SUMMARY FOR POLICY MAKERS

The Ocean is Losing its Breath

Declining Oxygen in the World's Ocean and Coastal Waters

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The Ocean is Losing its Breath

Declining Oxygen in the World's Ocean and Coastal Waters

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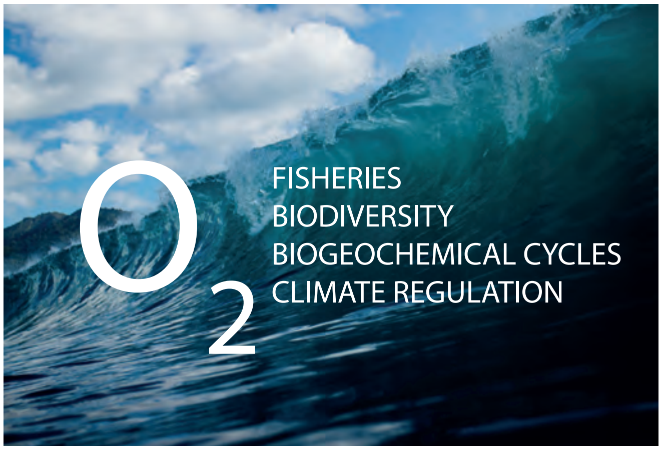
Declining oxygen in the world's oceans: 15 things to know

1. Oxygen is critical to the health of the ocean. It structures aquatic ecosystems and is a fundamental requirement for marine life from the intertidal zone to the greatest depths of the ocean.
2. Oxygen is declining in the ocean. Since the 1960s, the area of low oxygen water in the open ocean has increased by 4.5 million km^2, and over 500 low oxygen sites have been identified in estuaries and other coastal water bodies.
3. Human activities are a major cause of oxygen decline in both the open ocean and coastal waters. Burning of fossil fuels and discharges from agriculture and human waste, which result in climate change and increased nitrogen and phosphorus inputs, are the primary causes.
4. Deoxygenation (a decline in oxygen) occurs when oxygen in water is used up at a faster rate than it is replenished. Both warming and nutrients increase microbial consumption of oxygen. Warming also reduces the supply of oxygen to the open ocean and coastal waters by increasing stratification and decreasing the solubility of oxygen in water.
5. Dense aquaculture can contribute to deoxygenation by increasing oxygen used for respiration by both the farmed animals and by microbes that decompose their excess food and faeces.
6. Insufficient oxygen reduces growth, increases disease, alters behaviour and increases mortality of marine animals, including finfish and shellfish. The quality and quantity of habitat for economically and ecologically important species is reduced as oxygen declines.
7. Finfish and crustacean aquaculture can be particularly susceptible to deoxygenation because animals are constrained in nets or other structures and cannot escape to highly-oxygenated water masses.
8. Deoxygenation affects marine biogeochemical cycles; phosphorus availability, hydrogen sulphide production and micronutrients are affected.
9. Deoxygenation may also contribute to climate change through its effects on the nitrogen cycle. When oxygen is insufficient for aerobic respiration, microbes conduct denitrification to obtain energy. This produces N_2O – a powerful greenhouse gas – as well as N_2, which is inert and makes up most of the earth's atmosphere.
10. The problem of deoxygenation is predicted to worsen in the coming years. Global warming is expected to worsen deoxygenation during the twenty-first century due to continued greenhouse gas emissions. The global discharge of nitrogen and phosphorus to coastal waters may increase in many regions of the world as human populations and economies grow. It is expected that many areas will experience more severe and prolonged hypoxia than at present under the same nutrient loads.
11. Slowing and reversing deoxygenation will require reducing greenhouse gas and black carbon emissions globally and reducing nutrient discharges that reach coastal waters. Concerted international efforts can reduce carbon emissions.
12. The decline in oxygen in the ocean is not happening in isolation. At the same time, food webs are disturbed due to overfishing and physical destruction of habitats, and waters are getting warmer, more acidic, and experience higher nutrient loads. Management of marine resources will be most effective if the cumulative effects of human activities on marine ecosystems are considered.
13. More accurate predictions of ocean deoxygenation, as well as improved understanding of its causes, consequences and solutions, require expanding ocean oxygen observation, long-term and multi-stressor experimental studies, and numerical modelling.
14. Accurate oxygen measurements with appropriate temporal resolution and adequate spatial coverage in the marine environment are needed to document the current status of our ocean, to track changing conditions, to build and validate models that can project future oxygen levels, and to develop strategies to slow and reverse deoxygenation.
15. Steps required to restore the ocean's breath can directly benefit human health and well-being. Sewage treatment and limiting global warming, for example, have societal benefits that extend beyond improving oxygen in our ocean and coastal waters.

Deoxygenation occurs when processes that decrease oxygen exceed those that enrich water in oxygen. Both excess nutrients and increasing temperatures shift the balance between oxygen reduction and addition, and worsen deoxygenation.



2

The problem of declining oxygen in the ocean

Oxygen is critical to the health of the ocean. It structures aquatic ecosystems, impacts the biogeochemical cycling of carbon, nitrogen and other key elements, and is a fundamental requirement for marine life from the intertidal zone to the greatest depths of the ocean.[1]

Nearly all ocean organisms larger than a single cell, and even many microbes, require oxygen for survival. They depend on oxygen in the water in the same way that animals on land depend on oxygen in the air. A reduction in ambient oxygen below required levels causes physiological stress, behavioural changes and ultimately death of key marine species. 'If you can't breathe, nothing else matters'.[2]

Climate change is decreasing oxygen concentrations in the open ocean. The combined effects of climate change and excess nutrients (nitrogen and phosphorus from sources such as agricultural runoff and human waste) are leading to oxygen loss in coastal marine systems and semi-enclosed seas that are strongly influenced by their watershed. Global and regional models predict that the oxygen content of marine waters will continue to decline as atmospheric and ocean temperatures rise and human population size increases. Ocean health is expected to decline and human well-being may ultimately suffer (Fig. 1).

This technical brief presents a summary of scientific experiments, observations and numerical models addressing the following questions: How has the oxygen content in the open ocean and coastal waters changed over the past century and through geological time? What are the mechanisms behind this oxygen decline? How is ocean oxygen content predicted to change over the rest of the twenty-first century? What are the consequences of low and declining oxygen concentrations in the marine environment?

1 See the recent review paper written by the IOC-UNESCO GO_2NE expert group that was published in Science for a more technical treatment of this issue (Breitburg et al., 2018).

2 Motto formerly used by the American Lung Association.

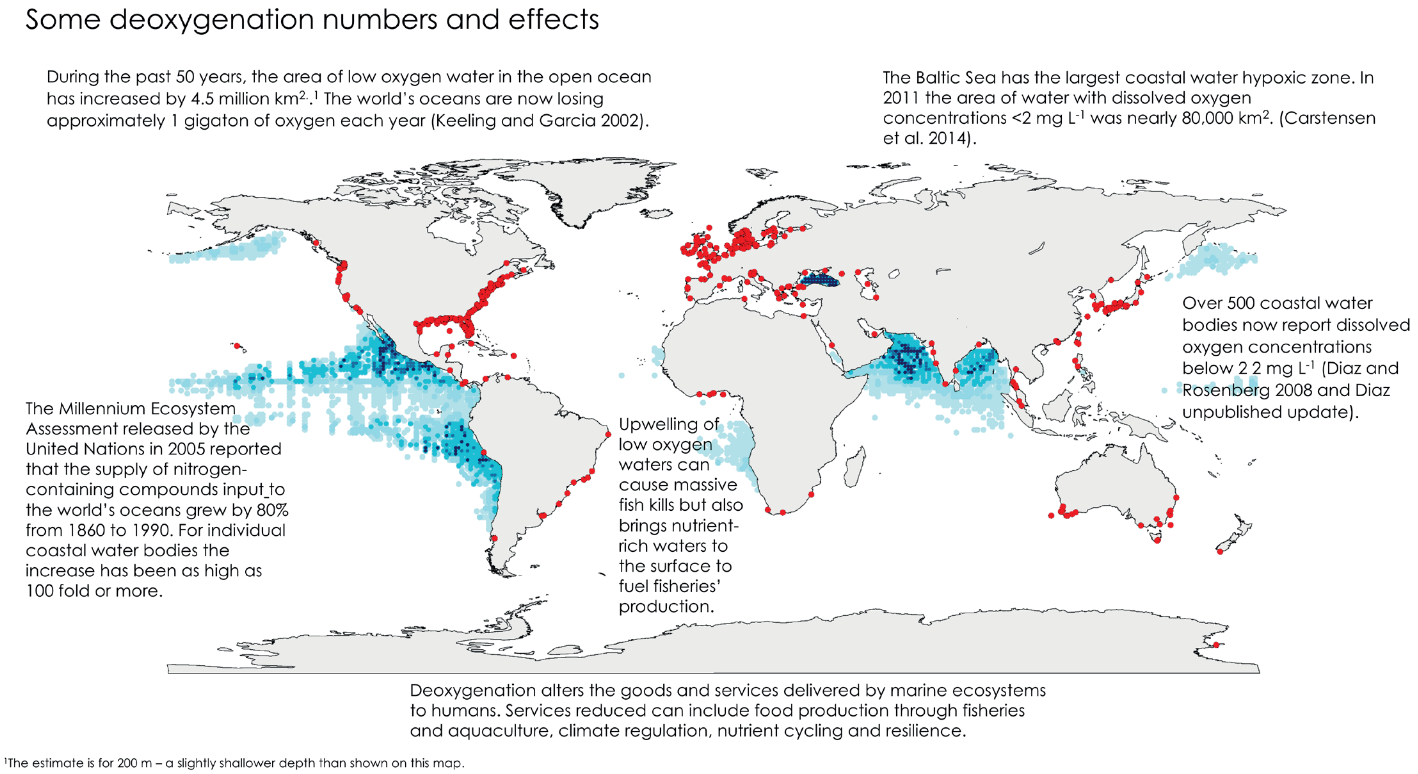


Figure 1. OMZs (blue) and areas with coastal hypoxia (red) in the world's ocean (adapted after Isensee et al., 2015; Breitburg et al., 2018; including oxygen effects from Keeling and Garcia, 2002; Diaz and Rosenberg, 2008; Carstensen et al., 2014).

Box 1. Definitions

Deoxygenation: A decline in the oxygen content of oceanic and coastal waters. Deoxygenation is a feature of our changing ocean.

Well oxygenated water: Water with oxygen concentrations sufficient to support oxygen-requiring biological and biogeochemical processes.

