

Declining oxygen in the global ocean and coastal waters

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One Sentence Summary: Declining oxygen in the world's ocean and coastal waters is reducing suitable habitat, altering biogeochemical cycles, and may cause feedbacks that further exacerbate deoxygenation and global warming.

PRINT SUMMARY:

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Background: Oxygen concentrations in both the open ocean and coastal waters have been declining since at least the middle of the 20th Century. This oxygen loss – or deoxygenation – is one of the most important changes occurring in an ocean increasingly modified by human activities that have raised temperatures, CO₂ levels, and nutrient inputs, and have altered the abundances and distributions of marine species. Oxygen is fundamental to biological and biogeochemical processes in the ocean. Its decline can cause major changes in ocean productivity, biodiversity, and biogeochemical cycles. Analyses of direct measurements at sites around the world indicate that oxygen minimum zones in the open ocean have expanded by several million km² and that hundreds of coastal sites now have oxygen concentrations low enough to limit the distribution and abundance of animals and alter the cycling of important nutrients.

Advances: In the open ocean, global warming, which is caused primarily by increased greenhouse gas emissions, is considered the primary cause of ongoing deoxygenation. Numerical models project further oxygen declines during the 21st Century even with ambitious emission reductions. Increasing global temperatures decrease oxygen solubility in water, increase the rate of oxygen consumption via respiration, and are predicted to reduce the introduction of oxygen from the atmosphere and surface waters into the ocean interior by increasing stratification and weakening ocean overturning circulation.

In estuaries and other coastal systems strongly influenced by their watershed, oxygen declines have been caused by increased loadings of nutrients (nitrogen and phosphorus) and organic matter, primarily from agriculture, sewage and the combustion of fossil fuels. In many regions, further increases in nitrogen discharges to coastal waters are projected as human populations and agricultural production rise. Climate change exacerbates oxygen decline in coastal systems through similar mechanisms as in the open ocean, and by increasing nutrient delivery from watersheds that will experience increased precipitation.

Expansion of low oxygen zones can increase production of N_2O , a potent greenhouse gas, reduce eukaryote biodiversity, alter the structure of food webs, and negatively affect food security and livelihoods. Both acidification and increasing temperature are mechanistically linked with the process of deoxygenation and combine with low oxygen conditions to affect biogeochemical, physiological and ecological processes. But an important paradox to consider in predicting large-scale effects of future deoxygenation is that high productivity in nutrient-enriched coastal systems and in upwelling areas associated with oxygen minimum zones also support some of the world's most productive fisheries.

Outlook: Major advances have been made in understanding patterns, drivers and consequences of ocean deoxygenation, but there is a need to improve predictions at large and temporal scales important to ecosystem services provided by the ocean. Improved numerical models of oceanographic processes that control oxygen depletion and the large-scale influence of altered biogeochemical cycles are needed to better predict the magnitude and spatial patterns of

deoxygenation in the open ocean, as well as feedbacks to climate. Developing and verifying the next generation of these models will require increased in situ observations and improved mechanistic understanding at a variety of scales. Models useful for managing nutrient loads can simulate oxygen loss in coastal waters with some skill, but their ability to project future oxygen loss is often hampered by insufficient data and climate model projections on drivers at appropriate temporal and spatial scales. Predicting deoxygenation-induced changes in ecosystem services and human welfare requires scaling effects that are measured on individual organisms to populations, food webs, and fisheries stocks, considering combined effects of deoxygenation and other ocean stressors, and increased research emphasis in developing nations. Reducing effects of other stressors may provide some protection to species negatively affected by low oxygen conditions. Ultimately, though, limiting deoxygenation and its negative effects requires a dramatic global decrease in greenhouse gas emissions as well as reductions in nutrient discharges to coastal waters.

Figure 1. Low and declining oxygen in the open ocean and coastal waters affects processes ranging from molecules to food security. Global map shows coastal sites where anthropogenic nutrients have exacerbated or caused oxygen declines to $<2 \text{ mg O}_2 \text{ l}^{-1}$ ($<63 \mu\text{mol O}_2 \text{ l}^{-1}$) (red dots), and ocean oxygen minimum zones at 300m depth (blue shades). Map created from data provided by R. Diaz, updated by members of the GO₂NE network and downloaded from the World Ocean Atlas (2009).

ONLINE FULL PAPER:

ABSTRACT: Oxygen is fundamental to life. Not only is it essential for the survival of individual animals, but it regulates global cycles of major nutrients and carbon. The oxygen content of the open ocean and coastal waters has been declining for at least the past half century largely due to human activities that have increased global temperatures and nutrients discharged to coastal waters. These changes have accelerated consumption of oxygen by microbial respiration, reduced solubility of oxygen in water, and reduced the rate of oxygen resupply from the atmosphere to the ocean interior, with a wide range of biological and ecological consequences. Further research is needed to understand and predict long-term, global and regional-scale oxygen changes and their effects on marine and estuarine fisheries and ecosystems.

Oxygen has been decreasing in the open ocean and coastal waters since at least the middle of the 20th century (1, 2, 3). This ‘ocean deoxygenation’ ranks among the most important changes occurring in marine ecosystems (1, 4-6) (Figs. 1, 2). The oxygen content of the ocean constrains productivity, biodiversity, and biogeochemical cycles. Major extinction events in Earth’s history have been associated with warm climates and oxygen-deficient oceans (7), and there is concern that anthropogenic activities could drive the ocean towards widespread oxygen deficiency within the next thousand years (8). In this paper we refer to ‘coastal waters’ as systems that are strongly influenced by their watershed, and the ‘open ocean’ as waters where such influences are secondary.

