

REVIEW SUMMARY

OCEANS

Declining oxygen in the global ocean and coastal waters

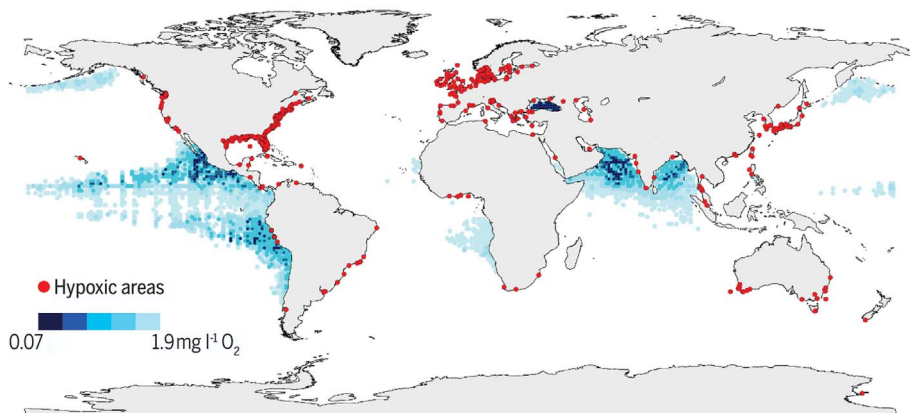
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BACKGROUND: Oxygen concentrations in both the open ocean and coastal waters have been declining since at least the middle of the 20th century. This oxygen loss, or deoxygenation, is one of the most important changes occurring in an ocean increasingly 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 square kilometers and that hundreds of coastal sites now have oxygen concentrations low enough to limit the distribution and abundance of animal populations and alter the cycling of important nutrients.

ADVANCES: In the open ocean, global warming, which is primarily caused 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. Rising 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 those in the open ocean, as well as by increasing nutrient



Low and declining oxygen levels in the open ocean and coastal waters affect processes ranging from biogeochemistry to food security. The global map indicates coastal sites where anthropogenic nutrients have exacerbated or caused O₂ declines to <2 mg liter⁻¹ (<63 μmol liter⁻¹) (red dots), as well as ocean oxygen-minimum zones at 300 m of depth (blue shaded regions). [Map created from data provided by R. Diaz, updated by members of the GO₂NE network, and downloaded from the World Ocean Atlas 2009].

delivery from watersheds that will experience increased precipitation.

Expansion of low-oxygen zones can increase production of N₂O, 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 biogeo-

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chemical, physiological, and ecological processes. However, an important paradox to consider in predicting large-scale effects of future deoxygenation is that high levels of productivity in nutrient-enriched coastal systems and upwelling areas associated with oxygen-minimum zones also support some of the world's most prolific fisheries.

OUTLOOK: Major advances have been made toward understanding patterns, drivers, and consequences of ocean deoxygenation, but there is a need to improve predictions at large spatial 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 on 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 placing an increased research emphasis on developing nations. Reducing the impacts of other stressors may provide some protection to species negatively affected by low-oxygen conditions. Ultimately, though, limiting deoxygenation and its negative effects will necessitate a substantial global decrease in greenhouse gas emissions, as well as reductions in nutrient discharges to coastal waters. ■

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REVIEW

OCEANS

Declining oxygen in the global ocean and coastal waters

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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 because of 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 levels have been decreasing in the open ocean and coastal waters since at least the middle of the 20th century (1–3). This ocean deoxygenation ranks among the most important changes occurring in marine ecosystems (1, 4–6) (Figs. 1 and 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 under current trajectories, anthropogenic activities could drive the ocean toward widespread oxygen deficiency within the next thousand years (8). In this Review, 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.