Hypoxia: The medical term hypoxia describes a condition in which the body or a part of the body is deprived of adequate oxygen. Similarly, all or a part of a water body can be deprived of adequate oxygen. There is no single oxygen concentration that serves as a definition of hypoxia because resident organisms and ecological processes vary in their oxygen requirements, and water bodies vary in their natural condition. Most numerical criteria are based on conditions that lead to sublethal biological effects: 2 mg L^{-1} O_2 (=1.4 ml L^{-1} = 63 µmol L^{-1}) is often used as a threshold, but many organisms are negatively affected at higher or lower oxygen concentrations.

Anoxia: The absence of oxygen. Under anoxic conditions, respiration of organic matter switches to sulfate reduction, and eventually to methane reduction. Traces of oxygen at nanomolar levels can inhibit anaerobic processes, such as denitrification, the conversion of nitrate (NO_3^-) into gaseous nitrogen (N_2) (Bristow et al., 2017).

Oxygen minimum zones (OMZs): OMZs are the places in the world ocean where oxygen saturation in the water column is at its lowest. The most intense OMZs have oxygen concentrations below about 5% saturation (<20 µmol L^{-1}), which are oxygen levels often used to delineate severe OMZs. In the open ocean, OMZs occur at depths of about 100–1,000 m; in deep basins of semi-enclosed seas, they can extend to the bottom.

Low oxygen areas: For simplicity in this document, we refer collectively to open ocean, coastal waters and semi-enclosed seas with oxygen conditions that are deficient for oxygen requiring biological and biogeochemical processes as 'low oxygen areas'. We avoid the phrase 'dead zone' because of the importance of microbial life in these habitats.

Measurement units: 1 mg L^{-1} (milligram per litre) = 0.7 ml L^{-1} (millilitres per litre) = 32 µmol L^{-1} (micromoles per litre) = 31 µmol kg^{-1} micromoles per kilogram) = 32,000 nmol L^{-1} (nanomoles per litre).

20°C seawater in equilibrium with the atmosphere (i.e. 100% air saturation) contains 7.4 mg dissolved oxygen per litre of water.

Marine water bodies: In this report, we refer to coastal waters as systems that are strongly influenced by their watershed and the open ocean as waters in which such influences are secondary. Coastal waters include systems such as estuaries, coastal lagoons and the coastal and shelf areas of semi-enclosed seas. The terms ocean and marine system are intended to be inclusive and refer to all coastal waters, semi-enclosed seas and the open ocean.

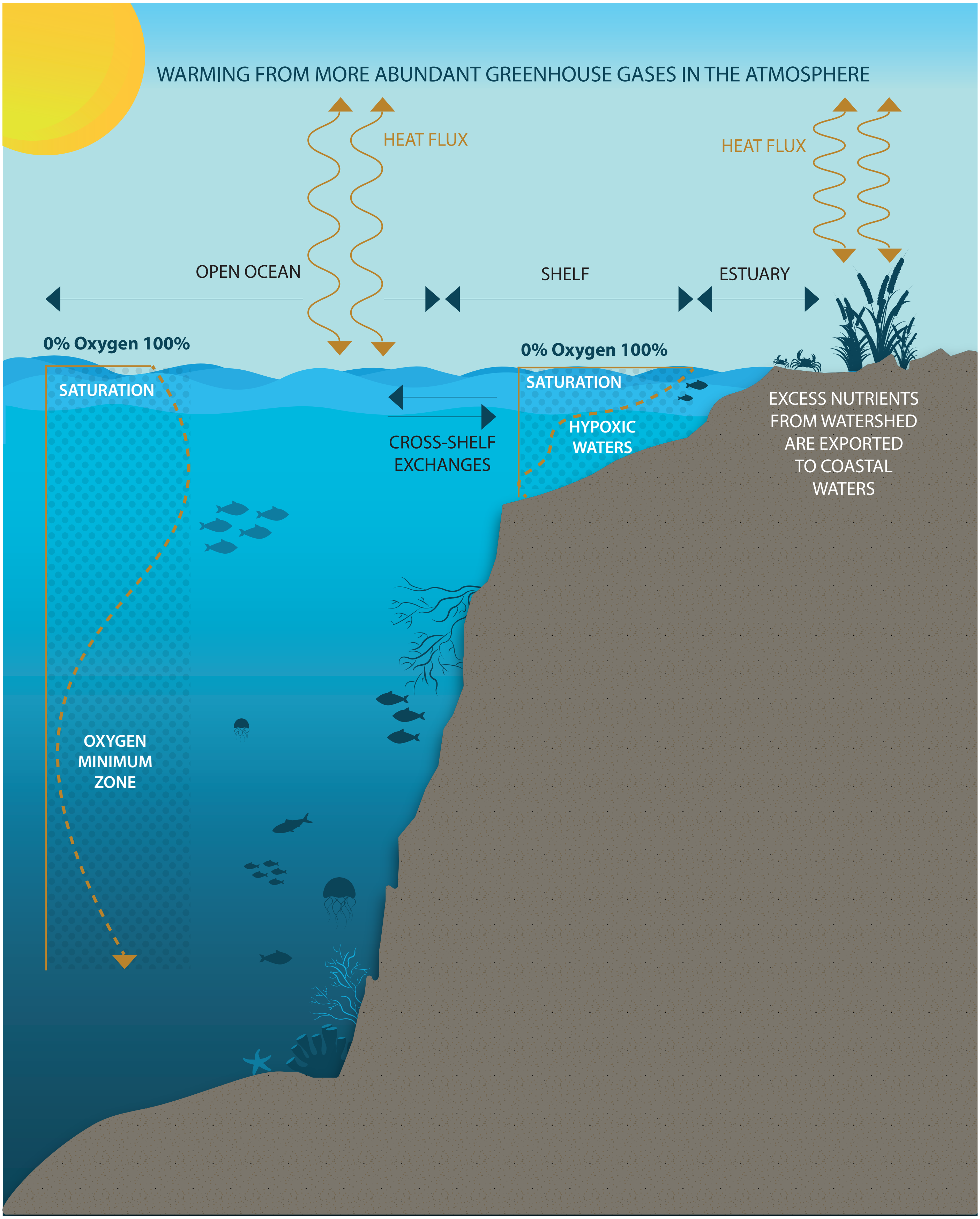


Figure 2. Deoxygenation in the ocean – causes and consequences (adapted from Denis Gilbert).

3

Human activities are causing oxygen declines in the open ocean and coastal waters

Low dissolved oxygen concentrations occur naturally in some habitats, including OMZs in the open ocean and deep basins of semi-enclosed seas, coastal upwelling zones and systems like deep fjords with limited tidal exchange (Box 2). The spatial extent, severity or duration of low oxygen events have increased in many of these areas, however, and low oxygen now occurs in water bodies that historically had high oxygen concentrations. Since the 1960s, over 500 hypoxic coastal water bodies have been identified (Diaz and Rosenberg, 2008; Isensee et al., 2015). The ocean is currently losing about 1.5–3.1 gigatons (1.5–3.1 billion tons) of oxygen each year (Keeling and Garcia, 2002; Schmidtko et al., 2017).

3.1 Excess nutrients

Nutrients – primarily nitrogen and phosphorus – from human waste, agriculture and industry, fertilize coastal waters. In a process called eutrophication, these nutrients stimulate photosynthesis, which increases the growth of algae and other organisms (Fig. 5). This results in more organic material sinking into deep water and to the sediment. Increased respiration by animals and many microbes eating or decomposing this organic material uses oxygen. The consequence can be oxygen concentrations that are far lower than those that would occur without human influence, and in some cases a complete lack of oxygen in bottom waters (Fig. 6). Strong density differences between surface and bottom waters (referred to as 'stratification'), due to temperature and salinity, can isolate bottom waters from the atmosphere and reduce or prevent re-oxygenation through ventilation. Semi-enclosed seas (e.g. the Black and Baltic Sea) can be sensitive to eutrophication and related deoxygenation because of their characteristic limited water exchange with the open ocean, and low ventilation rates.

The global discharge of nitrogen and phosphorus to coastal waters is expected to continue to increase in coming decades as populations and economies grow (Reed and Harrison, 2016), potentially increasing the risk of harmful algal blooms in coastal marine ecosystems (Seitzinger et al., 2010). These blooms can result in enormous amounts of organic matter sinking to the sea floor, fuelling further deoxygenation. Shifts in nutrient ratios can also influence trophic dynamics in coastal waters (Turner et al., 1998).

Some areas have made tremendous strides in reversing deoxygenation, but the problem persists or continues to worsen in many estuaries. Historical records of places like the Delaware River Estuary in the United States and the Thames River in the United Kingdom show that a change from the release of raw sewage to primary treated sewage can improve dissolved oxygen concentrations (Sharp, 2010). Thus, measures that are directly beneficial to human health can also reduce the problem of low oxygen in coastal waters.

Box 2. Natural low oxygen systems: OMZs and upwelling.

OMZs with lowest oxygen levels (shown in magenta in Fig. 3) form in the ocean adjacent to continents, generally at depths of 100–1,000 m, and occur in deep basins of semi-enclosed seas such as the Black and Baltic seas. Deep, oxygen-depleted waters can be lifted towards the surface and near shore, affecting shallow ecosystems in a process called 'upwelling' (Fig. 4).

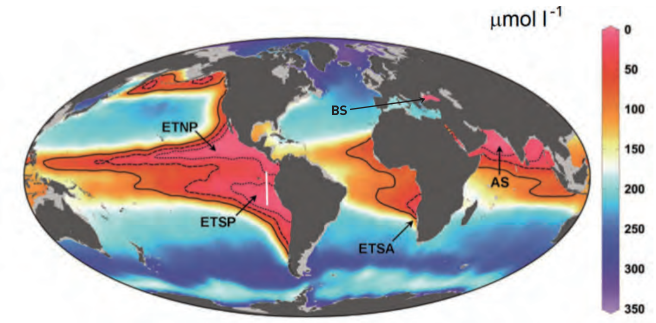


Figure 3. Dissolved oxygen concentrations at 300 m depth in the open ocean. Oxygen can be low enough to limit biological and ecological processes in large areas of the ocean (e.g. areas shown in red and orange, as well as magenta OMZs). ETNP, eastern tropical North Pacific; ETSP, eastern tropical South Pacific; ETSA, eastern tropical South Atlantic; AS, Arabian Sea; BS, Black Sea. (Figure adapted from Kavelage 2012).