The open ocean lost an estimated 2%, or 4.8 ± 2.1 petamoles (77 billion tons) of its oxygen over the past 50 years (9). Open-ocean oxygen minimum zones (OMZs) have expanded by an area

about the size of the European Union (4.5 million km², based on water with <70 μmol kg⁻¹ oxygen at 200 m depth) (10) and the volume of water completely devoid of oxygen (anoxic) has more than quadrupled over the same period (9). Upwelling of oxygen-depleted water has intensified in severity and duration along some coasts, with serious biological consequences (11).

Since 1950, more than 500 sites in coastal waters have reported oxygen concentrations $\leq 2\text{mg l}^{-1}$ ($=63\ \mu\text{mol l}^{-1}$ or $\cong 61\ \text{kg l}^{-1}$) – a threshold often used to delineate hypoxia (3, 12) (Fig. 1a). Fewer than 10 percent of these systems were known to have hypoxia prior to 1950. Many more water bodies may be affected, especially in developing nations where available monitoring data can be sparse and inadequately accessed even for waters receiving high levels of untreated human and agricultural waste. Oxygen continues to decline in some coastal systems despite substantial reductions in nutrient loads, which have improved other water quality metrics such as chlorophyll *a* that are sensitive to nutrient enrichment (13).

Oxygen is naturally low or absent where biological oxygen consumption through respiration exceeds the rate of oxygen supplied by physical transport, air-sea fluxes and photosynthesis for sufficient periods of time. A large variety of such systems exist, including the OMZs of the open ocean, the cores of some mode-water eddies, coastal upwelling zones, deep basins of semi-enclosed seas, deep fjords, and shallow productive waters with restricted circulation (14, 15). Whether natural or anthropogenically driven, however, low oxygen levels and anoxia leave a strong imprint on biogeochemical and ecological processes. Electron acceptors, such as Fe(III) and sulfate that replace oxygen as conditions become anoxic, yield less energy than aerobic respiration, and constrain ecosystem energetics (16). Biodiversity, eukaryotic biomass, and

energy-intensive ecological interactions such as predation are reduced (17-19), and energy is increasingly transferred to microbes (3, 16). As oxygen depletion becomes more severe, persistent and widespread, a greater fraction of the ocean is losing its ability to support high-biomass, diverse animal assemblages, and provide important ecosystem services.

But the paradox is that these areas – sometimes called ‘dead zones’ – are far from dead. Instead they contribute to some of the world’s most productive fisheries harvested in the adjacent, oxygenated waters (20-22) and host thriving microbial assemblages that utilize a diversity of biogeochemical pathways (16). Eukaryote organisms that use low-oxygen habitats have evolved physiological and behavioral adaptations that enable them to extract, transport and store sufficient oxygen, maintain aerobic metabolism, and reduce energy demand (23-26). Fishes, for example, adjust ventilation rate, cardiac activity, haemoglobin content, and O₂ binding, and remodel gill morphology to increase lamellar surface area (27). For some small taxa, including nematodes and polychaetes, high surface area to volume ratios enhance diffusion and contribute to hypoxia tolerance (26). Metabolic depression (23, 25, 28) and high H₂S tolerance (24) are also key adaptations by organisms to hypoxic and anoxic environments.

Causes of Oxygen Decline

Global warming as a cause of oxygen loss in the open ocean:

The discovery of widespread oxygen loss in the open ocean during the past 50 years depended on repeated hydrographic observations that revealed oxygen declines at locations ranging from the

NE Pacific (29) and N Atlantic (30), to tropical oceans (2). Greenhouse gas-driven global warming is the likely ultimate cause of this ongoing deoxygenation in many parts of the open ocean (31). For the upper ocean, oxygen and heat content are highly correlated for the period of 1958-2015 with sharp increases in both deoxygenation and ocean heat content beginning in the mid 1980s (32).

Ocean warming reduces the solubility of oxygen. Decreasing solubility is estimated to account for about 15% of current total global oxygen loss and more than 50% of the oxygen loss in the upper 1000 m of the ocean (9, 33). Warming also raises metabolic rates, thus accelerating the rate of oxygen consumption. Decomposition of sinking particles therefore occurs faster, and remineralization of these particles is shifted towards shallower depths (34) resulting in a spatial redistribution, but not necessarily a change in the magnitude of oxygen loss.

Intensified stratification may account for the remaining 85% of global ocean oxygen loss by reducing ventilation – the transport of oxygen into the ocean interior – and by affecting the supply of nutrients controlling production of organic matter and its subsequent sinking out of the surface ocean. Warming exerts a direct influence on thermal stratification and indirectly enhances salinity-driven stratification through its effects on ice melt and precipitation. Increased stratification alters the mainly wind-driven circulation in the upper few hundred meters of the ocean and slows the deep overturning circulation (9). Reduced ventilation, which may also be influenced by decadal to multidecadal oscillations in atmospheric forcing patterns (35), has strong subsurface manifestations at relatively shallow ocean depths (100-300 m) in the low to mid-latitude oceans and less pronounced signatures down to a few thousand meters at high

latitudes. Oxygen declines closer to shore have also been found in some systems, including the California Current and lower Saint Lawrence Estuary where the relative strength of various currents have changed and remineralization has increased (36, 37).

