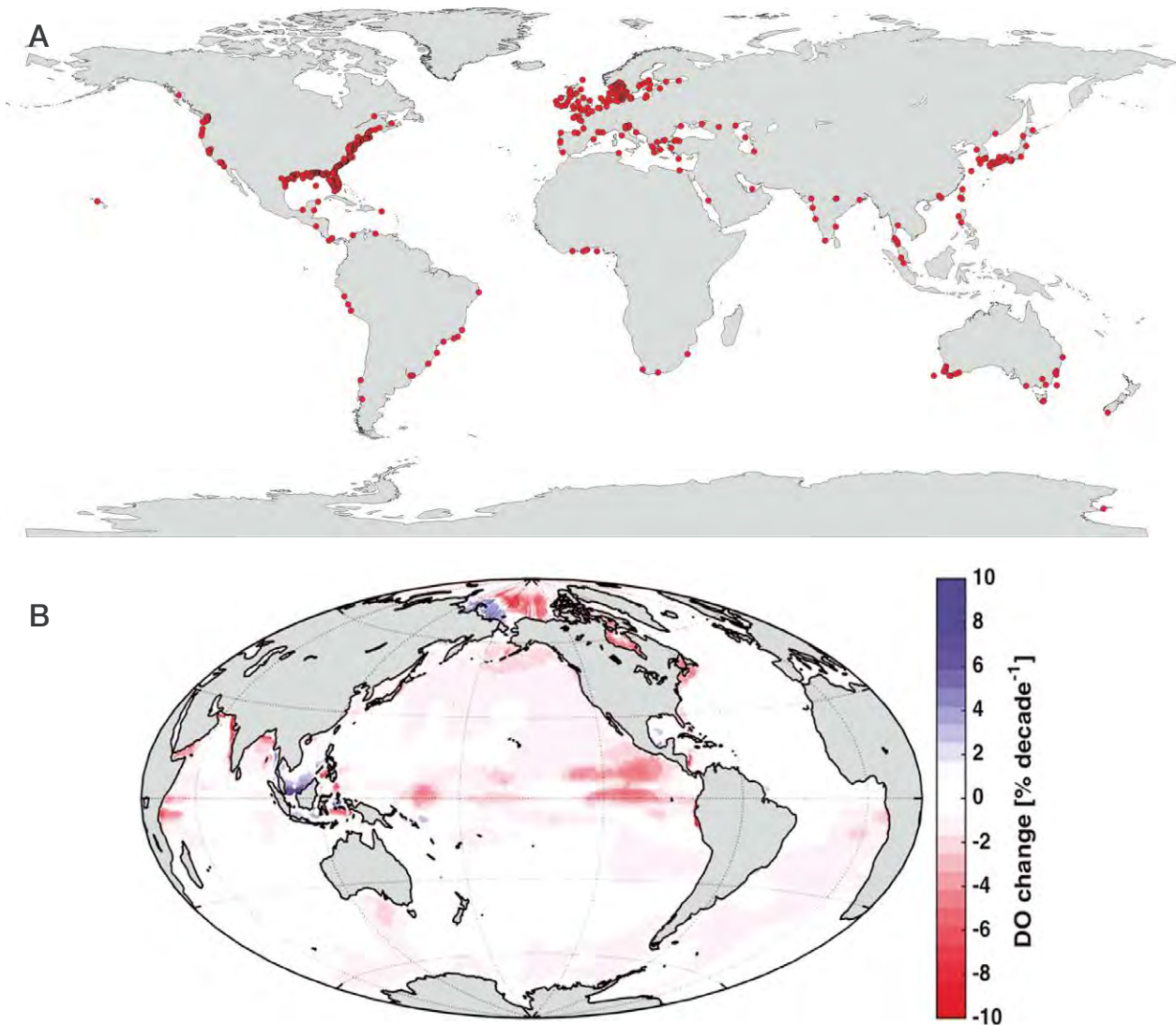


Figure 11.1 Oxygen has declined in both (A) coastal waters and (B) the open ocean since the middle of the 20th Century (reproduced from Breitburg et al., 2018). (A) Coastal waters that have reported oxygen concentrations $<2 \text{ mg L}^{-1}$ ($63 \text{ } \mu\text{mol L}^{-1}$ or $61 \text{ } \mu\text{mol kg}^{-1}$) (red dots) (Diaz & Rosenberg, 2008; Isensee et al., 2016). Most systems shown in this figure reported their first incidence of low oxygen after 1960. (B) Estimated change in oxygen content of the global ocean in percentage decade⁻¹ since 1960 (Schmidtke et al., 2017). Red tones denote oxygen declines, and blue tones increases.

restore this vital resource to healthier levels. Addressing deoxygenation will require action on multiple fronts, with mitigation and adaptation actions at the global, regional, national and local levels, and thus engagement of a broad range of stakeholders.

11.2 Solutions to slow and reverse oxygen decline

11.2.1 Warming-induced deoxygenation and eutrophication share common causes

Causes of global warming-driven and nutrient-driven oxygen decline are closely intertwined (Seitzinger & Phillips, 2017) (Figure 11.2). Combustion of fossil

fuel and agriculture are major contributors to both problems. Fossil fuel combustion, the major source of GHG emissions, also produces nitrogen oxides that are deposited onto land and directly into coastal waters, where they stimulate primary production and, ultimately, oxygen decline (Seitzinger & Phillips, 2017). Atmospheric deposition of iron and fixed nitrogen also stimulates primary production in the open ocean and may worsen oxygen decline in oxygen minimum zones (OMZs) (Ito et al., 2016). Agriculture, strongly associated with eutrophication of coastal waters, is estimated to be the source of 13% of global anthropogenic GHG emissions (FAO, 2014; including energy use in agriculture). Methane and nitrous oxide emissions associated with livestock production, comprised approximately 22%

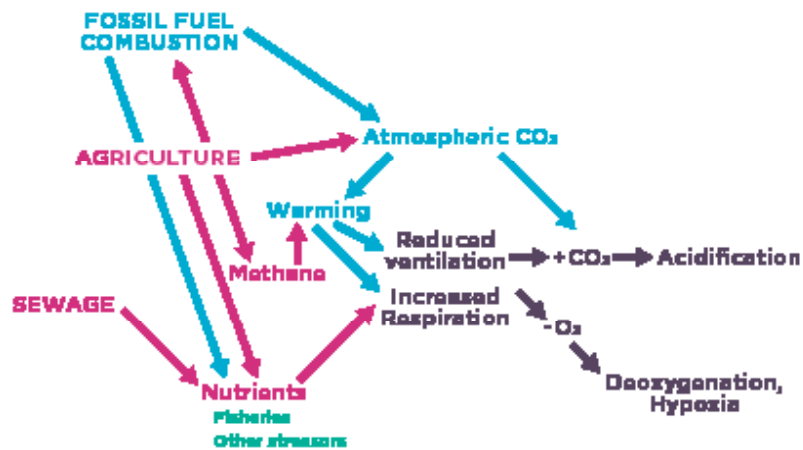


Figure 11.2 Linked causes and mechanisms of oxygen loss. Not shown are pathways for some greenhouse gases such as N₂O, or feedbacks, including the potential for deoxygenation and warming to increased production of greenhouse gases such as nitrous oxide and methane. Red = major pathways for nutrient sources and effects; blue = major pathways for warming and CO₂ enrichment; green = other stressors that can increase respiration, for example by altering food webs.

of total non-CO₂ GHG emissions (in CO₂ equivalents) in 2010 (Caro et al., 2014). The boom in agriculture, made possible, in part, by the invention and use of synthetic fertilizers (Figure 11.3), and transportation systems that enhance food distribution, have provided the tremendous benefit of feeding the growing human population. A side effect, however, is that agricultural fertilizers, and the sewage from livestock and humans, also fertilize coastal waters, increasing oxygen demand in these systems. Ensuring food security and adequate nutrition for the human population while minimizing the negative effects of agriculture on the environment is a challenge that must be met.