Major upwelling zones that can bring OMZ waters to the surface occur on the eastern side of the Atlantic and Pacific Oceans and are referred to as Eastern Boundary Upwelling Systems but upwelling also happens along other coasts throughout the world and may, in certain circumstances, bring low oxygen waters to the surface, e.g. in the Indian Ocean. Nutrients transported to the surface by upwelling support some of the most productive fisheries in the world. During upwelling events along some coasts, however, hypoxic and anoxic waters, and sometimes H_2S produced under anoxic conditions, can kill fish and other animals. In the waters along the Namibian coast of south-western Africa, for example, low oxygen events can cover 20,000 km^2 and last for several weeks, with severe ecosystem consequences (Weeks et al., 2002; Lavik et al., 2009).

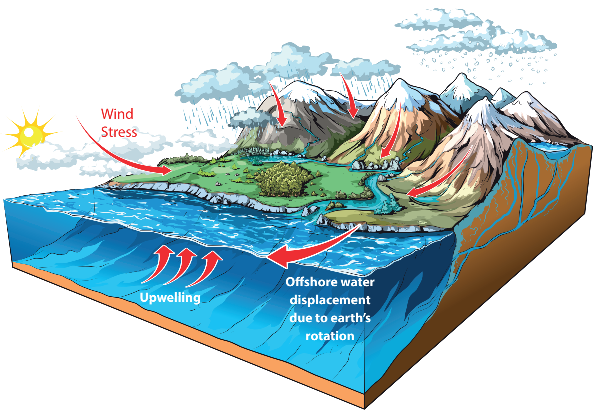


Figure 4. Coastal upwelling. When winds blow parallel to the coastline, the earth's rotation can move surface waters offshore. In response, cold, oxygen-depleted, nutrient-rich deep water is pulled towards the surface.

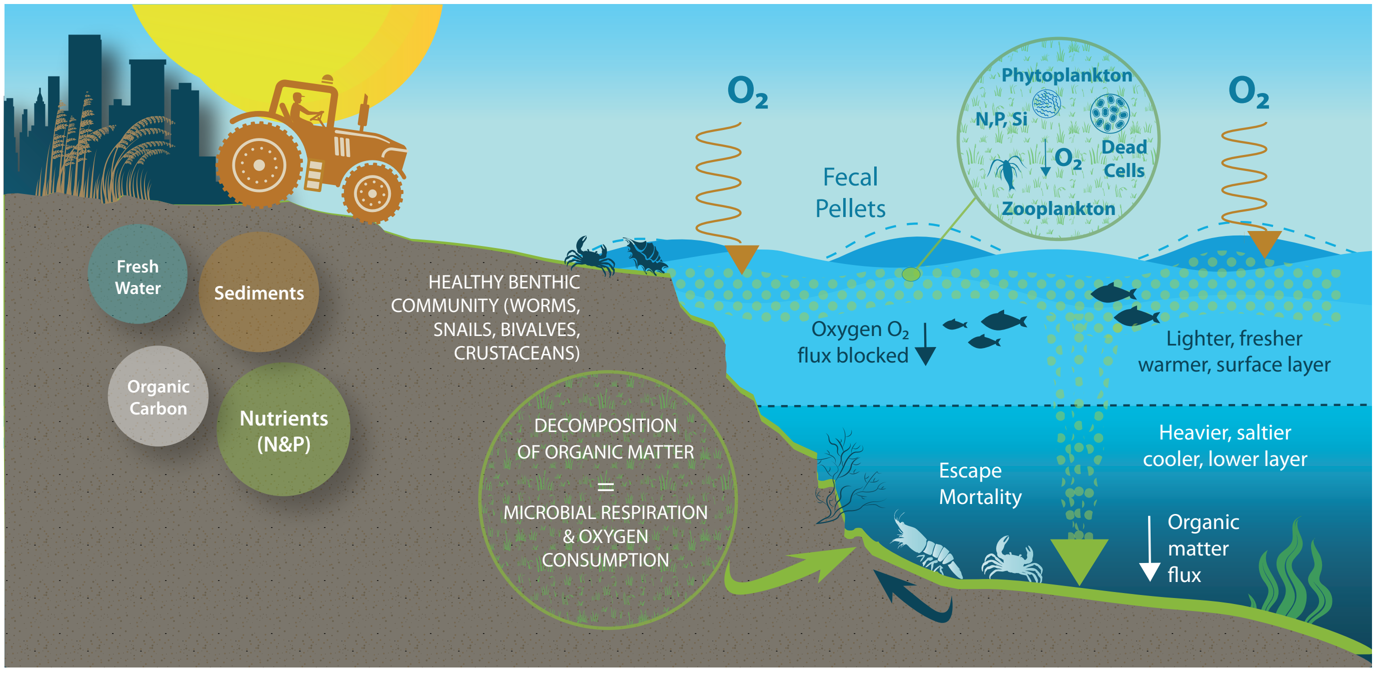


Figure 5. Impacts of excess nutrients (eutrophication) on ocean oxygen. (Figure modified from https://upload.wikimedia.org/wikipedia/commons/d/dd/Scheme_eutrophication-en.svg)

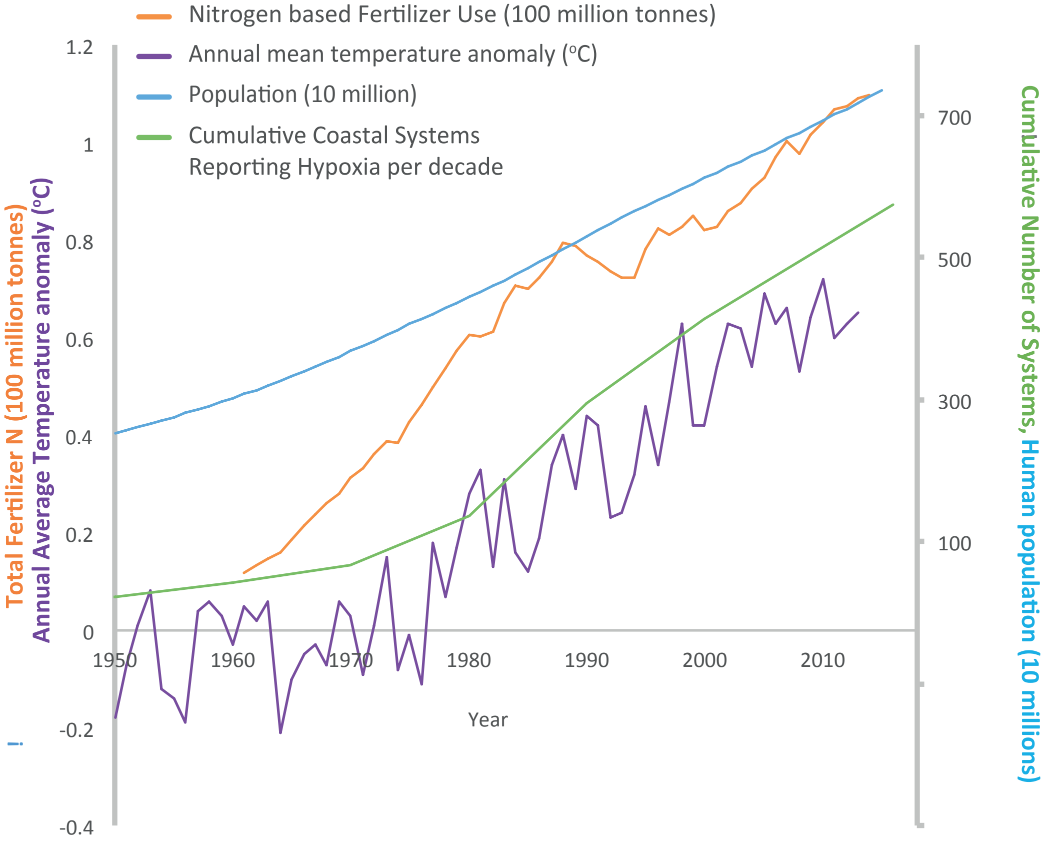


Figure 6. The number of water bodies in which hypoxia associated with eutrophication has been reported has increased exponentially since the 1960s; hundreds of systems worldwide have been reported with oxygen concentrations <2 mg L^{-1}, lasting from hours to years. The increasing severity and prevalence of this problem reflects the invention and increasing use of synthetic fertilizers and the growing human population. Global fertilizer use shown includes data for fertilizers with nitrogen, phosphate and potash. (Fertilizer use data: Earth Policy Institute, 2014, IFADATA, 2016; temperature anomaly data: GISS; cumulative number of hypoxic systems: Diaz and Rosenberg, 2008; Isensee et al., 2015; 2015 from Diaz unpublished data; global human population data: UNDESA, 2010).

Box 3. Management actions can greatly improve oxygen conditions, but some of the largest low oxygen areas remain.

Thames River Estuary

The low oxygen problem in the upper Thames River Estuary (United Kingdom) was greatly improved by management actions that reduced raw sewage and nutrients entering the river. Observations showed that conditions improved from anoxia (zero oxygen) to >10% oxygen saturation (Fig. 7) and fish species richness increased 10-fold through implementation of primary sewage treatment and offshore shipping of sewage sludge (Fig. 8; Tinsley, 1998). Additional steps are now in progress to improve remaining problems related to storm sewage overflows (National Audit Office, 2017).

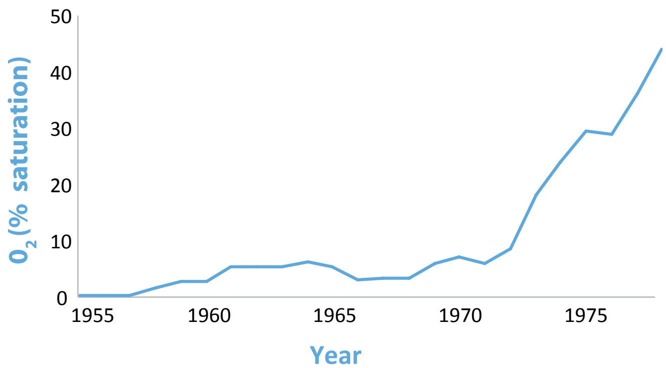


Figure 7. Recovery of oxygen saturation in the upper Thames River Estuary (UK). Source: adapted from Kemp et al., 2009.