There is general agreement between numerical models and observations about the total amount of oxygen loss in the surface ocean (38). There is also consensus that direct solubility effects do not explain the majority of oceanic oxygen decline (31). However, numerical models consistently simulate a decline in the total global ocean oxygen inventory only about half that of the most recent observation-based estimate and also predict different spatial patterns of oxygen decline, or in some cases, increase (9, 31, 39). These discrepancies are most marked in the tropical thermocline (40). This is problematic for predictions of future deoxygenation as these regions host large open-ocean OMZs, where a further decline in oxygen levels could have large impacts on ecosystems and biogeochemistry (Fig. 2A). It is also unclear how much ocean oxygen decline can be assigned alterations in ventilation versus respiration. Mechanisms other than CO₂-driven global warming may be at play in the observed ocean oxygen decline that are not well represented in current ocean models. For example, internal oscillations in the climate system, such as the Pacific Decadal Oscillation, affect ventilation processes and eventually oxygen distributions (35).

Models predict that warming will strengthen winds that favor upwelling and the resulting transport of deeper waters onto upper slope and shelf environments in some coastal areas (41, 42), especially at high latitudes within upwelling systems that form along the eastern boundary of ocean basins (43). 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 (43). Where the oxygen content of subsurface source waters declines, upwelling introduces water to the shelf that is both lower in oxygen and higher in CO₂. Along the central Oregon coast of the U.S. in 2006, for example, anoxic waters upwelled to depths of <50 m within 2 km of shore, persisted for 4 months, and resulted in large-scale mortality of benthic macro-invertebrates (11). There are no prior records of such severe oxygen depletion over the continental shelf or within the OMZ in this area (11).

Nutrient enrichment of coastal waters:

Sewage discharges have been known to deplete oxygen concentrations in estuaries since at least the late 1800s (44), and by the mid 1900s the link to agricultural fertilizer runoff was discussed (45). Nevertheless, the number and severity of hypoxic sites has continued to increase (Fig. 2B). The human population has nearly tripled since 1950 (46). Agricultural production has greatly increased to feed this growing population and meet demands for increased consumption of animal protein, resulting in a 10-fold increase in global fertilizer use over the same period (47). Nitrogen discharges from rivers to coastal waters increased by 43% in just 30 years from 1970 to 2000 (with more than 3 times as much nitrogen derived from agriculture as from sewage (49). 48),

Eutrophication occurs when nutrients (primarily N and P) and biomass from human waste and agriculture, and N deposition from fossil fuel combustion, stimulate the growth of algae and increase algal biomass. The enhanced primary and secondary production in surface waters

increases the delivery rate of degradable organic matter to bottom waters where microbial decomposition by aerobic respiration consumes oxygen. Once oxygen is low, behavioral and biogeochemical feedbacks can hinder a return to higher oxygen conditions (50). For example, burrowing invertebrates that introduce oxygen to sediments die or fail to recruit, and sediment phosphorus is released, fueling additional biological production in the water column and eventual increased oxygen consumption.

Coastal systems vary substantially in their susceptibility to developing low-oxygen concentrations. Low rates of vertical exchange within the water column reduce rates of oxygen resupply (51), and long water retention times favor the accumulation of phytoplankton biomass (14) and its eventual sub-surface degradation. Chesapeake Bay develops hypoxia and anoxia that persist for several months during late spring through early autumn and cover up to 30% of the system area. In contrast, the nearby Delaware Bay, which has weaker stratification and a shorter retention time, does not develop hypoxia in spite of similar nutrient loads (52). Manila Bay is adjacent to a megacity and also receives similar loads on an annual basis, but it becomes hypoxic principally during the wet southwest monsoon period, when rainfall increases nutrient loads and stratification (53).

Low oxygen in coastal waters and semi-enclosed seas can persist for minutes to thousands of years, and extend over spatial scales ranging from less than one to many thousands of km². Both local and remote drivers lead to temporal and spatial variations in hypoxia. Local weather can influence oxygen depletion in very shallow water through wind mixing and the effect of cloud cover on photosynthesis (54). At larger spatial scales, variations in wind direction and speed

(55), precipitation and nutrient loads (56), sea surface temperature (57) and the nutrient content of water masses transported into bottom layers of stratified coastal systems contribute to interannual and longer period variations in hypoxic volume, duration, and the rate of deoxygenation (14).

Climate change in coastal waters:

Warming is predicted to exacerbate oxygen depletion in many nutrient-enriched coastal systems through mechanisms similar to the open ocean –increased intensity and duration of stratification, decreased oxygen solubility, and accelerated respiration (4, 58, 59). The current rate of oxygen decline in coastal areas exceeds that of the open ocean (60), however, likely reflecting the combined effects of increased warming of shallow water and higher concentrations of nutrients. Higher air temperatures can result in earlier onset and longer durations of hypoxia in eutrophic systems through effects on the seasonal timing of stratification and the rate of oxygen decline (58). An ensemble modeling study of the Baltic Sea projects declining oxygen under all but the most aggressive nutrient reduction plans due to increased precipitation and consequent nutrient loads, decreased flux of oxygen from the atmosphere, and increased internal nutrient cycling. Even aggressive nutrient reduction is projected to yield far less benefit under climate change than under current conditions (61).

Because of regional variations in the effects of global warming on precipitation and winds, the rate and direction of change in oxygen content is expected to vary among individual coastal water bodies (4, 58). Where precipitation increases, both stratification and nutrient discharges are expected to increase, with the reverse occurring in regions where precipitation decreases.

Changes in seasonal patterns of precipitation and rates of evaporation can also be important.