11.2.2 Nutrient management

Reducing nutrient and carbon loads to coastal waters is the basic action required to slow and reverse oxygen depletion in eutrophic coastal waters, and is a focus of policy goals ranging from local municipalities to Goal



Figure 11.3 Stock of synthetic fertilizer ready for applying to crop © Photo-Loci / Alamy stock photo.

14 of the United Nations 2030 Agenda for Sustainable Development (Table 11.1; UN General Assembly, 2015). An important first step for governments is to set environmental quality objectives, as well as specific water quality criteria, to guide the process (Bricker et al., 1999; Ferreira et al., 2011; GO₂NE, 2018). The most effective efforts have utilized legal requirements (Andersen et al., 2017) and set specific targets. Aquatic monitoring programmes that provide a comprehensive picture of environmental conditions are essential to nutrient reduction efforts. They are needed to detect large- and small-scale changes indicative of degradation, as well as positive responses to nutrient management. A focus on data collection and management, with coordinated assessments and analyses, is also necessary to evaluate progress and to adaptively modify nutrient-reduction actions. Finally, long-term financial support for implementation of actions required to reduce nutrients and sewage inputs, for research to develop and identify the most effective actions, and for environmental monitoring to track progress must be established.



Figure 11.4 Boston Harbour © Terry Mathews / Alamy stock photo.

Evaluating cost effectiveness of the various possible actions to reduce nutrients from both point and non-point sources is a critical step needed to move beyond broad strategies. Both societal equity and the magnitude of nutrient reduction that is often required mean that reductions must come from the range of sectors contributing to the problem, including atmospheric deposition, industrial sources, wastewater treatment plants and agriculture. Reductions in nutrient loads from advanced wastewater treatment plants with both phosphorus and nitrogen removal have been clearly demonstrated to lead to improvements in water quality in diverse locations. Estuaries with heavy urban biochemical oxygen demand that had severe oxygen depletion in the past have also seen remarkable improvements in recent decades, such as Boston Harbour, MA, USA (Tucker et al., 2014) (Figure 11.4), the urban region of the Delaware estuary, USA (Sharp, 2010), and the Thames River Estuary, UK (Tinsley, 1998). Conditions in the Thames recovered from anoxia (zero oxygen) to >10% oxygen saturation through implementation of primary treatment of wastewaters, with a resulting 10-fold increase in fish species richness (Tinsley, 1998). The Thames example shows that even primary sewage treatment, the removal of biosolids, can result in a large improvement in systems currently receiving raw sewage (Figure 11.5).

Numerous measures can be taken to achieve sustainability in nutrient cycling to protect the environment and reduce the anthropogenic deoxygenation of coastal, shelf and ocean waters. Human-derived nutrients originate from four main sources: nutrients contained in waste from septic systems and wastewater treatment plants, fertilizer run off, livestock manure, and atmospheric deposition primarily of nitrogen from the burning of fossil fuels. Within the agricultural sector, improved manure management, more efficient fertilizer use, and other changes in crop production can make substantial contributions to reducing nutrients reaching coastal waters. Manure management to reduce nutrient losses to both the atmosphere and aquatic environments includes (i) effective manure handling, (ii) manure transport to other areas, and (iii) adjustment of livestock density (Oenema et al., 2007). Technical solutions to treat manure are becoming increasingly common to reduce its environmental impact (De Vries et al., 2015). To achieve sustainable agriculture, maximum limits on the amount of plant-available nutrients added to different crops, scaled to the optimum needed, can greatly reduce nutrient losses from agricultural fields (Kronvang et al., 2008). Implementing cost effective measures to reduce nutrient loads from agriculture is a major challenge but is needed to minimize the food system's environmental burden (Davis et al., 2016; Sharpley et al., 2015).

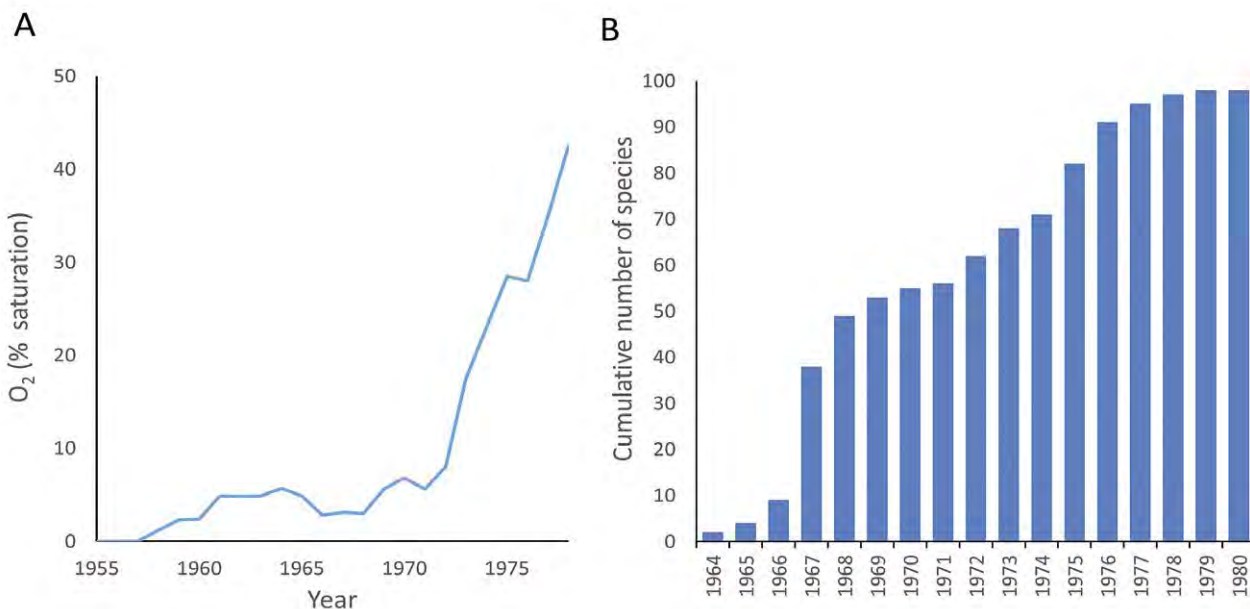


Figure 11.5 Recovery of (A) dissolved oxygen in the upper Thames River Estuary, UK, and (B) fish populations in the cumulative number of fish species recorded in the Thames between Kew and Gravesend. Conditions improved from anoxia (zero oxygen) to >10% oxygen saturation and a 10-fold increase in fish species richness through implementation of primary treatment and offshore shipping of sewage sludge in the early 1960s. Further improvements in sewage treatment during the 1970s resulted in large further improvements in dissolved oxygen and fish species richness (Tinsley, 1998). (A) adapted from Kemp et al. (2009); (B) adapted from Andrews (1984).