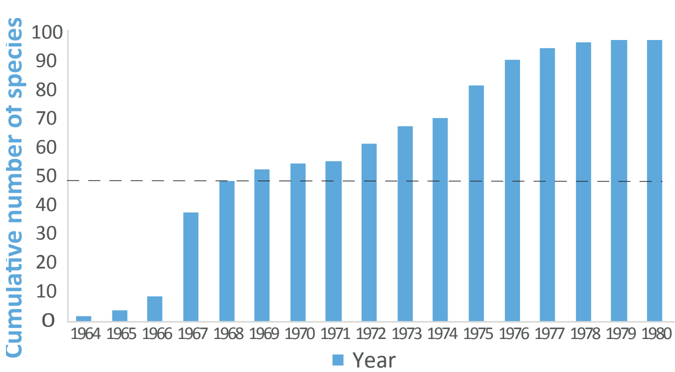


Figure 8. The cumulative number of fish species recorded in the Thames between Kew and Gravesend from 1964 to 1980. Source: adapted from Andrews, 1984.

Baltic Sea

In contrast, low oxygen in the Baltic Sea has expanded. Wide areas of bottom water become hypoxic seasonally along with deep basins that remain hypoxic or anoxic for years to decades. And though management actions have been put in place to reduce nutrient loads, they have not been sufficient to substantially reduce or eliminate low oxygen (Figs. 9, 10; Carstensen et al., 2014).

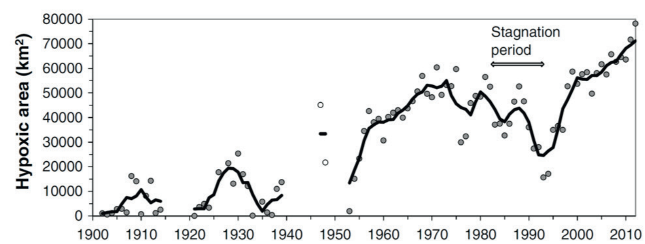


Figure 9. Sea floor area covered by water with <2 mg L^{-1} dissolved oxygen from 1900 to 2011 in the Baltic Sea. © National Academy of Sciences, Carstensen et al., 2014.

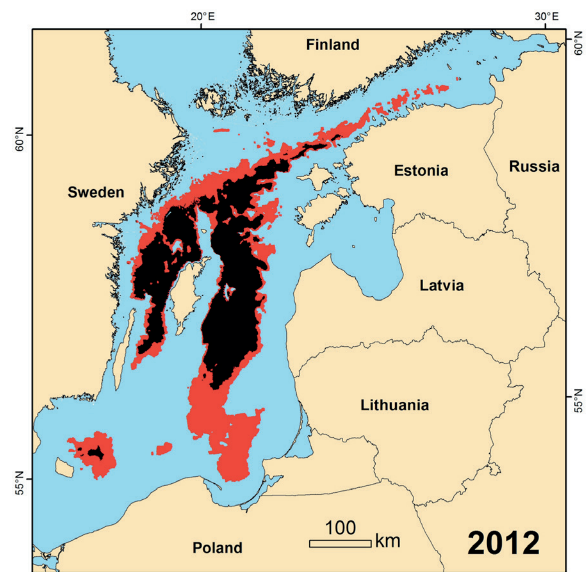


Figure 10. Estimated spatial extent of hypoxia <2 mg L^{-1} (red) and anoxia (black) during 2012 in the Baltic Sea. © National Academy of Sciences, Carstensen et al., 2014.

3.2 Climate change

Over the past 50 years, the open ocean lost approximately 0.5–1 petamoles of oxygen per decade, which translates into 1–2%, or 2.4–4.8 petamoles (77–154 billion tons of O_2) less oxygen in our current ocean than five decades ago (e.g. Bopp et al., 2013; Schmidtko et al., 2017). The result is the expansion of OMZs by an area about the size of the European Union (4.5 million km^2, based on water with <70 µmol kg^{-1} oxygen at 200 m depth) (Stramma et al., 2010), and a quadrupling of the volume of anoxic water completely devoid of oxygen over the same period (Schmidtko et al., 2017). Climate change caused by increasing anthropogenic emissions of greenhouse gases contributes to this decline (Fig. 11; Stramma et al., 2008; Keeling et al., 2010; Helm et al., 2011; Stramma et al., 2012; Schmidtko et al., 2017). Regional variation in the patterns of oxygen change has also been influenced by natural climate variability, nutrients and aerosol pollution (Ito, 2016; Levin, 2018).

Climate change is predicted to worsen deoxygenation during the twenty-first century, even under future climate scenarios that assume greatly reduced greenhouse gas emissions (i.e. RCP 2.6, Fig. 12). The rising atmospheric and seawater temperatures reduce the mixing of atmospheric oxygen into mid-depth and deep parts of the ocean by increasing density differences in the water column, decreasing vertical mixing and altering ocean circulation patterns. Warmer water holds less oxygen, so oxygen concentrations are declining even near the ocean's surface.

However current models do not reproduce observed patterns for oxygen changes in the ocean's tropical thermocline and generally simulate only about half the oceanic oxygen loss inferred from observations (Oschlies et al., 2018). Models therefore need to evolve in order to improve the representation of fine scale ocean-atmosphere interactions and ocean-sediment coupling, mesoscale activities (Bettencourt et al., 2015), the impact of deoxygenation and acidification on primary production, vertical export and biogeochemical cycles as well as the possibility of transition, adaptation, and/or extinction of living organisms.

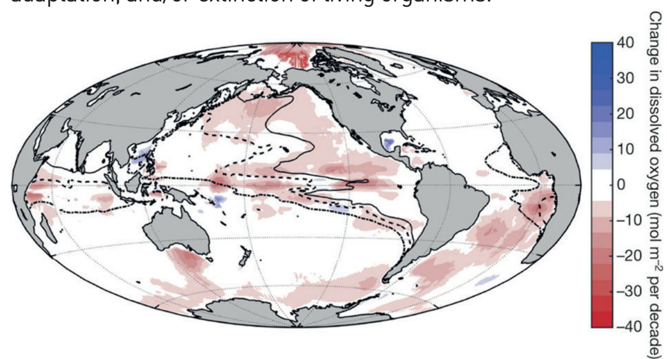


Figure 11. Change in dissolved oxygen per decade since 1960 (colour coded) from surface waters to the ocean bottom. Lines indicate boundaries of OMZs; dashed-dotted lines indicate regions with less than 80 µmol kg^{-1} oxygen anywhere within the water column. Source: Schmidtko et al., 2017.

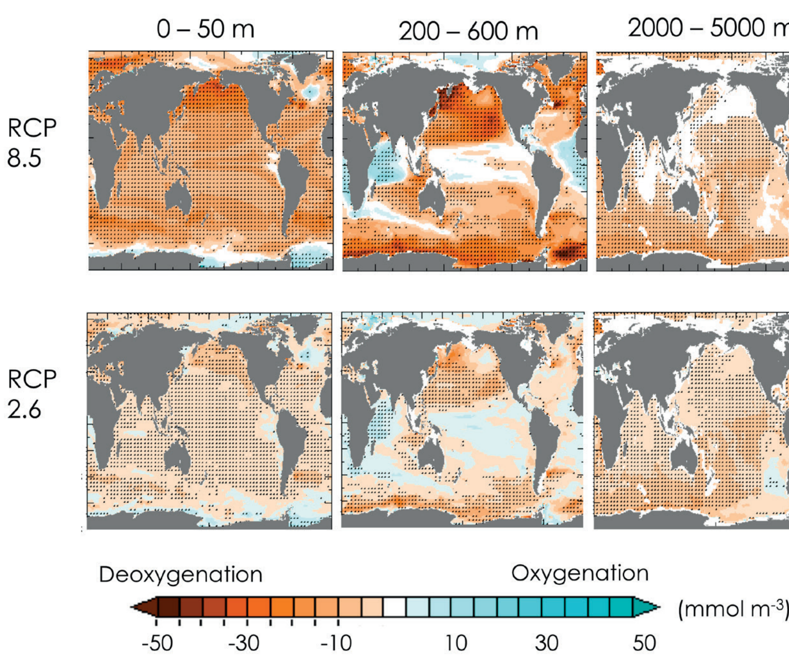


Figure 12. Projected change in dissolved oxygen concentrations between the 1990s and 2090s predicted by an ensemble of models run under the RCP8.5 ('business as usual') and RCP2.6 scenarios (based on Bopp et al., 2013; figures provided by L. Bopp). Models generally agree that oxygen in both the surface layer and the deep ocean will decline throughout the globe under both emission levels. There is large uncertainty in the magnitude, and in mid-latitudes, even the direction of change in oxygen content at 200–600 m depths, including many low latitude OMZ regions. Improving the consistency of these projections is critical because of the large role the OMZs play in global biogeochemical cycles and the ecology of the oceans as a whole. A refinement of current model formulations and improved resolution, together with improved observation techniques, are needed to improve prediction of the oxygen content of the future ocean. Note: Stippling in figures indicates that 80% of models agree on the direction, but not necessarily the magnitude, of change.

Models predict that warming will strengthen winds that favour upwelling and the resulting transport of deeper waters onto upper slope and shelf environments in some coastal areas (Sydeman et al., 2014; Feely et al., 2008), especially at high latitudes within upwelling systems that form along the eastern boundary of ocean basins (Wang et al., 2015). The predicted magnitude and direction of change is not uniform, however, either within individual large upwelling systems or among different systems. Upwelling in the southern Humboldt, southern Benguela and northern Canary Eastern Boundary upwelling systems is predicted to increase in both duration and intensity by the end of the twenty-first century (Wang et al., 2015).

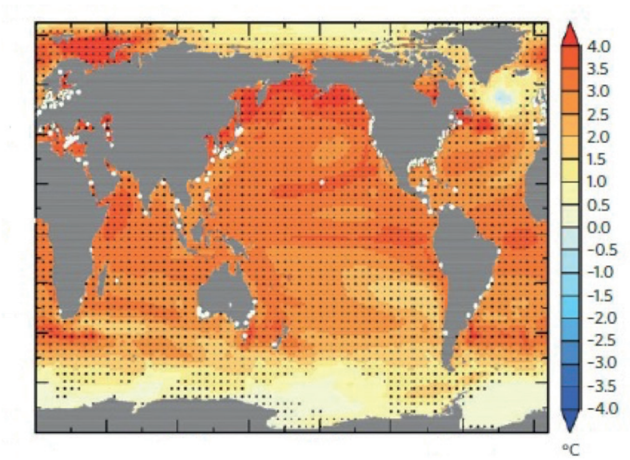


Figure 13. Most coastal hypoxic zones (shown in white) occur in regions with a predicted end-of-century water temperature increase of >2°C (Altieri and Gedan, 2015). Figure from Levin and Breitburg (2015) showing projected changes in water temperature by the 2090s under Bopp et al. (2013) RCP8.5 model projections.