Coastal wetlands that remove nutrients before they reach open water are predicted to be lost as sea levels rise, decreasing capacity to remove excess nitrogen, but the rate of wetland inundation and the ability of wetlands to migrate landward will vary.

Effects of ocean deoxygenation

Oxygen influences biological and biogeochemical processes at their most fundamental level (Fig. 3). As research is conducted in more habitats and using new tools and approaches, the range of effects of deoxygenation that have been identified, and understanding of the mechanisms behind those effects, has increased significantly. Although 2 mg l^{-1} ($61 \text{ } \mu\text{mol kg}^{-1}$) is a useful threshold for defining hypoxia when the goal is to quantify the number of systems or spatial extent of oxygen-depleted waters, a more appropriate approach when considering biological and ecological effects is to simply define hypoxia as oxygen levels sufficiently low to affect key or sensitive processes. Organisms have widely varying oxygen tolerances even in shallow coastal systems (19). In addition, because temperature affects not only oxygen supply (through its effect on solubility and diffusion) but also the respiratory demand by organisms, oxygen limitation for organisms is better expressed as a critical oxygen partial pressure below which specific organisms exhibit reduced metabolic functions than by oxygen concentration (62, 63).

Biological responses

Ocean deoxygenation influences life processes from genes to emergent properties of ecosystems (Fig. 4). All obligate aerobic organisms have limits to the severity or duration of oxygen

depletion for which they can compensate. Low oxygen can reduce survival and growth and alter behavior of individual organisms (3, 4, 26, 64). Reproduction can be impaired by reduced energy allocation to gamete production, as well as interference with gametogenesis, neuroendocrine function, and hormone production, and can ultimately affect populations and fisheries (65-67). Exposure to hypoxia can trigger epigenetic changes expressed in future generations even if these generations are not exposed to hypoxia (68). Brief, repeated exposure to low oxygen can alter immune responses, increase disease, and reduce growth (69, 70).

In both oceanic and coastal systems, vertical and horizontal distributions of organisms follow oxygen gradients and discontinuities, and migratory behavior is constrained in response to both oxygen availability and the ways that oxygen alters the distributions of predators and prey (64, 71). Because oxygen tolerances and behavioral responses to low oxygen vary among species, taxa, trophic groups, and with mobility (19), encounter rates, feeding opportunities, and the structure of marine food webs change. Movement to avoid low oxygen can result in lost feeding opportunities on low oxygen-tolerant prey, and can increase energy expended in swimming (19, 70). Hypoxia impacts on vision, a function that is highly oxygen intensive, may contribute to these constraints in part through changing light requirements (72).

The presence and expansion of low water column oxygen reduces diel migration depths, compressing vertical habitat and shoaling distributions of fishery species and their prey (73-75). For pelagic species, habitat compression can increase vulnerability to predation as animals are restricted to shallower, better-lit waters, and can increase vulnerability to fishing by predictably aggregating individuals at shallower or lateral edges of low oxygen zones (71, 76-78). For

demersal species, hypoxia-induced habitat compression can lead to crowding and increased competition for prey (73), potentially resulting in decreased body condition of important fishery species such as Baltic cod (79).

In contrast, migration into and out of hypoxic waters can allow some animals to utilize oxygen-depleted habitats for predator avoidance or to feed on hypoxia-tolerant prey, and then to return to more highly oxygenated depths or locations (23, 80). Habitat compression may also enhance trophic efficiency in upwelling regions, contributing to their extraordinary fish productivity (20, 21). Some hypoxia-tolerant fish and invertebrate species expand their ranges as OMZs expand (28, 81) and their predators and competitors are excluded.

Multiple stressors

Deoxygenation is mechanistically linked to other ocean stressors, including warming (82) and acidification (83), and thus it is often their combined effects that shape marine ecosystems (84, 85). Because hypoxia limits energy acquisition, it is especially likely to exacerbate effects of co-occurring stressors that increase energy demands (65). The thermal tolerance of ectotherms is limited by their capacity to meet the oxygen demands of aerobic metabolism (62). Increased temperature elevates oxygen demand while simultaneously reducing oxygen supply, thus expanding the area of the oceans and coastal waters where oxygen is insufficient. Through this mechanism, ocean warming is predicted to result in shifts in the distribution of fishes and invertebrates poleward by 10s-100s km per decade, shifts into deeper waters, and local extinctions (63, 86). Models project that warming combined with even modest O₂ declines (less than 10 μmol kg⁻¹) can cause declines in important fishery species that are sensitive to low

oxygen (87). Physiological oxygen limitation in warming waters is also predicted to reduce maximum sizes of many fish species, including some that support important fisheries (88).

Increased respiration that causes deoxygenation also amplifies the problem of ocean acidification because the by-product of aerobic respiration is carbon dioxide. Temporal and spatial variations in oxygen in sub-pycnocline and shallow eutrophic waters are accompanied by correlated fluctuations in CO₂. In highly productive estuarine, coastal, and upwelling regions, oxygen concentrations and pH can exhibit extreme fluctuations episodically and on diel, tidal, lunar and seasonal cycles (83, 89). Elevated CO₂ can sometimes decrease the oxygen affinity of respiratory proteins (90), reduce tolerance to low oxygen by increasing the metabolic cost of maintaining acid-base balance (91), and reduce responses to low oxygen that would otherwise increase survival (92). Neither the occurrence nor the magnitude of cases where acidification exacerbates the effects of low oxygen are currently predictable (83).