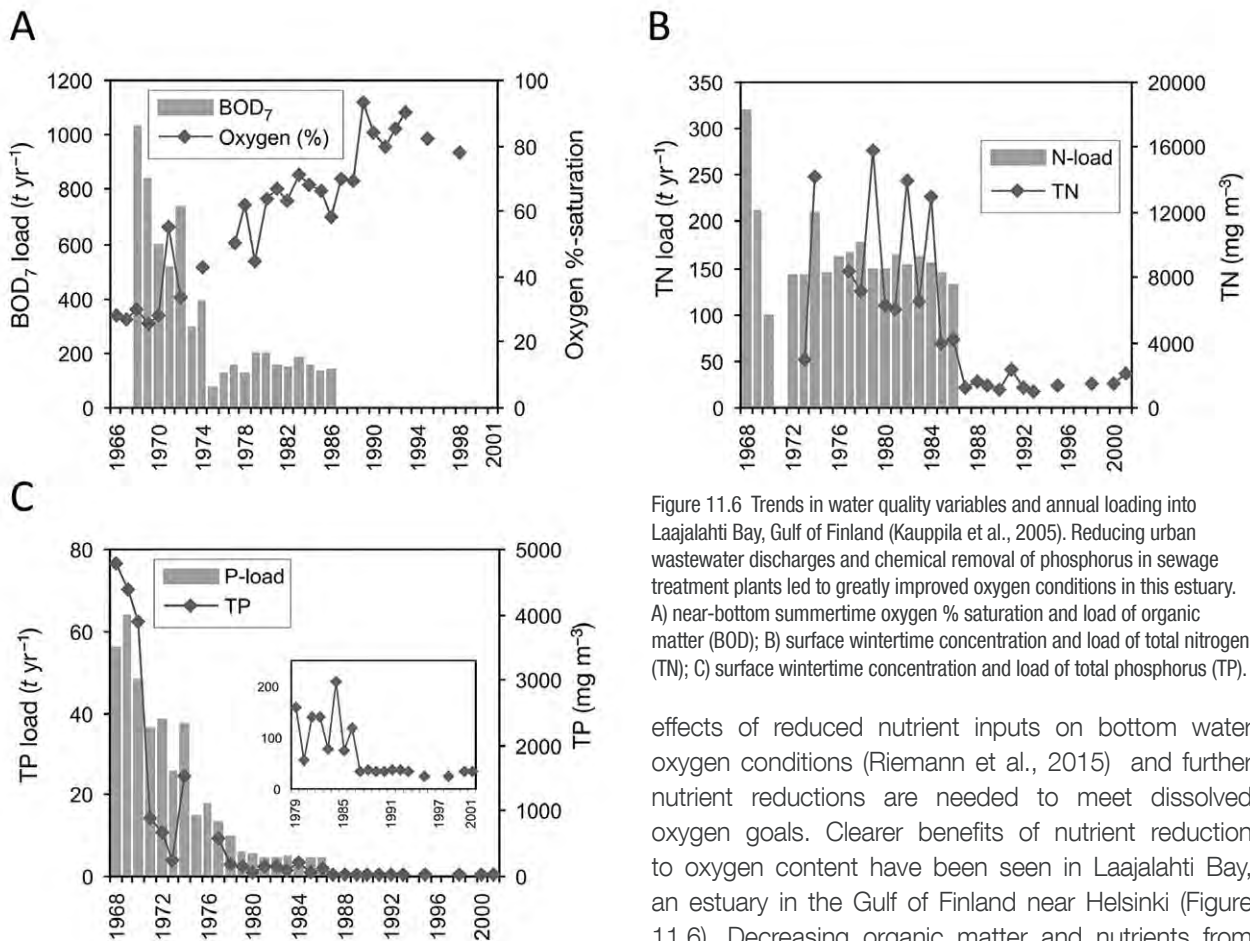


Figure 11.6 Trends in water quality variables and annual loading into Laajalahti Bay, Gulf of Finland (Kauppila et al., 2005). Reducing urban wastewater discharges and chemical removal of phosphorus in sewage treatment plants led to greatly improved oxygen conditions in this estuary. A) near-bottom summertime oxygen % saturation and load of organic matter (BOD); B) surface wintertime concentration and load of total nitrogen (TN); C) surface wintertime concentration and load of total phosphorus (TP).

effects of reduced nutrient inputs on bottom water oxygen conditions (Riemann et al., 2015) and further nutrient reductions are needed to meet dissolved oxygen goals. Clearer benefits of nutrient reduction to oxygen content have been seen in Laajalahti Bay, an estuary in the Gulf of Finland near Helsinki (Figure 11.6). Decreasing organic matter and nutrients from urban wastewater has led to dramatic increases in near-bottom summertime oxygen saturation (Kauppila et al., 2005).

Effective environmental monitoring and assessment systems have been established regionally and nationally during the late 20th century, e.g. Australia (<http://www.ozcoasts.gov.au/indicators/introduction.jsp>), Chesapeake Bay, USA (U.S. Environmental Protection Agency, 1996), and San Francisco Bay, USA (Cloern et al., 2017). Progress in nutrient reduction has, however, often been slow. An exception can be found in Denmark where measures have included large changes in agricultural practices and significant improvements in sewage treatment (Kronvang et al., 2008), resulting in approximately 50% reduction in nitrogen and 75% reduction in phosphorus discharges to Danish coastal waters (Rieman et al., 2016). Nearly three decades after the first mitigation measures were implemented, most key ecosystem components (chemical and biological variables) show evidence of a healthier coastal ecosystem, demonstrating the importance of nutrient reductions and the impact on coastal communities. However, the Danish experience also demonstrates the complexity of the problem of deoxygenation in coastal waters: frequent stratification and higher water temperatures have counteracted the expected positive

One of the major challenges for reducing hypoxia is that deoxygenation is driven by multiple factors. In diverse ecosystems such as Chesapeake Bay and the Baltic Sea, river- or inflow-induced stratification, respectively, and nutrient load are highly correlated with hypoxia (Hagy et al., 2004). Wind speeds and directions during summer are key secondary variables explaining interannual variability in hypoxia and anoxic volumes (Carstensen et al., 2014; Testa et al., 2017). It is also increasingly recognized that there is a legacy of excess external nutrient loading from the last century in the sediments of many coastal and shelf ecosystems that contributes to continued eutrophication despite large-scale nutrient reductions. The legacy of a higher sediment respiratory demand following eutrophication has been shown for other coastal systems (Turner et al., 2008) whereby repeated hypoxic events lead to an increased susceptibility of further hypoxia and accelerated eutrophication. Nutrients previously buried in the sediments can be returned to the water column