Increasing temperatures are expected to worsen the problem of deoxygenation in coastal waters throughout the world (white dots in Fig. 13; Rabalais et al., 2014; Altieri and Gedan, 2015). Higher seawater temperatures are also extending the duration of seasonal hypoxia in estuaries and coastal waters. Geographic variation in these patterns and precipitation is likely (Rabalais et al., 2014; Sinha et al., 2017), emphasizing the need to incorporate local climate predictions in projections of deoxygenation. Some regions will experience reduced precipitation in a warmer world, which could reduce nutrients discharged to coastal waters. Shifts in current patterns may also reduce water temperatures in some locations.

Box 4. Combined environmental cost of hypoxia and nitrogen loads.

Rising ocean temperatures can worsen oxygen depletion and make restoration more difficult. Nutrient reduction policies can contribute to solutions by decreasing oxygen depletion. However, these policies will only have a significant effect on combating hypoxia if they account for realistic future climate scenarios.

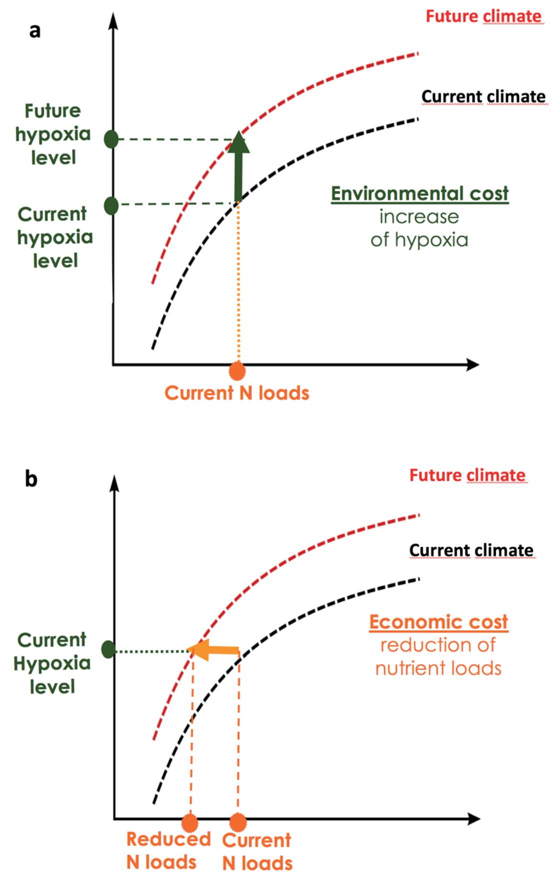


Figure 14. In a warming world, coastal waters in many areas are expected to experience more severe and prolonged hypoxia than at present under the same nutrient loads. Under such conditions, if the level of nutrient (N) discharge is unchanged, society will incur the environmental (a) and economic (b) costs associated with increased hypoxia. If the goal is to keep the level of hypoxia unchanged, nutrients will need to be reduced more than if temperatures were cooler and the economic cost associated with a reduction of the N discharge to the sea will increase. (Figure modified from Capet et al. (2013) for the Black Sea shelf.)

4

Why is deoxygenation a problem?

4.1 Climate regulation and nutrient cycling

The oxygen content of the ocean and coastal waters exerts an important influence on the biogeochemical cycles of nitrogen (N), phosphorus (P) and carbon (C) in the water and sediments directly and through its effect on the types of organisms that live in an area (Fig. 15). With a decrease in oxygen, species shift from long-lived, deep-burrowing, slow-growing animals that can irrigate and mix the sediments and bring oxygen into anoxic sediments, to small species that live closer to the sediment surface (Levin et al., 2009). Currently, large volumes of seawater in areas such as the Bay of Bengal are at a tipping point where a loss of oxygen of just a few nmol L^{-1} could result in large changes in nitrogen balance of the ocean (Bristow et al., 2017).

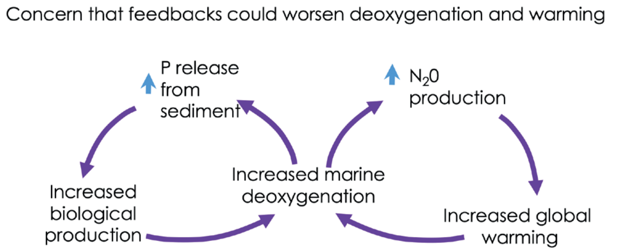


Figure 15. There is concern that expanding low oxygen areas may influence biogeochemical cycles in ways that further exacerbate deoxygenation and global warming. Phosphorus (P) released from sediments under oxygen deficient conditions in eutrophic coastal systems can fuel further primary production, and therefore worsen deoxygenation. Whether this process is offset by other factors in the open ocean is currently under debate. Major research efforts are underway to better understand how much production of N_2O, a potent greenhouse gas, will increase as OMZs expand, and whether the increased N_2O will escape into the atmosphere. Another potent greenhouse gas, methane, is produced in anoxic waters and sediment, but the ocean contributes only a small percentage of the methane released into the atmosphere (Naqvi et al., 2010; Ruppel and Kessler, 2016).

Box 5. Ecosystem services.

Ecosystem goods and services are the products of ecosystems upon which human societies depend (Daily, 1997). Ecosystem services of well-oxygenated oceans and coastal waters include the regulating and supporting services related to climate and biogeochemical cycles, the provisioning service of seafood production, cultural services of tourism and livelihood, supporting services of adaptation capacity and resilience.

4.2 N_2O greenhouse gas production

Nitrous oxide (N_2O) – a powerful greenhouse gas with a climate change potential more than 260 times that of CO_2 – is formed as a by-product when microbes reduce nitrate to gaseous nitrogen (denitrification) and oxidize ammonium to nitrate. Denitrification can only occur where oxygen concentrations are extremely low. It was shown that even traces of oxygen at nanomolar levels can inhibit anaerobic processes, such as denitrification (Bristow et al., 2017). Open ocean OMZs now account for a large fraction of the global ocean production of N_2O of 4 Tg N yr^{-1} (Nevison et al., 2003; Naqvi et al., 2010). In a warming ocean, the expansion and intensification of the open ocean OMZs and the increasing emergence of low-oxygen sites in coastal areas could contribute to global climate change (Fig. 15).

4.3 Phosphorus release

Large amounts of phosphorus (P) are released from sediments under anoxic and extremely low oxygen conditions. When P is released and mixed into surface waters, it can increase the production of algae and of cyanobacteria, which can use N_2 as a nitrogen source (Fig. 15). The increased expansion of hypoxia in the Baltic Sea, for example, reduces the amount of P buried and absorbed into sediments, and enhances the pool of easily mobilized P in the water column (Conley et al., 2009).

4.4 Hydrogen sulphide

When oxygen is completely exhausted, anoxic conditions prevail and the degradation of organic matter leads to the production of toxic hydrogen sulphide (H_2S). In some upwelling regions, H_2S is released directly into the atmosphere and can be recognized by its 'rotten egg' odour. The effects on living organisms and coastal fisheries can be serious. In severely affected areas, H_2S kills a variety of invertebrates and fishes, causes anomalous dislocation of mobile species and leads seabirds to feed on floating dead marine organisms (Weeks et al., 2002).

4.5 Micronutrient cycling

Oxygen gradients that occur at the upper and lower edges of OMZs favour a complex succession of organisms that use different types of aerobic and anaerobic respiration processes (Wright et al., 2012). Once oxygen is completely depleted, microorganisms with anaerobic respiratory pathways dominate. Nitrate (macronutrient), manganese, iron, sulphate and CO_2 are utilized sequentially in order of decreasing energy yield for the organism. The products and by-products synthesized during these processes alter the abundance of micronutrients and their availability to marine organisms.

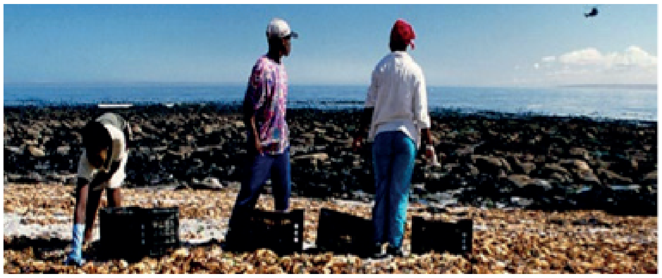
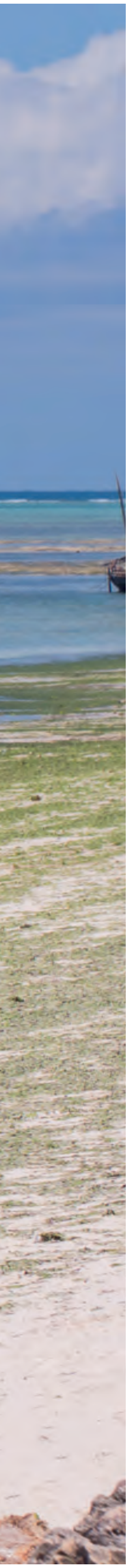


Figure 16. Low oxygen caused by algal blooms in South Africa. Rock lobsters attempting to escape low oxygen become stranded on the shore. © Claudio Velasquez. http://www.dlist.org/sites/default/files/image_library/741.jpg.

4

5

Deoxygenation disrupts the biological and ecological functioning of marine ecosystems



Deoxygenation can result in a sharp reduction in biodiversity as organisms dependent on aerobic respiration fail to recruit, remain or survive.

Large mobile species such as fish and crustaceans can be sensitive to low oxygen and migrate away. Carnivory, which is oxygen intensive, is reduced in low oxygen conditions (Sperling et al., 2013).

Dead fish washed up on shore are an obvious consequence of low oxygen events, but many animals fall to the bottom where they decompose and fuel further deoxygenation but are never seen (Fig. 16). Underwater photo of the Baltic © https://upload.wikimedia.org/wikipedia/commons/thumb/4/45/Fishkillk.jpg/220px-Fishkillk.jpg.

As O_2 declines, less of the energy generated by oceanic primary production is transferred to higher trophic levels, like fish and shellfish, while more is used by microorganisms.

Deoxygenation can disrupt the connectivity among life stages or populations at different locations. Many marine organisms have both pelagic and benthic (bottom-dwelling) life stages and require sufficient oxygen in both habitats to complete their life cycle. Many species also migrate vertically between deep and shallow waters and require oxygen in both habitats to feed or avoid predators.