Other co-varying factors such as nutrients and fisheries dynamics can mask or compensate for effects of deoxygenation, complicating management decisions. Fisheries management is designed to adjust effort and catch as population abundance changes (93). Thus, direct and indirect effects of deoxygenation on a harvested population may not be easily traceable in monitoring or catch data because management actions adjust for the loss in abundance. In addition, high nutrient loads can stimulate production in habitat that remains well oxygenated, at least partially offsetting lost production within hypoxic habitat (52). Total landings of finfish, cephalopods and large mobile decapods are positively correlated with nitrogen loads (22) in spite of hypoxia in bottom waters (52). The conflation of habitat loss and nutrient enrichment is

prominent in upwelling zones, as well as eutrophic coastal waters. Increased upwelling of nutrient-rich, oxygen-depleted waters from the 1820s to the twentieth century has increased primary and fish productivity off the coast of Peru, for example (94). However, there are limits to the extent of hypoxia that can form before total system-wide fisheries landings decline. In addition, individual species dependent on degraded habitat can decline while other species able to use more highly-oxygenated habitats within the same system thrive (52).

Biogeochemistry

Oxygen availability affects remineralization processes and associated sources and sinks of important nutrient elements, such as nitrogen, phosphorus and iron. Even when occurring in relatively small, low-oxygen regions, the effects of oxygen-dependent nutrient cycling processes are communicated to the wider ocean by circulation. Hence, local changes within OMZs can impact nutrient budgets, biological productivity and carbon fixation on regional to global scales, and changes in oxygen-depleted bottom waters of coastal systems can affect entire water bodies.

In addition to nitrogen, phosphorus and iron, which are discussed in more detail below, a wide range of other elements are affected by oxygen conditions. Hydrogen sulphide, which is toxic to most aerobic organisms, is produced in anoxic sediments and can be released to the overlying water column – especially during upwelling events (16). Methane, a potent greenhouse gas, is also produced in anoxic sediments but methanotrophic activity limits its release to the atmosphere (95). Hypoxia increases conversion of As(V) to more toxic AS(III) (96). Cadmium, copper, and zinc form sulphide precipitates in the presence of anoxic or extremely oxygen-

deficient waters and sulphides (97). This process 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.

Where oxygen is extremely low or absent, anaerobic remineralisation of organic matter by denitrification and anaerobic ammonium oxidation (anammox) leads to a net loss of bioavailable nitrogen through the formation of dinitrogen gas N_2 . Recent investigations have reported functionally anoxic conditions within open ocean OMZs (98) and have shown that traces of oxygen at nanomolar levels can inhibit anaerobic processes, such as denitrification (99). Total loss of bioavailable nitrogen from the open ocean is currently estimated to be 65-80 TgN y^{-1} from the water column and 130-270 TgN y^{-1} from sediments (100). Analysis and modeling 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 TgN y^{-1}) of global benthic denitrification (101). Similarly enhanced benthic denitrification has been observed at very low bottom-water oxygen concentrations in eutrophic coastal systems (102, 103) and in the oxycline of the water column similar to OMZs (104). Certainly there is genetic potential for water column denitrification to occur once anoxic conditions are reached.

A by-product of both nitrification and denitrification is nitrous oxide, N_2O , a potent greenhouse gas (105). The amount of N_2O produced is strongly dependent on prevailing oxygen conditions. Production of N_2O is enhanced at the oxic/suboxic boundaries of low-oxygen waters, but N_2O is further reduced to N_2 in anoxic conditions (95), 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 total oceanic N₂O emission to the atmosphere and expansion of these systems may significantly enhance oceanic N₂O emissions (95). Record air-sea N₂O fluxes have recently been observed above the OMZ in the eastern tropical South Pacific (106).

Although the understanding of the relationships among oxygen, remineralization of bioavailable N, and production of N₂O have greatly increased, the consequences of a shift in these relationships in a warming world with increased O₂-depleted waters are less well understood. Continued 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 (99). 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 (107). However, the feedbacks that link nitrogen loss and nitrogen fixation remain enigmatic (101). The direction and magnitude of change in the N₂O budget and air-sea N₂O flux are also unclear because increased stratification could reduce the amount of N₂O that reaches the surface ocean and escapes to the atmosphere (108).

The supply of phosphorus and iron released from the sediments is generally enhanced under anoxic conditions (109, 110). These nutrients have the potential to further stimulate biological production if they 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 (111) and in some systems, deep waters supply as much phosphorus to productive surface layers as do watershed discharges (112). 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 and iron from the sediment. There is evidence for this positive feedback in enclosed seas like the Baltic, where enhanced nitrogen fixation in response to deoxygenation has led to the recent proliferation of undesirable cyanobacterial blooms that can be toxic and have adverse impacts on ecosystems and society (102). Enhanced phosphate and iron levels may generally favor nitrogen fixation by diazotrophs, especially in the presence of nitrogen loss when ordinary plankton are driven towards nitrogen limitation.

Predicting oxygen decline:

Sound management of marine ecosystems is based on reliable predictions under a range of future scenarios and an understanding of associated uncertainties. Numerical models that can project effects of climate change and eutrophication on oxygen availability in the open ocean and in coastal systems can offer these predictions. Current state-of-the-art global models generally agree that the total amount of oxygen loss will be a few percent by the end of the century (31), a decline that could have substantial biogeochemical and ecological effects. However, there is little agreement among models about the spatial distribution of future low oxygen zones having $< 100 \mu\text{mol O}_2 \text{ kg}^{-1}$ (113), or the spatial patterns of O_2 changes that have occurred over the past several decades (40). This uncertainty currently limits our ability to reliably predict the regional impact of climate warming on open-ocean OMZs and hence on oxygen-sensitive biogeochemical

processes, including the nitrogen budget. More realistic and detailed inclusion of mechanisms other than CO₂-driven global warming, such as atmospheric nutrient deposition and decadal-to-multi-decadal scale climate variability (especially fluctuations in wind patterns), may improve agreement among models, and therefore their ability to predict the spatial distribution of past and future low oxygen areas.