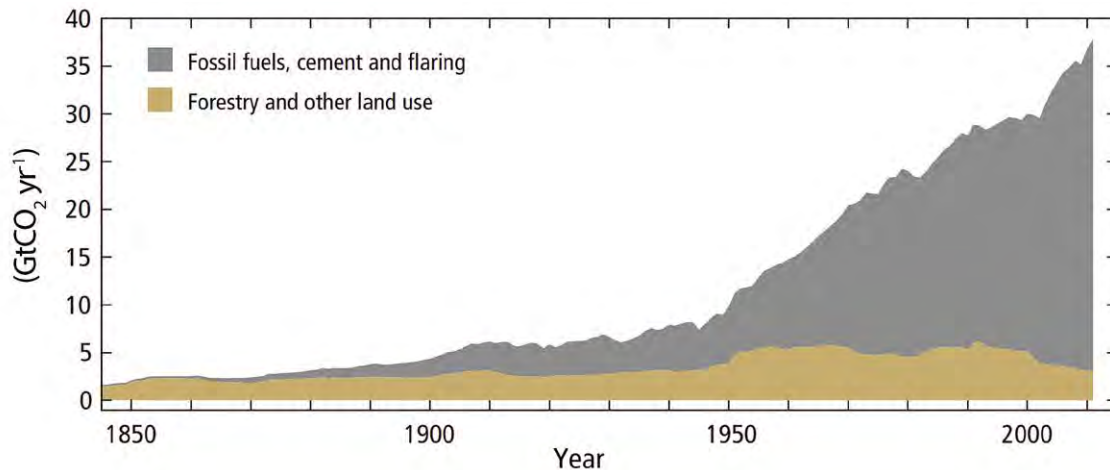


Figure 11.7 Global CO₂ emissions have increased more than 10 fold since 1900 (modified from IPCC, 2014).

causing an increase in eutrophication (Conley et al., 2009a).

Geoengineering has been suggested as a complementary measure to nutrient reduction strategies to reduce coastal hypoxia. However, two such efforts carried in the Baltic Sea demonstrate the mixed success and potential for unintended negative consequences of this approach. In both of these cases, oxygen-rich surface water was pumped into the deep water to enhance the burial of phosphorus. Pumping surface water downward in Sandöfjärden, Finland expanded the bottom area below the pycnocline, and the basin went from hypoxic to anoxic because of the warming of bottom water (Rantjärvi, 2012). In By Fjord, Sweden, pumping increased oxygen concentrations and induced deep-water renewals by inflowing water from an adjacent estuary (Stigebrandt et al., 2015). Reduced phosphorus regeneration from sediments was observed, but the long-term benefits of this effort are uncertain. More research is needed on the potential for implementation of sea-based measures and their long-term efficiency in order to better understand their impacts. Important issues including costs, legality, financial liability and, not least, potential environmental impacts, must be addressed before implementation occurs (Conley et al., 2009b).

11.3 Reducing the threat of global warming

Reducing the rate of oxygen decline in the global ocean, and minimizing the contribution of global warming to deoxygenation of coastal waters, requires a dramatic climate mitigation effort, primarily through global cessation of greenhouse gas (GHG) emissions due to human activities (IPCC, 2014, 2018). Restoring oxygen

lost over the past century on less than millennial time scales will almost certainly require reducing atmospheric GHG concentrations to levels lower than the present, through active GHG removal (IPCC, 2014, 2018). Both approaches (emission reductions and active removal) are likely to be necessary to achieve the objectives of the United Nations Framework Convention on Climate Change (UNFCCC, 1992): ‘...stabilization of GHG concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system’. An international commitment to achieve global net zero emissions by 2100 — in order to keep global temperature increase “well below 2 °C” — was made through the 2015 Paris Agreement (UNFCCC, 2016), but national mitigation commitments are currently insufficiently aggressive to achieve that goal (Hansen & Sato, 2016). Human activities have caused an estimated 1 °C increase in global temperatures above pre-industrial levels, and current estimates indicate that global temperatures are now increasing at a rate of 0.2 °C per decade (IPCC, 2018).

Global anthropogenic GHG emissions increased by an order of magnitude during the 20th century, and nearly doubled between 1970 and 2010 (Edenhofer et al., 2014) (Figure 11.7). Energy production is the largest contributor to global greenhouse gas emissions (72% in 2013; Figure 11.8). Thus, the goal to decarbonize the electric grid through renewable energy, and fully electrify the energy supply, can be considered as joint priorities. However, the pace of those transitions is not currently on track to meet the goals of the 2015 Paris Agreement (REN21, 2019). Growth in global energy consumption averaged 1.5% per year between 2006 and 2016. During that time, the contribution to total energy consumption from all renewables, combined

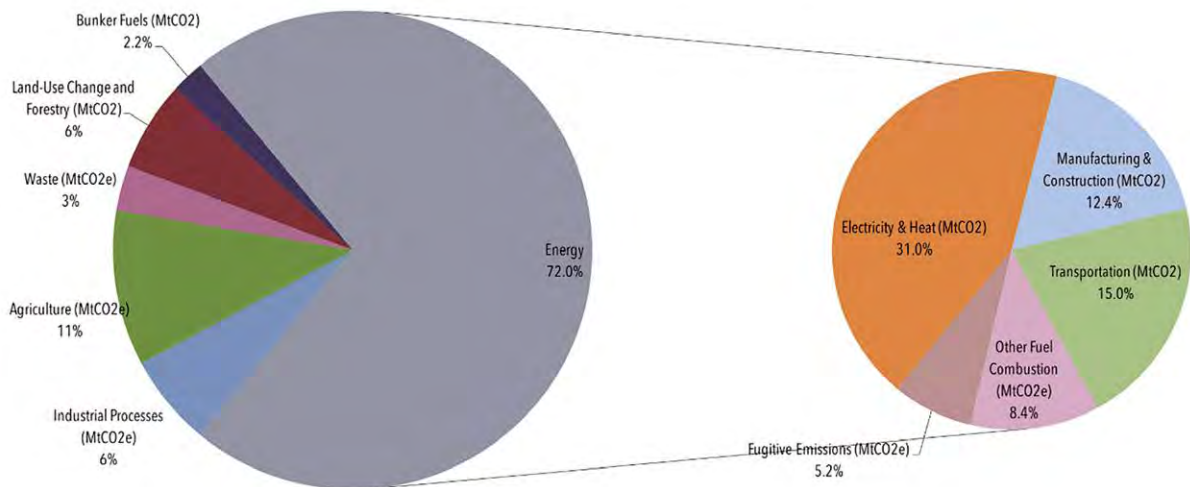


Figure 11.8 The largest global sources of greenhouse gas emissions are electricity and heat, transportation, manufacturing, and agriculture. (Center for Climate Change Solutions, 2017).

(including both traditional biomass and modern renewables) increased only slightly more, by 2.3% annually (REN21, 2019). Eighty per cent of global energy was still generated from fossil fuels in 2017, with less than a 1% decline in contribution to total energy production in the decade 2005-2015 (World Bank – IEA Statistics, 2018). Progress in reducing GHG emissions from heating and cooling, and from transportation, the largest power consumption contributors other than electricity generation, has also lagged (REN21, 2019).

Somewhat more encouraging is the trend to a decarbonized future within sectors and within individual nations and regions. Despite continued subsidies for fossil fuel consumption (estimated at US\$300 million in 2017), 2018 marked the fifth consecutive year that global investment in new renewable power capacity

exceeded US\$230 billion. The contribution to total energy consumption by modern renewables, dominated by wind, solar, and hydropower (Figure 11.9), increased by 4.5% per year between 2006 and 2016, a rate more than three times that of total energy consumption (REN21, 2019). China, currently the largest producer of GHG emissions, also has the highest annual investment in new renewable power and fuels, and a near-complete phase-out of fossil fuels by 2050 is planned in several European countries (France, Norway, Sweden and the UK) in order to meet legal net-zero emission targets (Climate Home News, 2019).