5

Avoidance of low oxygen and differential tolerances of predators and their prey can change food-web interactions both within the hypoxic waters and in the surrounding, more highly oxygenated waters to which they escape.

There is not much oxygen in water compared to air, and animals need to work hard to extract it.

	Overal Mass	Oxygen
One Litre of Air	1.3 g	0.3 g
One Litre of Water	1000 g	0.008 g (100% saturation) 0.004 g (50% saturation) 0 g (anoxic)

5.1 Impact of deoxygenation on food security

Deoxygenation reduces the quality and quantity of habitats that support fisheries and are available for aquaculture production. Large-scale mortality of finfish and shellfish caused by insufficient oxygen occurs worldwide in systems that range from highly eutrophic tropical estuaries in India (Ram et al., 2014), to upwelling regions (Pitcher et al., 2014), and to northern semi-enclosed seas, such as the Baltic and Black seas, (Capet et al., 2013). Chronic exposure to hypoxia also increases disease susceptibility (Breitburg et al., 2015b; Lehmann et al., 2016), interferes with reproduction (Thomas et al., 2015) and reduces growth rates. Although there are important fisheries based on species inhabiting OMZs (Gallo and Levin, 2016), most harvested species require a much more highly oxygenated environment.

Deoxygenation can reduce the abundance and diversity of species that are important to food security and local economies. Substantial efforts are needed to better understand the link between declines in wild fisheries and deoxygenation on the scale of fish stocks because effects of deoxygenation can be masked by other anthropogenic effects on ocean and coastal waters. For example, additional nutrient input that causes low oxygen in coastal waters can simultaneously increase food available to fished species, and it can be difficult to quantify effects of lost habitat on populations that are kept well below historical levels by fishing (Breitburg et al., 2009a; Breitburg et al., 2009b; Rose et al., 2009).

5.2 Habitat compression

Mobile species that are important to human welfare and economies often avoid low oxygen by swimming or crawling away. They can become more concentrated and more reliably caught in nearby areas or shallower depths where oxygen concentrations are higher (Fig. 17). Fisheries target these high oxygen 'refuge' areas. Although short-term economic benefits may result, there is concern that this fishing strategy contributes to unsustainable management of ocean resources and can lead to overharvesting of affected stocks in both coastal areas (Craig and Bosman, 2013) and the open ocean (Stramma et al., 2012).

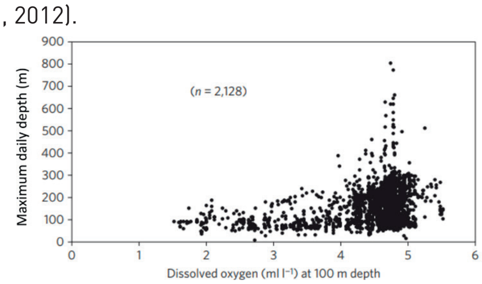


Figure 17. Vertical expansion of OMZs in the tropical north-east Atlantic restricts habitat of billfishes and tunas to a narrower surface layer, potentially increasing their vulnerability to surface fishing gear and threatening the sustainability of pelagic fisheries targeting these species (Stramma et al., 2012). This change in habitat usage may be due to either the effect of low oxygen on the fish themselves or the effect of low oxygen on depth distributions of their prey. Data show the maximum daily depth of blue marlin compared to the dissolved oxygen concentration at 100 m. (Data figure from Stramma et al., 2012; photo © Joe Fish Flynn/Shutterstock.com).

5.3 Aquaculture

Finfish and crustacean aquaculture can be particularly susceptible to deoxygenation because animals are constrained in nets or other structures and cannot escape to more highly-oxygenated habitat. For the same reason, crabs and lobsters caught in traps can suffer high mortality when oxygen concentrations decline (Grantham et al., 2004).

Figure 18. A fish kill, due to low oxygen concentrations, in Bolinao, Philippines, in 2002, resulted in the loss of thousands of kilos of fish in aquaculture pens and cages, and economic losses of 500 million Philippine pesos (San Diego-McGlone et al., 2008). Many people who ate fish killed by low oxygen developed histamine fish poisoning (Cayabyab et al., 2002). Photo © Gerry Albert Corpuz / bulatlat.com.

Aquaculture itself can also contribute to deoxygenation. Not only do densely kept animals use oxygen as they respire, but microbial decomposition of excess fish food and faeces also consumes oxygen. When this increased respiration and insufficient water flow take place at the same time, oxygen concentrations can decline. Fish kills have occurred in aquaculture pens throughout East and South-East Asia (Fig. 18; Rice, 2014).

Although bivalve aquaculture does not generally present as large a problem as finfish aquaculture in contributing to hypoxia because food is not added, it can still be susceptible to low oxygen-induced mass mortality (Han et al., 2013). Studies of hanging mussel aquaculture also indicate that biodeposits can organically enrich the sediment below the mussels, thereby increasing oxygen demand and the potential for hypoxia (Cranford et al., 2009).

Low oxygen affects animals in habitats ranging from coral reefs to estuaries to the deep sea

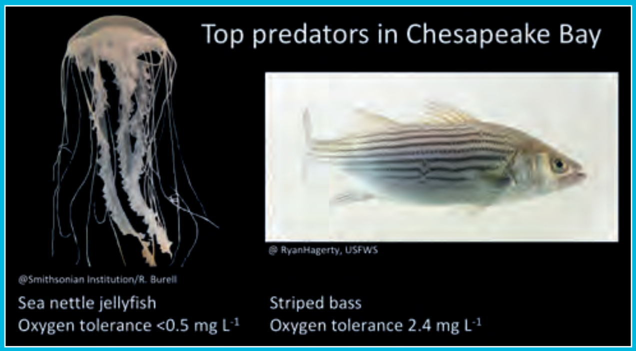
Large declines in midwater fish have been observed during the expansion of OMZs off Southern California over the past quarter of a century (Koslow et al., 2011; Koslow and Couture, 2015.)

Food webs and biological processes are disrupted at different oxygen concentrations in different habitats, reflecting conditions to which organisms are adapted. But even within the same ecosystem, different species can have vastly different oxygen tolerances.

Avoidance of bottom waters that are cooler as well as low in oxygen can result in a 'thermal squeeze', leading to metabolic stress and reduced growth efficiencies of some coastal fishes (Coutant, 1985; Niklitschek and Secor, 2005; Brandt et al., 2009).

Massive mortality of mussels and other bivalves used for food have been caused by hypoxia in coastal waters worldwide (e.g. Zaitsev and Mamaev, 1997). Chronic exposure to milder hypoxia can reduce fish and bivalve populations by interfering with reproduction (Thomas et al., 2007; Long et al., 2014).

Hypoxia can eliminate large burrowing animals, reducing geochemical heterogeneity and leading to loss of habitat for sediment-dwelling fauna (Middelburg and Levin, 2009).



Jellyfish can store oxygen in their jelly (mesoglea) and can be abundant in waters that fish avoid. Their tolerance of low oxygen allows jellyfish to be efficient predators at oxygen concentrations that compromise the escape behaviour of fish on which they prey (Breitburg et al., 1997; Shoji et al., 2005).

The loss of sessile, reef-forming species such as oysters or corals can have significant negative effects on biodiversity and ecosystem function through loss of habitat complexity and water filtration capacity (Coleman and Williams, 2002; Alteri et al., 2017).

6

Understanding deoxygenation as one of the many human impacts on our ocean and coastal waters

The decline in oxygen in the ocean and coastal waters is not happening in isolation (Doney, 2010; Breitburg et al., 2015b; Levin and Le Bris, 2015). Marine food webs are altered, and the planet's waters are getting warmer and more acidic. Fisheries reduce the abundance of target and bycatch species and can degrade habitat. These environmental changes/impacts are called 'stressors' when they result in undesirable changes to individual organisms, food webs or ecosystems. When two or more stressors affect the same physiological or ecological process, their combined effects can be greater than, less than, or qualitatively different from changes that would be predicted by simply summing up the independent effects of each stressor, making both prediction and management more difficult (Fig. 19). A concern is that the combined effects of multiple stressors may reduce the resilience of communities and ecosystems – not just negatively affect individual organisms.

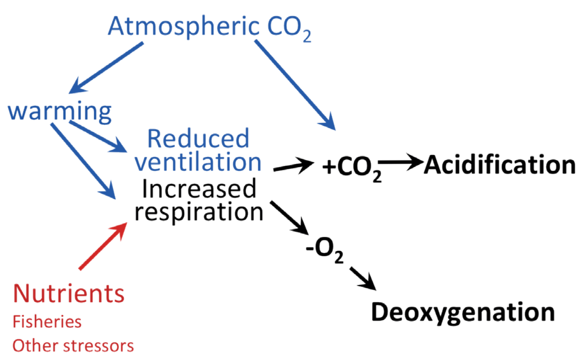


Figure 19. Global warming, acidification and deoxygenation are linked. Increasing carbon dioxide concentrations in the earth's atmosphere result in higher ocean temperatures, more acidic conditions and deoxygenation (Gruber, 2011; Breitburg et al., 2015b; Gattuso et al., 2015). The warming caused by greenhouse gases, including CO_2, lowers oxygen solubility in seawater, increases respiration rates of individual organisms, increases stratification of the water column, and inhibits the exchange between surface waters rich in oxygen and subsurface waters low in oxygen. Respiration by microbes, plants and animals depletes oxygen and produces CO_2, causing further acidification. Nutrients increase total respiration in water bodies by increasing the total production of organic biomass. (Figure modified from Breitburg et al. 2015b; Note that the size of arrows does not indicate the relative importance of these processes.)

Projections need to consider different stressors acting simultaneously and sequentially

Warmer temperatures simultaneously reduce the oxygen content of water and increase oxygen requirements of animals (Fig. 20; Pörtner, 2010; Vaquer-Sunyer and Duarte, 2011), making this combination particularly worrying.