Predicting oxygen levels in individual coastal water bodies requires modeling the variability in these systems, which is tightly governed by interactions with the land, atmosphere, sediment and offshore waters at small space and time scales. This can be achieved by current estuary-specific and regional 3-D coupled hydrodynamic-water quality models (67); these and other state-of-the-art modeling approaches deserve broader implementation. However, model performance can be hampered by the use of forcing data, such as river discharges and atmospheric conditions, that lack sufficiently resolved spatial and temporal detail. Projections of future deoxygenation also require reliable information on changes in key parameters and interactions under a range of climate change and nutrient management scenarios, and benefit from the use of approaches that explicitly model connections along the river-estuary-adjacent ocean or sea continuum.

Projections of local changes in timing and magnitude of precipitation and warming are especially important. Future characteristics of human populations, such as rates of population growth, the effect of climate change on the geography of population centers, and the effects of education and income on demands for improved sanitation and animal protein are also needed because of their influence on nutrient discharges at both local and global scales.

Improving predictions critical for management in both the open ocean and coastal systems will require increased observations from field measurements and experiments to constrain and refine models. Ideally, such data should include representations of future environmental conditions. An improved mechanistic understanding of feedbacks that limit or exacerbate oxygen depletion and alter oxygen-sensitive biogeochemical cycles is especially important. In the open ocean information is needed on transport mechanisms, such as small-scale mixing processes (114), stirring, and transport by mesoscale structures (115) that influence oxygen distributions.

Advanced observation networks can provide data to underpin the development of an improved mechanistic understanding and the refinement of current models. Drifters and autonomous platforms ranging from ARGO floats to tethered arrays provide real-time data and have the potential to increase knowledge of oxygen dynamics at small spatial and temporal scales that are ultimately needed for both regional and global models. High-resolution measurements have revealed the small-scale patchiness of oxygen-sensitive processes in space and time (99, 106) and have provided new understanding of the biogeochemistry of OMZs (98). Optical oxygen sensors mounted on ARGO floats or gliders can now use atmospheric oxygen to perform ongoing, *in situ* calibrations throughout the float (116) or glider lifetime. The accuracy of autonomous measurements of *in situ* oxygen concentrations $\leq 1 \mu\text{mol kg}^{-1}$ has been improved by the development of Switchable Trace amount OXygen (STOX) sensors (117), and novel trace oxygen optical sensors can now provide precise oxygen quantification in OMZs and detect oxygen concentrations as low as $\sim 5 \text{ nmol kg}^{-1}$ (118). The new platforms and sensors make possible the implementation of regional and global oxygen observatories targeted towards a much improved monitoring and, eventually, modelling and management of deoxygenation. For

coastal waters, it is also important to develop sensors that are affordable for use in low-income developing countries (LIDC) and can be used to generate reliable data from citizen science.

Predicting effects at large scales of space, time and ecological organization

Improved management and conservation of open-ocean and coastal systems requires predictions of the effects of deoxygenation at spatial, temporal, and ecological scales most relevant to the ecosystem services provided by these waters. Although research has clearly shown that low oxygen zones reduce habitat for species dependent on aerobic respiration and that exposure to suboptimal oxygen levels leads to a host of negative effects on individuals, identifying effects of expanding deoxygenation at the scale of populations or fisheries stocks has been difficult, particularly for mobile species (52, 119). A similar problem applies to scaling up oxygen-sensitive biogeochemical processes to predict feedbacks on global ocean nutrient inventories and the earth's climate.

Scaling to predict effects on food webs and fisheries is confounded by compensatory mechanisms, such as increased production of planktonic prey under high nutrient loads, and increased encounter rates between predators and their prey where they are squeezed into smaller oxygenated habitat space (52, 119, 120). In addition, populations maintained below their habitat-dependent carrying capacity by fisheries or other factors may not be as strongly affected by loss of habitat as species nearer their carrying capacity. In these cases, habitat suitable for feeding and other life functions may remain sufficient even where their size is reduced by low oxygen.

The most promising approaches to scaling employ a suite of methods ranging from detailed mechanistic studies, to large-scale field efforts, and new and increasingly sophisticated analyses and modeling tools that address spatial processes (*120*), temporal fluctuations (*121, 122*) and the role of co-occurring stressors. Considering the effects of early hypoxia exposure on later life stages after they migrate to more highly oxygenated habitat can indicate the large spatial scales over which even spatially limited hypoxia can have effects (*123*). Paleoecological approaches are critical for gaining a long-term perspective beyond the time scale of biological and oceanographic observation (*94, 124*). Even sophisticated approaches will not always provide support for large-scale negative effects of deoxygenation, but eliminating deoxygenation as a major cause of population declines is also important to effective management.