As noted above, global warming can be slowed either by reducing emissions, or by the active removal of greenhouse gases from the atmosphere, also known as

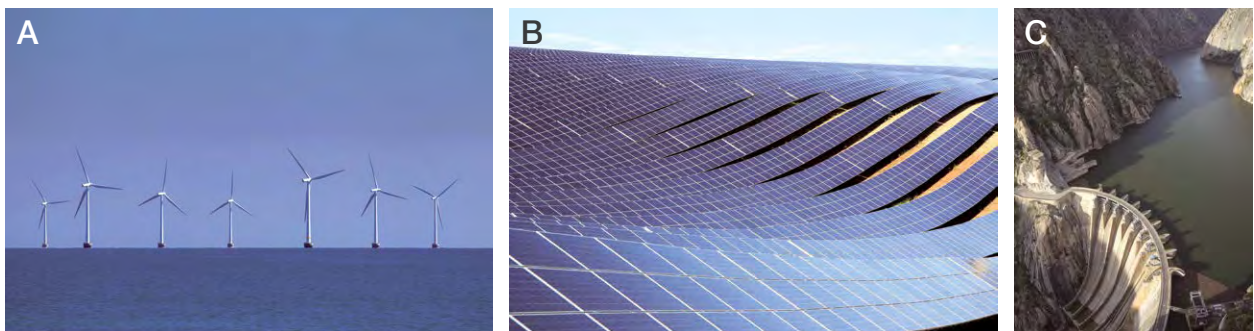


Figure 11.9 (A) Offshore wind turbines in the Baltic Sea © Arterra / Alamy stock photo (B) Large solar panel farm in France © Helene Roche /Alamy stock photo (C) Hydro-electric dam on River Duro, Spain © M Afoto / Alamy stock photo.

sink enhancement or negative emissions, as well as by reducing emissions.

Within scenario-based integrated assessment models, bioenergy with carbon capture and storage (BECCS) and increased forestation are the techniques most commonly considered for CO₂ removal (Fuss et al., 2014). A wide range of other approaches have also been proposed (CBD, 2016; Minx et al., 2018); those, that involve ocean-based CO₂ removal and have recently been assessed by Gattuso et al. (2018). For all methods, the feasibility of large-scale removal is contentious, either for technical, environmental or governance reasons (Smith et al., 2016; Williamson, 2016). Nevertheless, IPCC (2014) considered that 'warming caused by CO₂ emissions is effectively irreversible over multi-century timescales unless measures are taken to remove CO₂ from the atmosphere'.

Other proposed climate interventions involve sunlight reflection methods (SRM), also known as solar radiation management. Sunlight reflection methods include stratospheric aerosol spraying, marine cloud brightening and increasing the albedo of the land or ocean surface. Although they are theoretically capable of reducing global temperatures, high uncertainty and

risk are involved (Sillmann et al., 2015), with low public and political acceptability (CBD, 2016). The potential implications of different carbon removal and SRM techniques have been considered by several studies in the specific context of ocean acidification (Gattuso et al., 2018; Keller et al., 2014; Williamson & Turley, 2012). However, those considering effects on ocean oxygen (other than direct temperature effects) are more limited. One widely discussed approach, iron fertilization, would exacerbate mid-water and seafloor deoxygenation (Williamson et al., 2018).

Solving the problem of global warming clearly requires strong commitments in four areas- policy, technology, finance and patterns of consumption (Figure 11.10). Nations will need to adopt very ambitious policies that go beyond those aimed at limiting warming to less than 2 °C if the goal is to halt and reverse ocean deoxygenation. The much smaller increment in warming that occurred between the mid-20th century and present was sufficient to contribute to substantial ocean oxygen decline (Schmidtko et al., 2017). The global ocean is projected to lose 2% of its Year 2000 oxygen content under RCP 2.6, the scenario that is projected to keep global temperature rise below 2 °C (Bopp et al., 2013). The acceptability of a 2% decline in global ocean oxygen is a societal question, not a scientific one, but limiting oxygen loss to 2% would likely cause far less environmental harm than oxygen loss projected for GHG scenarios that result in more severe warming.

Continued rapid advances in technology and future innovation can provide the promise of cleaner energy and healthy societies (Nuttall, 2017), and ambitious development and implementation are key to meeting goals to limit global warming. Development and implementation of policies and technology will require direct investment as well as financial mechanisms that increase the cost-effectiveness and encourage public acceptance of the transformative changes that are required. Both policies and financial resources are also required to ensure justice and equity in the face of changes that will occur.

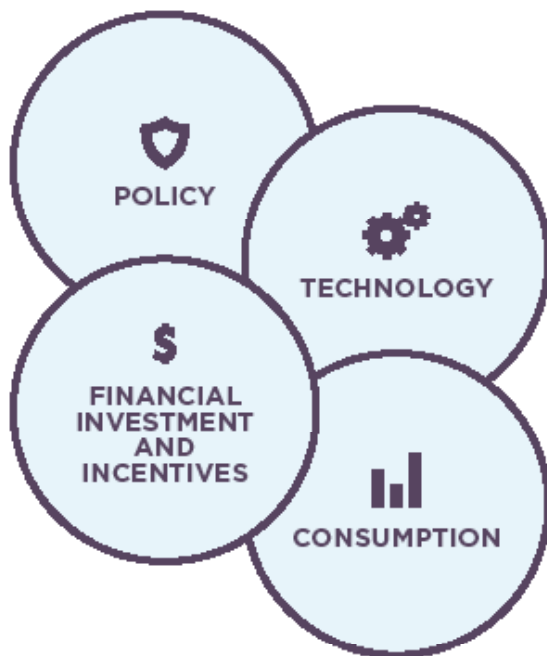


Figure 11.10 Success in addressing global warming requires major emphasis on policy development and implementation, technology development and transfer, economic investment and incentives, and patterns of consumption.

The good news is that all actions taken to reduce emissions of CO₂ and other greenhouse gases, through the Paris Agreement, other policy instruments and financial incentives, will help to mitigate ocean deoxygenation. Efforts taken at national, regional and local levels all contribute to solutions (Table 11.1).

Table 11.1 Examples of governance actions that address ocean deoxygenation.

Governance Unit	Entities	Mitigation	Adaptation
Local/State	Climate Action Committees, local promulgation of European Climate-ADAPT programme	City commitments to reduce C emissions (e.g. Climate action plans)	Wetland restoration, fisheries management, nutrient reduction programs, green infrastructure
Larger region within a nation	West Coast Acidification and Hypoxia Panel - unified management actions	Carbon Cap and Trade	Coordinated science priorities, fisheries management
National	National Ocean Policy, Clean Air and Water Acts	Regulating CO ₂ as a pollutant, Nutrient legislation, water quality limits, Blue carbon initiatives, Carbon Cap and Trade	Research and development programmes, Ecosystem-based fisheries management policies, National Sanctuaries/Protected Areas
Regional/ Transnational	UN - Regional Fisheries Management Organizations	EU Water Framework Directive	Oxygen-sensitive fisheries management for Vulnerable Marine Ecosystems (VMEs), fishing grounds
International	UNFCCC UN General Assembly	Paris Agreement (CO ₂ emissions), 2030 Agenda Sustainable Development Goal 14.1	Classification of oxygen as an essential ocean variable for Global Ocean Observing System (GOOS) (science)

11.4 Adaptation in the face of oxygen decline

Given that the ocean has already lost substantial amounts of oxygen (IPCC, 2019; Levin, 2018; Schmidtko et al., 2017), and that many regions and ecosystems will continue to experience deoxygenation, it is beneficial to consider adaptation strategies that may help preserve fisheries and other ecosystem functions and services in affected and adjacent waters. Options include adaptive, ecosystem-based management of fisheries, spatial planning to create refugia that enhance ecosystem resilience, actions that reduce local stress on ecosystems, capacity building and socio-ecological shifts that ameliorate impacts on people. An additional category involves observation, monitoring and mechanistic studies that can improve understanding of hypoxia impacts in space and time and will facilitate management and adaptation.