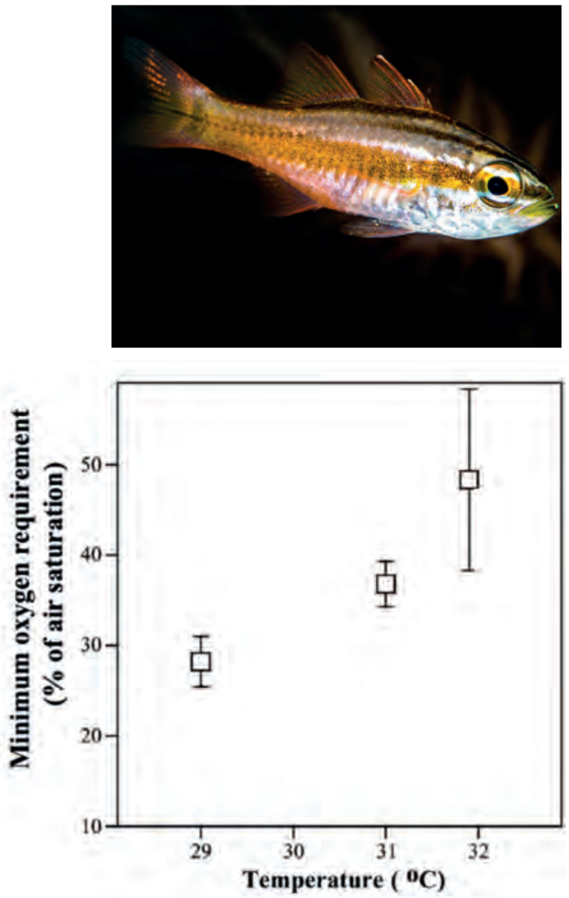


Figure 20. Oxygen requirements of fish increase with increasing temperatures. In the case of this coral reef cardinal fish, a 3°C temperature rise increased the oxygen required to sustain life by 40%. Modified from Nilsson et al., 2010. Photo © Subphoto/Shutterstock.com.

The combined effects of hypoxia and acidification are sometimes more severe than effects of either stressor alone (Gobler et al., 2014; Reum et al., 2016) but are difficult to predict (Gobler and Baumann, 2016). In some animals, increased CO_2 content of the surrounding waters reduces the ability of blood pigments to bind to oxygen (Seibel, 2015) or suppresses responses that would otherwise increase survival under low oxygen conditions (Miller et al., 2016).

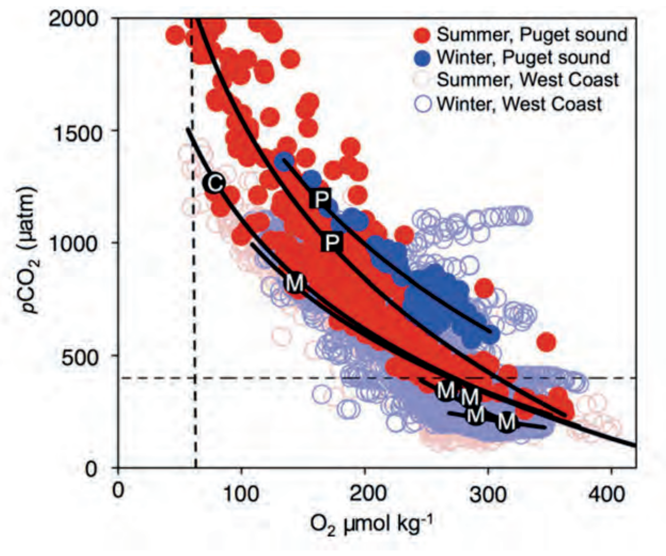


Figure 21. Low dissolved oxygen and acidification (low pH, high pCO_2) occur together. Relationships between pCO_2 and O_2 in the top 50 m of the water column during summer upwelling (May to October) and winter downwelling seasons (November to April). Regression lines are overlaid for summer and winter; lines labelled M, P and C correspond to mooring, Puget Sound and open coast datasets, respectively. For reference, approximate present-day pCO_2 levels (390–400μatm) are indicated by the dashed horizontal line and the hypoxia threshold (60 μmol kg^{-1}) is indicated with a dashed vertical line. Source: Reum et al., 2016.

Ignoring the complex ways that the marine environment has been altered can make it difficult to correctly identify the causes and effects of deoxygenation and develop effective management strategies.

Box 6. Measures to improve the understanding, predicting and minimizing impacts of oxygen decline in the ocean.

Scientific progress and the incorporation of sound science in management and policy are imperative. Further progress in understanding, predicting and minimizing impacts of oxygen decline require:

- Expanding oxygen observations in the marine environments, especially in regions where the sparsity and quality of data challenge a sound assessment of the current status and patterns of oxygen change;
- Experiments to complement observations and improve the 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;
- Improved 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;
- Capacity-building activities for communities in coastal areas of the developing world, to improve observations on core oceanographic parameters, especially oxygen, and the impact of deoxygenation on fisheries and biodiversity will have to be given high priority, and
- Clear and accurate translation of science results to society.

7

Observing oxygen decline and its effects

Accurate oxygen measurements with appropriate temporal resolutions and adequate spatial coverage of the open ocean and coastal waters can document the current status of our ocean, track changing conditions and validate models. These measurements and models can help managers separate natural variability from human-caused changes, and develop and evaluate strategies to improve ocean health and the sustainable use of ocean resources in the face of degraded conditions. Oxygen measurements are particularly powerful tools for understanding and managing marine systems when combined with measurements of a suite of other parameters, such as nutrient concentrations and parameters describing ocean acidification. Together, these measurements can help describe patterns and predict biological and biogeochemical effects of multiple stressors in the open ocean and coastal waters.

New optical oxygen sensors as well as more traditional technologies are currently used in coastal waters – sometimes in extensive networks or shipboard sampling programmes designed to provide better understanding of relationships among land use, nutrient discharges, climate and oxygen content. Remotely deployed sensors, such as Argo floats (Fig. 22), which record oxygen and other water quality parameters every few minutes for extended periods of time, have greatly increased our understanding of temporal and spatial variability influencing organisms and biogeochemical processes and our ability to detect short-term episodes of severe oxygen depletion that can cause massive mortality of marine animals.

Mobile platforms, which include devices like profiling systems, gliders, floats and powered autonomous underwater vehicles, can use optical oxygen sensors to provide observations over a wide range of spatial and temporal scales (Pizarro et al., 2016). Oxygen sensors are also used in cabled observatories (e.g. Matabos et al., 2012; Chu and Tunnicliffe, 2015) and moorings (e.g. Send and Nam, 2012), with data telemetered to shore, and in remotely operated and human-occupied vehicles working in deep water. For some moored sensors, cabled observatories and remotely operated vehicle programmes, it is possible to view oxygen conditions in real time (Fig. 23).

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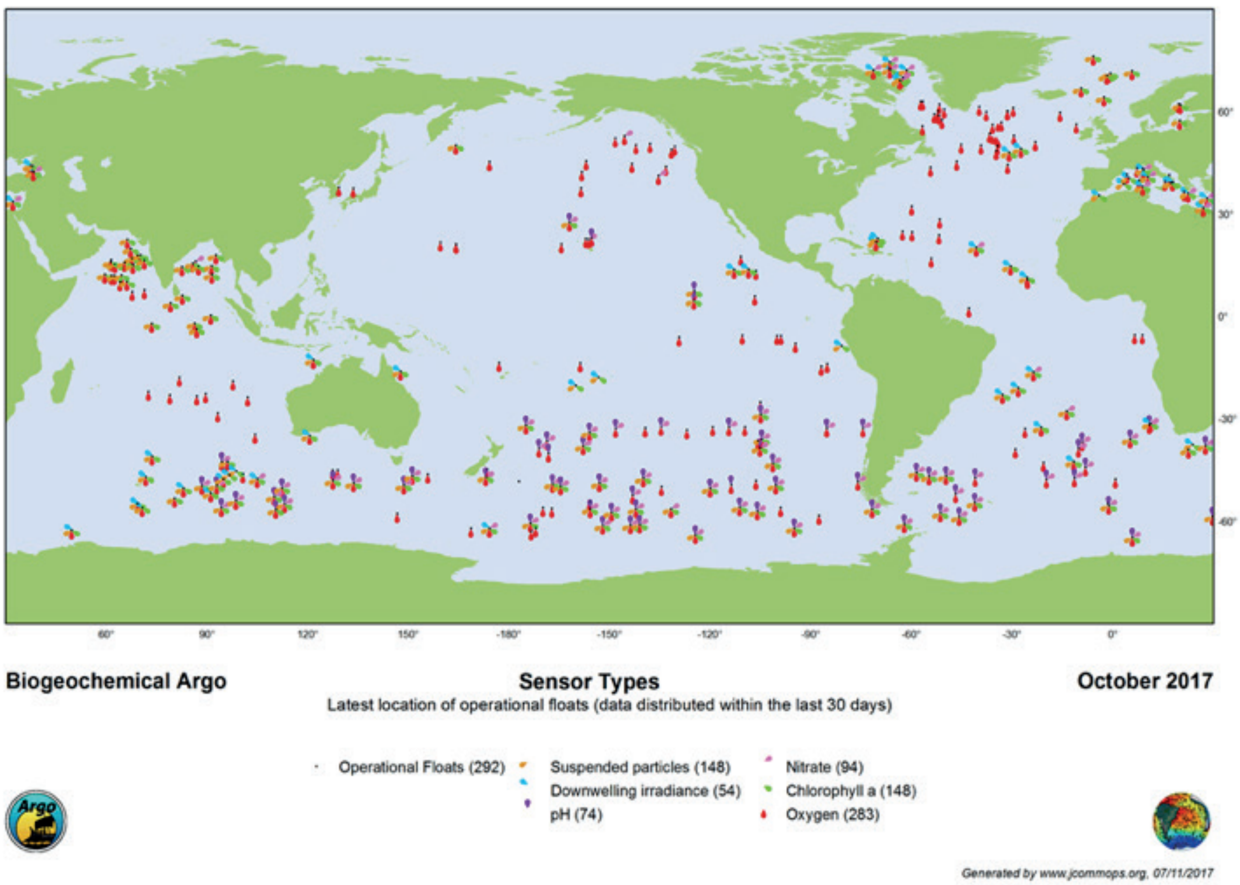
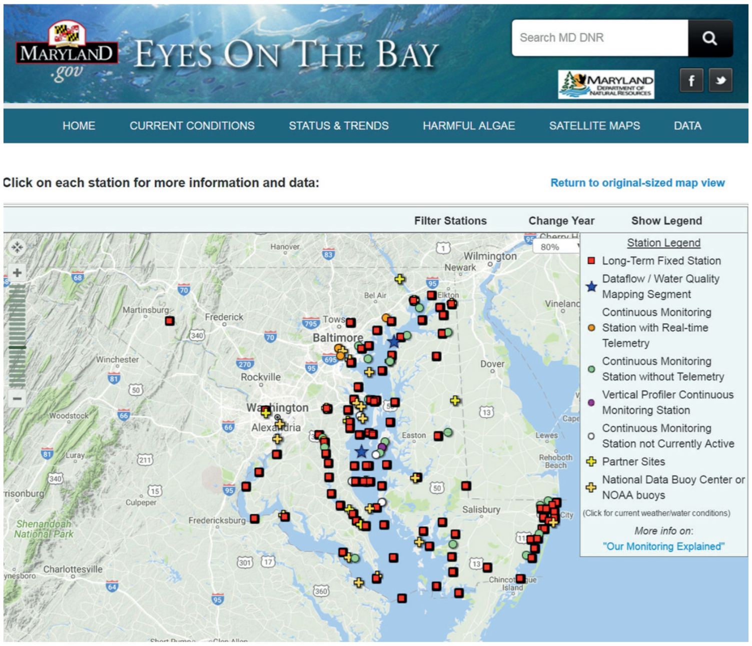


Figure 22. Map showing the locations of 292 operational Argo floats equipped with biogeochemical sensors, of which 283 had an oxygen sensor in October 2017. Argo floats freely drift in the ocean at a parking depth of 1,000 m and perform vertical profiles of temperature, salinity, oxygen and other parameters every 10 days between 2,000 m depth and the sea surface. Sources: Map: JCOMMOPS.