Increased research is most needed in locations where deoxygenation is likely to impact local economies and food security. Place-based, artisanal fisheries with little capacity to relocate as local habitat degrades are more likely to suffer from deoxygenation than industrialized fisheries with highly mobile fishing fleets. Aquaculture, in particular, can be a critical intersection between deoxygenation and societal effects because aquaculture itself can cause deoxygenation (*125*), and animals restrained in nets and cages are unable to escape harmful oxygen conditions. But critically, much of the world's marine aquaculture is done in LIDC. Fish kills in aquaculture pens (*125*) can compromise livelihoods and can directly harm to human health where low incomes and food insecurity lead to consumption of fish killed by low oxygen conditions (*126*). Coral reefs contribute to food security and to local economies through their value to tourism and storm protection, as well as food production. Recent research indicates that low oxygen may be

an increasingly important factor in mortality of corals and associated fauna in some regions, and that low-oxygen problems on coral reefs are likely underreported (127).

Reducing deoxygenation and its negative effects

Local, national and global efforts are required to limit further oxygen declines, restore oxygen to previously well-oxygenated environments, and enhance the resilience of ecosystems affected by deoxygenation. At their most basic level, the actions needed to address deoxygenation – reducing nutrient loads to coastal waters and reducing greenhouse gas emissions globally – have substantial benefits to society above and beyond improving oxygen conditions. Improved sanitation can benefit human health directly, while also reducing coastal nutrient loads.

Eliminating excess and inefficiently applied fertilizer can reduce costs to farmers (128), and can reduce emissions of N₂O (129), as well as decrease nitrogen loads to waterways. Eliminating emissions from combustion of fossil fuels can reduce greenhouse gas production, and result in reduced atmospheric deposition of nitrogen that stimulates primary production in coastal waters (130). Reducing or eliminating greenhouse gas emissions can, more generally, reduce the threats from global warming and ocean acidification and simultaneously reduce ocean deoxygenation.

Improved management of fisheries and marine habitats that are sensitive to the development and effects of low oxygen helps to protect economies, livelihoods and food security (Fig. 5).

Failure to reduce nutrient loads – at all or sufficiently – is the primary reason that oxygen levels have not improved in most coastal systems. But some of the reasons for slow progress are inherent in the problem itself. High sedimentary oxygen demand can continue for decades as accumulated organic matter degrades (e.g., (57)), phosphorus may continue to be released from

sediments once oxygen thresholds have been crossed (102), and nitrogen leached from soils and dissolved in groundwater continues to enter waterways for decades (131). Increasing temperatures can require greater reductions in nutrients to meet the same oxygen goals (57, 61). Because of changing conditions and the non-linearity of ecological processes, ecosystems may not return to their pre-disturbed state even if conditions that caused the initial deoxygenation are eased (132).

Per capita reductions in nutrient discharges and greenhouse gas emissions will need to increase as the global population continues to increase just to maintain current conditions. Nevertheless, substantial improvements have been seen in some coastal systems through implementation of a wide range of strategies to reduce input of nutrients and biomass (133). Some of the most striking improvements have been in systems like the Thames and Delaware River estuaries where steps to keep raw sewage out of the rivers and, eventually, to treat wastewater, dramatically decreased biological oxygen demand (133). In the Maryland portion of Chesapeake Bay, where both point- and non-point source nutrient reduction strategies have been implemented, oxygen concentrations $<0.1 \text{ mg l}^{-1}$ ($<3 \text{ } \mu\text{mol kg}^{-1}$) have rarely been measured since 2014 – a marked contrast to the first 30 years of frequent monitoring (1984-2013) (134). In one Chesapeake tributary, the Potomac River, nitrogen reductions due to improvements in air quality have played the major role in water quality improvements (135). Additionally, improved understanding of deoxygenation may enable a range of adaptive, protective actions for fisheries and the habitats that sustain them (Fig. 5).

An integrated framework that combines modeling, observations and experiments in a multiple stressor environment and involves the full range of stakeholders (e.g., scientists, local governments, intergovernmental bodies, industrial sectors, and the public) will facilitate the development and implementation of the most ecologically and economically effective plans to reverse deoxygenation (Fig. 6). Networks of research scientists, such as the IOC-UNESCO Global Ocean Oxygen Network (GO₂NE, <http://www.unesco.org/new/en/natural-sciences/ioc-oceans/sections-and-programmes/ocean-sciences/global-ocean-oxygen-network/>), as well as groups with more limited geographic and disciplinary scope, can help bring the most up to date information to the process, and build capacity in parts of the world where improved technology and training are needed. Key to effective management is raised awareness of the phenomenon of deoxygenation, its causes, consequences and remediation measures.

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136. (A) Map created from data in (8) and updated by R. Diaz and authors. B. Image reproduced from (9) with permission.
137. (A) <https://www.mpi-bremen.de/Binaries/Binary1454/OMZ.jpg>, based on data from the World Ocean Atlas 2013. (B) Image from (119). Images reproduced with permission.
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139. Surgeonfish: By Uxbona (Own work) [CC BY 3.0 (<http://creativecommons.org/licenses/by/3.0>)], via Wikimedia Commons. Downloaded 27 September 2017 from https://commons.wikimedia.org/wiki/File:Maldives_Surgeonfish,_Acanthurus_leucosternon.jpg; Mobile Bay hypoxia event: public domain (US federal government photograph) downloaded from <http://www.pensapedia.com/wiki/File:Jubilee-Mobile-Bay-Alabama-crabs-flounders.jpg>. Anoxic sediment: B. Fertig, photographer, courtesy of the

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140. Figure 5: Walney Offshore Windfarm: photograph by David Dixon [CC BY-SA 2.0 (<https://creativecommons.org/licenses/by-sa/2.0>)], via Wikimedia Commons.