Where deoxygenation occurs, it can be critical to integrate the oxygenation regime into fisheries management through spatial restrictions that protect oxygen-stressed populations, and through closures and landings limits that reduce overfishing on species vulnerable to direct and indirect negative effects of low oxygen (e.g. Roberts et al., 2012). Because different fish and invertebrate life

stages can vary in their vulnerabilities to low oxygen, it may be possible to achieve protection of populations by regulating size limits, gear type, or fishing locations to reduce pressure on the most vulnerable stage or ontogenetic phase. Regulations that require avoidance of particular fishing depths or time periods could reduce fishing pressure in hypoxia-stressed locations (e.g. McClatchie et al., 2010) or seasons, and during episodic hypoxia events.

Spatial planning and the creation of protected areas are increasingly being used to enhance ecosystem resilience in the face of climate change (Le Cornu et al., 2018; Micheli et al., 2012). The effectiveness of area-based spatial management under climate change has been questioned (Johnson et al., 2018). But proactive efforts exist; climate-informed spatial management has incorporated ocean acidification (Queiros et al., 2016), sea-level rise and warming (Le Cornu et al., 2018). All major climate stressors have been modelled for deep seabed mining conservation applications (Dunn et al., 2018), as well as for deep-ocean fisheries management in relation to vulnerable marine ecosystems (FAO, 2019); modelling of potential interactions between deoxygenation and other stressors could inform management and policy. Creation of no-take marine reserves with flexible boundaries that take into account

changes in hypoxia distribution, and flexible timing to accommodate hypoxic seasons or events could reduce fishing stress and physical disturbance (Micheli et al., 2012). Hypoxia-induced habitat loss for cowcod (*Sebastes levis*), for example, was a consideration incorporated in management and closures in the US Channel Islands (McClatchie et al., 2010).

Habitat restoration has rarely been considered as an adaptive measure to protect species stressed by low oxygen. Creation or restoration of new nursery, spawning or feeding habitats could facilitate recruitment and contribute to population resilience, while providing additional ecosystem-scale benefits (Petr, 2000). In general, steps that relieve sources of mortality other than low oxygen exposure may help protect populations in systems with hypoxic waters (Breitburg et al., 2009).

Enhanced scientific capacity to monitor oxygen, detect hypoxic events, characterize their spatial and temporal dynamics, and place these in a broader oceanographic and anthropogenic context will aid adaptation to ocean deoxygenation by improving mechanistic understanding, modelling skills, and predictive power. Monitoring networks can facilitate quick-response capabilities. The ability to rapidly assess the consequences of episodic hypoxia for habitat structure, recruitment, and other

effects can facilitate rapid, adaptive management decisions and could reduce further impacts on habitat, facilitate recolonization, and aid recovery. Open data access allowing the incorporation of local information in regional and global oxygen syntheses will advance these goals (Breitburg et al., 2018). Improved understanding of thresholds or tipping points as a function of region or ocean basin is needed to inform management practices (Chu & Gale, 2017; Chu & Tunnicliffe, 2015). The Argo float programme (Figure 11.11) has offered unprecedented synoptic and regional views of oxygen in the open ocean (Martz et al., 2008; Takeshita et al., 2013), and local, national and regional monitoring programmes have done the same in coastal waters. A combination of raised awareness, technology transfer, and instrumentation training to build capacity in developing countries is needed. Additionally, development of inexpensive, easy to maintain and simple to deploy, continuous oxygen monitoring tools and platforms will enable engagement of more countries and regions. Creative use of fishing vessels, ferry lines, shipping infrastructure, and smart cables could be considered.

In addition, although still in the developmental phase, there is growing evidence that fishes themselves can be “mobile monitors” of their habitats and that

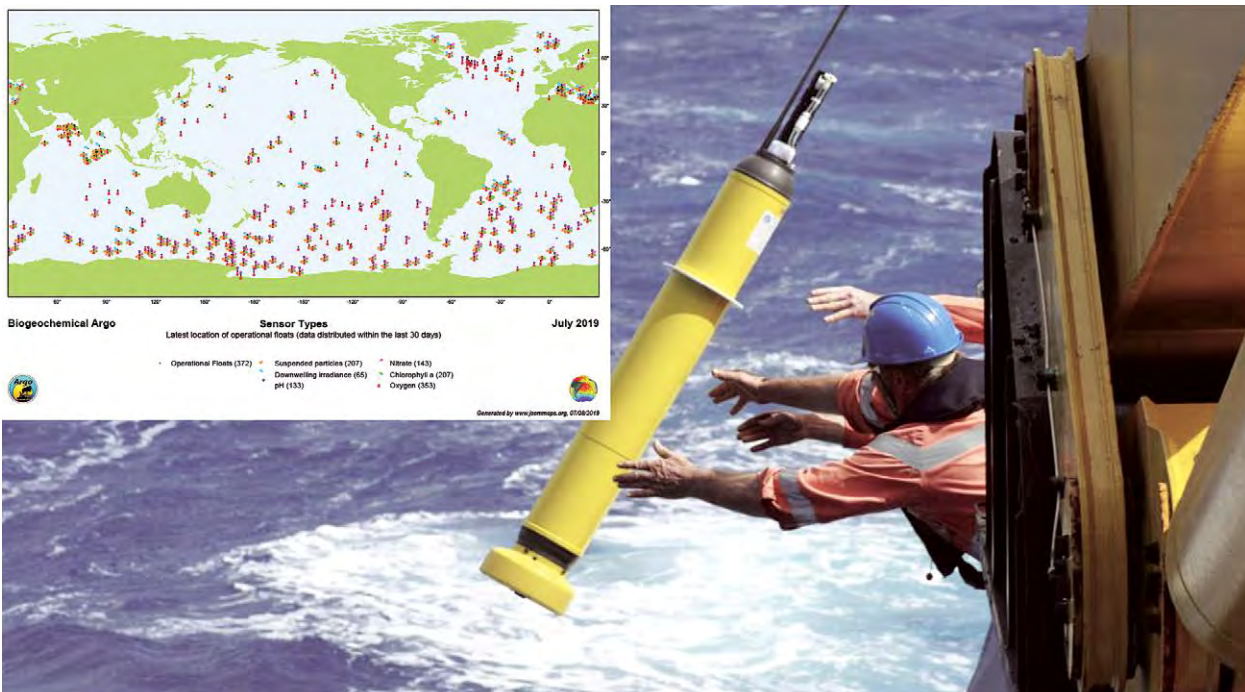


Figure 11.11 The deployment of an Argo Float in the Indian Ocean. Map showing the locations of 372 operational Argo floats equipped with biogeochemical sensors, of which 353 have an oxygen sensor in July 2019. Argo floats freely drift in the ocean at a parking depth of 1,000 m, and perform vertical profiles of temperature, salinity, oxygen and other parameters every 10 days between 2,000 m depth and the sea surface. (Sources: Map JCOMMOPS; photo: CSIRO <https://blog.csiro.au/bio-robots-make-a-splash-in-the-indian-ocean/>; images and figure legend from GO₂NE, 2018).