1. Extensive data collection by continuous sensors and shipboard measurements identifies patterns and problems.
2. Data are made accessible to managers, scientists and the public.
3. Experiments and biological monitoring inform oxygen criteria developed to sustain living resources.
4. Numerical models and statistical analyses identify relationships among land use, nutrients and oxygen concentrations
5. Management strategies are developed to limit nutrient loads to levels that yield oxygen concentrations suitable for living resources.
6. Monitoring is continued to ensure oxygen concentrations remain at or above management targets.

Figure 23. Field monitoring, numerical modelling and experiments are all used to identify spatial patterns and trends in oxygen in coastal waters and to develop solutions. On the left, a public website allows all stakeholders to access data collected at monitoring sites in the Maryland portion of Chesapeake Bay, USA. Source: Maryland Department of Natural Resources, http://eyesonthebay.dnr.maryland.gov/.

Experiments, field monitoring and numerical modelling at scales ranging from genes to ecosystems are contributing to our understanding of the effects of oxygen decline. Because oxygen loss so often occurs with changes in other environmental factors, attributing specific impacts to hypoxia can be a major challenge, but is critical for the development of tailored management strategies. Approaches for addressing this challenge include: examining biological responses across natural multi-stressor gradients in the modern ocean (e.g. Sperling et al., 2016) and in the past (Norris et al., 2013), conducting laboratory and field experiments with multiple stressors (reviewed in Gunderson et al., 2016), and use of multiple geochemical proxies (Gooday et al., 2010; Limburg et al., 2015).

In spite of scientific advances, major questions and uncertainties remain. Progress is ultimately limited by financial support available to operate and continue to improve oxygen monitoring technology, to integrate oxygen information into a single accessible, quality-controlled data system, to monitor and test effects of low oxygen on ecological and biogeochemical processes, and to incorporate the newly generated knowledge into advanced modelling tools.

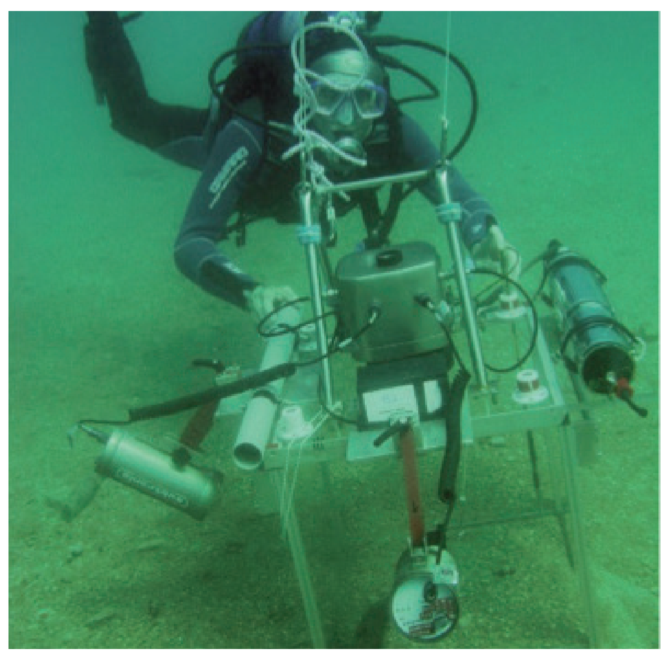


Figure 24. Experiments in the Adriatic investigating the impact of low oxygen concentration in the seawater on the behaviour of bottom-dwelling animals. © http://phys.org/news/2010-07-oxygen-marine-biologists-bottom.html.

Box 7. Using paleo-records to understand long-term dynamics of dissolved oxygen in the ocean.

What the past can tell us

Paleo-records (paleontological, sedimentological and biogeochemical data from sediment cores) are essential to understanding the long-term dynamics of dissolved oxygen levels, its climate drivers and ecosystem impacts. Direct oxygen concentration measurements and related biological monitoring data records often started only a few decades ago. Multi-decadal, centennial, millennial, or even longer time series, using paleo-records, extend the oxygen history beyond the period of monitoring, telling us about ecosystem status in the past, the possible climatic process involved and helping to identify trends in the future.

Past oxygen levels can be reconstructed qualitatively from sediment cores (Gooday et al., 2009; Moffitt et al., 2015b). Indicators of oxygen depletion include hypoxia-resistant species of foraminifera and ostracods, as well as laminated sediments that are formed during extended periods of low oxygen when organisms that otherwise disturb sediment layers are absent (Fig. 25). For example, the start of coastal benthic ecosystem degradation due to oxygen deficiency is clearly related to industrialization (Rabalais et al., 2010; Yasuhara et al., 2012, 2017). Sediment core records show a substantial biodiversity decline for the past 100-200 years, in estuaries and enclosed seas, e.g. Chesapeake Bay and Osaka Bay (Cooper, 1995; Alvarez Zarikian et al., 2000; Yasuhara et al., 2012). The primary cause of the ecosystem degradation including the decline in biodiversity was likely oxygen depletion caused by eutrophication and, more recently, by climate change (Yasuhara et al., 2012; Carstensen et al. 2014; Yasuhara et al., 2017).

Furthermore, geochemical indicators, trace metal concentrations, biomarkers and changes in stable isotopic composition, serve as proxies for past oxygen conditions. Although quantitative estimation remains difficult, these paleo-proxies have been successfully applied to reconstruct past oxygen histories (Cooper and Brush, 1993; Rabalais et al., 2007; Gutiérrez et al., 2009; Moffitt et al., 2015a; Moffitt et al., 2015b).

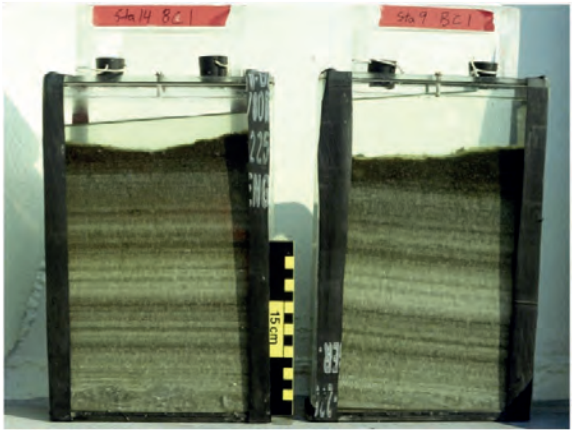


Figure 25. Lamination of sediments from the Black Sea indicate an environment with too little oxygen to support burrowing animals. Source: Schimmelmann et al. (2016).

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8

What can be done to reduce deoxygenation and protect ecosystem services exposed to low oxygen

Specific steps to slow and reverse deoxygenation will vary among locations depending on the cause of the problem, co-occurring stressors and locally specific capacities and demands. However, the general strategy for restoring the ocean's oxygen and minimizing the impacts of deoxygenation will require:

- Reduction of greenhouse gas emissions that cause atmospheric and ocean warming;
- Reduction of nutrient inputs that exacerbate oxygen loss in coastal waters and semi-enclosed seas;
- Inclusion of climate change effects in developing nutrient reduction strategies;
- Alleviation of anthropogenic stressors that threaten resilience and increase vulnerability of marine ecosystems to deoxygenation;
- Adoption of marine spatial planning and fisheries management strategies addressing deoxygenation vulnerabilities and the protection of affected species and habitats;
- Recognition of ocean deoxygenation as one of multiple climate stressors; and
- Work to unify research, management and policy actions in the coastal and open ocean across biology, geochemistry and physics, across problems of warming, acidification and deoxygenation, and across academic, industry, government and regulatory sectors.

These steps can be enhanced and facilitated by promoting global awareness and the exchange of information about ocean deoxygenation through global, regional and local efforts, including scientific efforts such as the Intergovernmental Oceanographic Commission's expert group 'the Global Ocean Oxygen Network' (GO_2NE), ocean literacy and education.

Although it is known that oxygen is critical to the biology, ecology and biogeochemical cycling of the oceans, and to the influence of the oceans on the earth's climate, major uncertainties remain – especially in our ability to scale up from small spatial scales and short time periods to fish stocks, global oxygen patterns and future times. Continued research, observation analysis and community engagement are required to not only detect the spatial and temporal extent of ocean deoxygenation, but also to advance the understanding of underlying processes to develop adaption and mitigation strategies. The ingredients needed to make those advances – data, modelling and experiments – are in hand or are being developed.

Ocean health and human health are connected. The steps that are required to restore the ocean's breath can result in direct benefits for society.

8

9

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SUMMARY FOR POLICY MAKERS

The Ocean is Losing its Breath

Declining Oxygen in the World's Ocean and Coastal Waters

'The Ocean is Losing its Breath' presents a summary of scientific experiments, observations and numerical models addressing the following questions: How has the oxygen content in the open ocean and coastal waters changed over the past century and through geological time? What are the mechanisms behind this oxygen decline? How is ocean oxygen content predicted to change over the rest of the twenty-first century? What are the consequences of low and declining oxygen concentrations in the marine environment?

This document was prepared by a group of concerned scientists from across the world, the IOC expert group, the Global Ocean Oxygen Network GO_2NE, established in 2016, which is committed to providing a global and multidisciplinary view on deoxygenation, with a focus on understanding its various aspects and impacts.

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