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<https://serc.si.edu/sites/default/files/styles/slideshow-wide/public/> (Unrestricted use provided by Smithsonian Institution).

141. Image sources from left of each row. Argo float deployment:

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anniversary of the signing of the 1974 Helsinki Convention: photograph by Tuukka Troberg, downloaded from <http://www.helcom.fi/helcom-at-work/events/helcom-40-years/jubilee-photos/>. Other images created by authors of this paper

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Figure 1. Oxygen has declined in both the open ocean and coastal waters during the past half century. A. Coastal waters where oxygen concentrations $\leq 61 \mu\text{mol kg}^{-1}$ ($63 \mu\text{mol l}^{-1}$ or 2 mg l^{-1}) have been reported (red) (3, 8). B. Change in oxygen content of the global ocean in $\text{mol O}_2 \text{ m}^{-2} \text{ decade}^{-1}$ (9). Most of the coastal systems shown in this figure reported their first incidence of low oxygen after 1960. In some cases, low oxygen may have occurred earlier but was not detected or reported. In other systems, like the Baltic Sea, that reported low oxygen prior to 1960, low oxygen areas have become more extensive and severe (59). Dashed-dotted, dashed and solid lines in lower figure delineate boundaries with oxygen concentrations $< 80, 40$ and $20 \mu\text{mol kg}^{-1}$ anywhere in the water column (9)

Figure 2. Dissolved oxygen concentrations (A) at 300 m in the open ocean and (B) at the bottom of the Baltic Sea during 2012 (59). In the upper figure, major eastern boundary and Arabian Sea upwelling zones, where oxygen concentrations are lowest, are shown in magenta, but low oxygen occurs more extensively than these major OMZs; large areas of the global ocean at this depth have waters with $< 100 \mu\text{mol O}_2 \text{ l}^{-1}$ (outlined and indicated in red). Labeled regions are the Eastern Tropical North Pacific, Eastern Tropical South Pacific, Eastern Tropical South Atlantic and Arabian Sea. Low oxygen areas of the Baltic, shown in the lower figure, have expanded to $60,000 \text{ km}^2$ during some recent years as a result of limited exchange, high anthropogenic nutrient loads and warming waters (59; red $\leq 63 \mu\text{mol O}_2 \text{ l}^{-1}$ [2 mg l^{-1}], black = anoxia). Image sources (137).

Figure 3. Life and death at low oxygen levels. (A) Animals using low oxygen habitats exhibit a range of physiological, morphological and behavioral adaptations. For example, teribellid worms (*Neoamphitrite* sp., Annelida) with large branchaea and high hemoglobin levels can survive in the extremely low oxygen levels found at 400 m in the Costa Rica Canyon. (B) Fishkills in aquaculture pens in Bolinao, Philippines had major economic and health consequences for the local population. (C) The ctenophore, *Mnemiopsis leidyi*, is more tolerant of low oxygen than trophically equivalent fishes in its native habitat in Chesapeake Bay and can use hypoxic areas from which fish are excluded. (D) A low oxygen event caused extensive mortality of corals and associated organisms in Bocas del Toro, Panama. These events may be a more important source of mortality on coral reefs than previously assumed. Image sources (138).

Figure 4. Oxygen exerts a strong control over biological and biogeochemical processes in the open ocean and coastal waters. Whether oxygen patterns change over space, as with increasing depth, or over time, as the effects of nutrients and warming become more pronounced, animal diversity, biomass and productivity decline with declining oxygen. At the edge of low oxygen zones where nutrients are high and predators and their prey are concentrated into oxygenated habitat, productivity can be very high, but even brief exposures to low oxygen can have strong negative effects. Top: well-oxygenated coral reef with abundant fish and invertebrate assemblages; middle: low oxygen event in Mobile Bay, USA, in which crabs and fish crowd into extreme shallows where oxygen is highest; bottom: anoxic mud devoid of macrofauna. Image sources (139).

Figure 5. Multiple management actions can help to mitigate deoxygenation (left). Key among these are reductions in anthropogenic nutrient inputs from land, which will reduce algal blooms and subsequent oxygen drawdown; greenhouse gas emissions, which will slow warming; and waste production from aquaculture, which contributes to oxygen consumption. Adaptive measures (right) can reduce stress and may increase resilience of marine ecosystems that face deoxygenation. Examples include creating protected areas that can serve as refugia in hypoxic areas or during hypoxic events, incorporating oxygen effects on population distribution and dynamics into catch limits and closures as has been done for rockfish, and adopting gear regulations that reduce stress on vulnerable fisheries or ecosystems. Both types of actions benefit from enhanced oxygen and biological monitoring, including access to real time data that can elicit quick management responses, as well as more synthetic analyses that might reveal spatial and temporal trends (bottom). Image sources (140).

Figure 6. Monitoring in coastal waters and the open ocean documents deoxygenation and, in some cases, improved oxygen conditions. In shallow water, handheld, continuous and shipboard sensors are used worldwide. In the open ocean as well as nearshore waters, global arrays of sensors like the ARGO floats, shipboard measurements, and deep platforms and profilers, provide data to validate global models. Archiving data in well-documented databases accessible by all stakeholders facilitates scientific and management advances and public engagement. Experiments and field studies at scales ranging from genes to ecosystems provide information to predict effects of low oxygen on ecological processes and services, and are used to develop fisheries and ecosystem models. Model projections and analyses of deoxygenation and its effects inform management and policy at both local and multinational scales, and provide the basis for strategies to combat deoxygenation. Image sources (141).