lifetime exposure to hypoxia can be tracked through geochemical proxies in fish otoliths (ear-stones), the small, calcified structures that form part of the hearing and balance system (Limburg et al., 2011, 2015). Because otoliths grow throughout life and lay down annual increments like tree rings, they can record the chemistry of waters in which fish develop, and chemical proxies can be developed from the trace elemental composition of otolith rings. In combination with age information derived from ring counts, it is possible to generate powerful chronologies of hypoxia experienced directly by fishes (Limburg et al., 2011) that can aid in the management of species and populations sensitive to the effects of hypoxia (Figure 11.12).

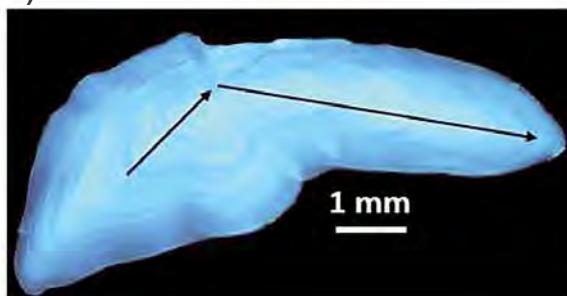
There are also important scientific-sociological linkages to consider in developing adaptation strategies to minimize the negative effects of oxygen decline. Deoxygenation is most likely to impact local economies, livelihoods and food security in areas where either artisanal or subsistence fisheries rely on vulnerable resources, aquaculture facilities are susceptible to hypoxia, or tourism relies on vulnerable ecosystems (Breitbart et al., 2018). Hypoxia-induced mortality in aquaculture (San Diego-McGlone et al., 2008) can compromise livelihoods or harm human health (Cayabyab et al., 2002). A lack of human mobility to track resources or move to unaffected areas for economic, cultural or other reasons, may mean that adaptation requires shifting sources of food, jobs and income. Linking governance actions across sectors (environment, fisheries, labour and other ministries or agencies) and jurisdictions (watershed, coastal, marine) would be key to effective integrated management of hypoxia for ecosystems and people.

11.5 Governance and collaboration

Locally designed and implemented actions can be successful at mitigation of low oxygen conditions, and for adaptation to locally degraded conditions, where the cause of deoxygenation and the affected water body fall within a single jurisdiction. But this is rarely the case even for the problem of excess anthropogenic nutrients, and is even less likely for deoxygenation caused by global warming. Collaborative efforts among governance units within nations are required where watersheds, airsheds and fisheries management units cross jurisdictional boundaries of villages, cities and provinces. Even where manifestations of problems are geographically confined, larger economic and political boundaries influence options for solutions. At large scales, regional and broader international collaboration in science, policy development and implementation are critical to solving, mitigating, and adapting to the problem of ocean deoxygenation.

International and regional scientific collaboration and cooperation are key to building capacities, to raising awareness, to improving management strategies and to informing policy decisions. The complexity, severity and geographic extent of problems like ocean deoxygenation requires that the best science from across the globe on a wide range of topics be used, and that there is a continued effort to build scientific capacity in both developed and developing nations. The IPCC and its working groups, with hundreds of members, authors, reviewers and editors from nations throughout the world is a model of the efforts that can be marshalled to address problems at a global scale. Scientific understanding and collaboration are proving

A)



B) Baltic Sea cod, 2014, severe hypoxia

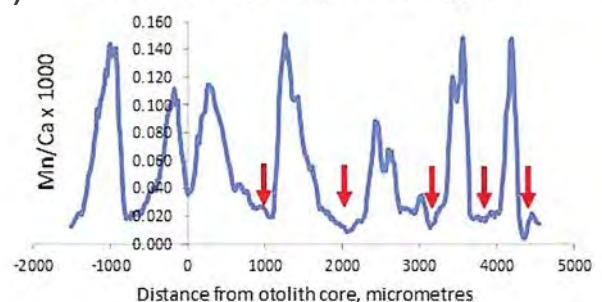


Figure 11.12 (A) Otolith cross section and (B) Mn/Ca ratios of a Baltic Sea cod, *Gadus morhua*. The peaks in Mn/Ca on the graph correspond to seasonal hypoxia exposure. Baltic cod exposed to increasing amounts of hypoxia, as shown in the chemical signature in their otoliths, experience a decline in body size (Limburg & Casini, 2018). The incidence of hypoxia exposure in these fish is increasing over time, with greater exposure during the current decade (2010s). Foregone biomass (losses from hypoxia exposure) is yet to be calculated for the entire population, but for three-year-old cod, those exposed to high levels of hypoxia (> 75% of the year), weight is estimated to be 64% lower than for cod residing in low levels of hypoxia (< 25% of the year). Black arrows on the otolith photos show the tracks of a laser that was used to sample the otoliths for the chemical analyses. Red arrows on (B) indicate wintertime minima.

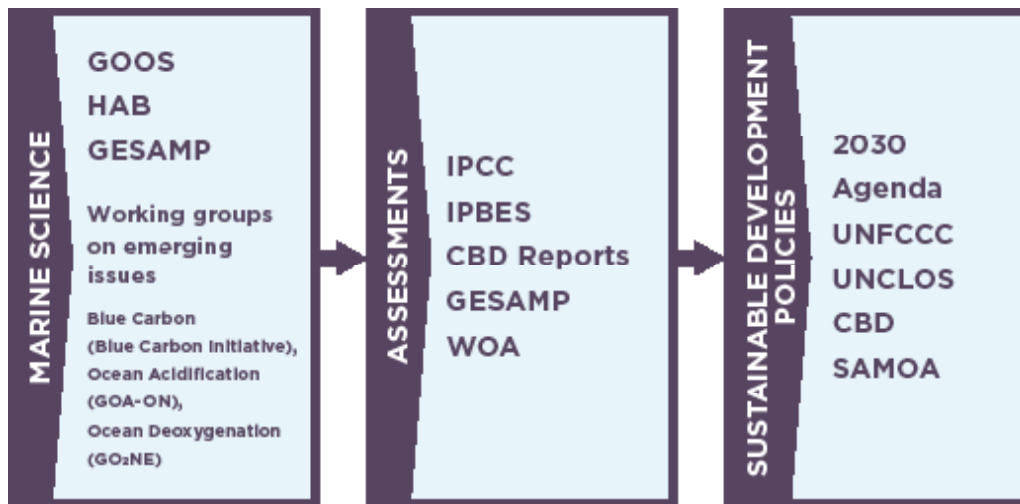


Figure 11.13 From Science to Policy. Examples of the different stages and instruments involved in the marine science-policy interface, starting from marine science, to assessments, to sustainable development policies. Acronyms and abbreviations not defined elsewhere: IPCC = Intergovernmental Panel on Climate Change; IPBES = Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services; CBD = Convention on Biological Diversity; UNCLOS = United Nations Convention on the Law of the Sea; SAMOA = SIDS [Small Island Developing States] Accelerated Modalities of Action pathway.

critical to identifying a wide range of ocean problems and their solutions from the accumulation of plastic in the ocean (e.g. GESAMP WG 40 - Group of Experts on the Scientific Aspects of Marine Environmental Protection Working Group focusing on sources, fate and effects of plastics and micro-plastics in the marine environment) to the implementation of harmful algae blooms warning systems (IOC-UNESCO, 2017).

The science-policy interface is especially important as climate and ocean change increasingly affect ocean health and marine resources. In response to this need, UN organizations and NGOs coordinate interdisciplinary scientific working groups and programmes, focusing on emerging issues, important to ocean and human health, including ocean acidification (Global Ocean Acidification Observing Network (GOA-ON)), coastal Blue Carbon ecosystems (the Blue Carbon Initiative), and Harmful Algae Blooms (IOC HAB Programme). The information and findings compiled and obtained by these working groups contribute directly to global assessments, including the Intergovernmental Panel for Climate Change and the World Ocean Assessment, which in turn are the basis for global sustainable development policies, such as the 2030 Agenda for Sustainable Development (UN General Assembly, 2015) and the UNFCCC (UN General Assembly, 1994) (Figure 11.13)

In 2016 the IOC-UNESCO established the 'Global Ocean Oxygen Network' (GO₂NE) expert group as the first international body with a primary focus on the

causes and impacts of decreasing oxygen levels on the ocean, including its coastal waters (IOC/EC-XLIX/2 Annex 6, IOC EC-XLIX, Dec. 4.1 (III)). The charge of GO₂NE includes the science of physical, chemical and biological processes, marine and human life, and the ecological goods and services the ocean provides. GO₂NE aims to provide needed scientific input, facilitate communication among different stakeholders, and help support decision makers to take measures required to stem increasing deoxygenation at local, regional and global scales. This global effort is expanding to include focused working groups, such as the regional group the Western Pacific Ocean Oxygen Network (WESTPAC O₂NE), and to work on important topics collaboratively with other international scientific working groups (e.g. the International Ocean Carbon Coordination Project working group VOICE - Variability in the Oxycline and Its Impacts on the Ecosystem, and the Scientific Committee on Oceanic Research (SCOR) working group 155 focusing on Eastern Boundary Upwelling Systems (EBUS): diversity, coupled dynamics and sensitivity to climate change). These groups are indispensable in the identification of specific steps to slow and reverse deoxygenation and its effects, which vary among locations depending on the cause of the problem, and co-occurring stressors.

Scientific cooperation will be critical to ensure that ocean oxygen levels are sufficient to continue to support vital marine ecosystem services, and to manage ocean resources in a sustainable manner (Agenda 2030, Sustainable Development GOAL 14)

Box 11.1. Further progress in the science of ocean deoxygenation is needed to better predict the patterns and consequences of ocean oxygen decline, and to inform policies and technological solutions to reduce further decline (GO₂NE, 2018). Critical areas include:

- Expanding oxygen observations in the open ocean and coastal waters, including through integration with existing programmes and networks, targeting regions where more data will improve assessment of the current status and patterns of oxygen change.
- Experiments and observations to improve understanding of critical mechanisms that control the patterns and effects of oxygen declines.
- Numerical models with improved ability to predict current effects of low oxygen and other stressors, future changes in oxygen levels, and potential benefits of management options at global, regional and local scales.
- Assessments of effects on human economies and societies, especially where oxygen declines threaten fisheries, aquaculture and livelihoods.
- Development of a data management system, with rigorous quality control and leadership by a globally recognized oceanography data centre that provides open access for use in science and policy.
- Continued improvement of oxygen monitoring equipment, including sensors that accurately measure ultra-low oxygen concentrations and low-cost sensors that will make more extensive monitoring in undersampled coastal waters possible.
- Capacity building in coastal areas of the developing world for observations on core oceanographic parameters, especially oxygen, and on the impact of deoxygenation on fisheries and biodiversity, will have to be given high priority.

(Voluntary Commitment GO₂NE: #OceanAction15767: Enhancing global ocean oxygen science from local seas to the global ocean to preserve ocean health and human well-being). Focused working groups will help to broaden understanding and contribute to the underlying science regarding the influence of nutrient pollution on increasing deoxygenation (SDG 14.1). They support the implementation of sustainable fisheries (SDG 14.7), and aim to improve the knowledge of how reduced oxygen levels are linked to additional stressors, such as harmful algal blooms, ocean acidification and global warming, that combine to reduce marine ecosystem resilience and ecosystem services (SDG 14.3).

11.6 Improving predictions of future patterns and effects

Solutions to ocean deoxygenation, and development of adaptation strategies in its presence, depend on sound and sufficient science. As this report shows, great strides have been made in understanding the causes, consequences and future patterns of ocean oxygen decline. But there are still great challenges in projecting the current information to the large temporal and spatial scales needed to implement sound policies and to improve predictions of future conditions and impacts on human welfare (Breitburg et al., 2018) (Box 11.1.).

Natural and social science advances are also critical to increasing the recognition of ocean deoxygenation as an important consequence of human alterations to our global environment. To date, little direct evaluation of the ecosystem services threatened or already impaired by deoxygenation has occurred. Yet these evaluation exercises could readily be performed. A pluralistic approach to ecosystem services valuation, adopting multiple metrics, will provide a more complete picture of services at risk (Limburg et al., 2002).

11.7 Concluding comments: The way forward

Curtailling ocean oxygen loss due to climate change, restoring oxygen lost as a result of excess nutrient discharges, and minimizing negative effects of deoxygenation now and in the future, require steps that are straightforward in their simplest expression, but difficult, and costly to put into practice. Ultimately, however, the societal cost of inaction is too great to ignore. The path towards improved oxygenation of the earth's ocean and coastal waters requires:

- Reduction of greenhouse gas emissions that cause atmospheric and ocean warming.
- Reduction of nutrient inputs to the ocean that exacerbate oxygen loss in coastal waters.

- Inclusion of climate change effects in developing nutrient reduction strategies.
- Alleviation of anthropogenic stressors (e.g. pollution, overfishing, trawling or mining/drilling disturbance) that threaten resilience and increase vulnerability of marine ecosystems to deoxygenation.
- Adoption and implementation of marine spatial planning and fisheries management strategies that identify deoxygenation vulnerabilities and protect species and habitats.
- Recognition of ocean deoxygenation as one of multiple climate-induced stressors.
- Unification of research, management and policy actions across coasts and the open ocean, across biology, geochemistry, and physics, and the social sciences, across problems of warming, acidification and deoxygenation, and across academic, industry, government and regulatory sectors (IOC, 2018).

Under the Paris Agreement nations declared their intent through nationally determined contributions (NDCs). While 70% of the 161 nations submitting NDCs recognized the importance of the ocean for climate mitigation and most recognized ocean warming, only one made the link to ocean deoxygenation (Gallo et al., 2017), suggesting the need for much stronger communication with international policy makers such as delegates to the UNFCCC. Our hope is that this report represents a step towards greater recognition of ocean deoxygenation as an environmental, societal and economic problem, and contributes to solutions.

11.8 References

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