The open ocean lost an estimated 2%, or 4.8 ± 2.1 petamoles (77 billion metric 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 $<70 \mu\text{mol kg}^{-1}$ oxygen at 200 m of 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 $\leq 2 \text{ mg liter}^{-1}$ ($=63 \mu\text{mol liter}^{-1}$ or $\approx 61 \mu\text{mol kg}^{-1}$), a threshold often used to delineate hypoxia (3, 12) (Fig. 1A). Fewer than 10% of these systems were known to have hypoxia before 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 levels of 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, hemoglobin 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 northeast Pacific (29) and northern 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

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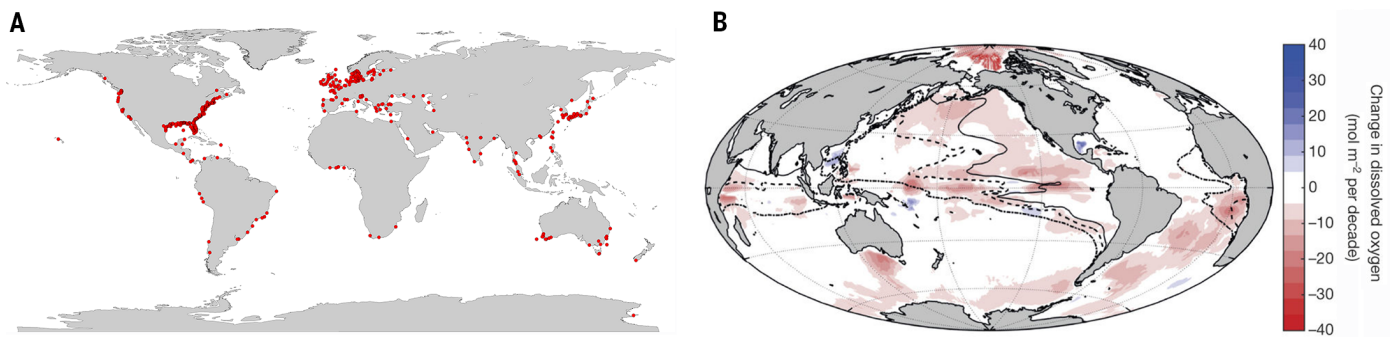


Fig. 1. Oxygen has declined in both the open ocean and coastal waters during the past half-century. (A) Coastal waters where oxygen concentrations $\leq 61 \mu\text{mol kg}^{-1}$ ($63 \mu\text{mol liter}^{-1}$ or 2 mg liter^{-1}) have been reported (red) (8, 12). [Map created from data in (8) and updated by R. Diaz and authors] (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 here reported their first incidence of low oxygen levels after 1960. In some

cases, low oxygen may have occurred earlier but was not detected or reported. In other systems (such as the Baltic Sea) that reported low levels of oxygen before 1960, low-oxygen areas have become more extensive and severe (59). Dashed-dotted, dashed, and solid lines delineate boundaries with oxygen concentrations <80 , 40 , and $20 \mu\text{mol kg}^{-1}$, respectively, at any depth within the water column (9). [Reproduced from (9)]

ocean (31). For the upper ocean over the period 1958–2015, oxygen and heat content are highly correlated 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 $\sim 15\%$ of current total global oxygen loss and $>50\%$ 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. Therefore, decomposition of sinking particles occurs faster, and remineralization of these particles is shifted toward 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 to 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 equal to 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 attributed to alterations in ventilation versus respiration. Mechanisms other than greenhouse gas-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 21st 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 CO_2 . Along the central Oregon coast of the United States in 2006, for example, anoxic waters upwelled to

depths of $<50 \text{ m}$ 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 (48), with more than three times as much nitrogen derived from agriculture as from sewage (49).

Eutrophication occurs when nutrients (primarily N and P) and biomass from human waste and agriculture, as well as 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 levels are 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 subsurface 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 may extend over spatial scales ranging from less than one to many thousands of square kilometers. 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 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 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 those of 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, owing 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 the understanding of the mechanisms behind those effects, has increased substantially. Although 2 mg liter⁻¹ (61 μmol kg⁻¹) is a useful threshold for defining hypoxia when the goal is to quantify the number of systems or the 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 in terms of 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 levels 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

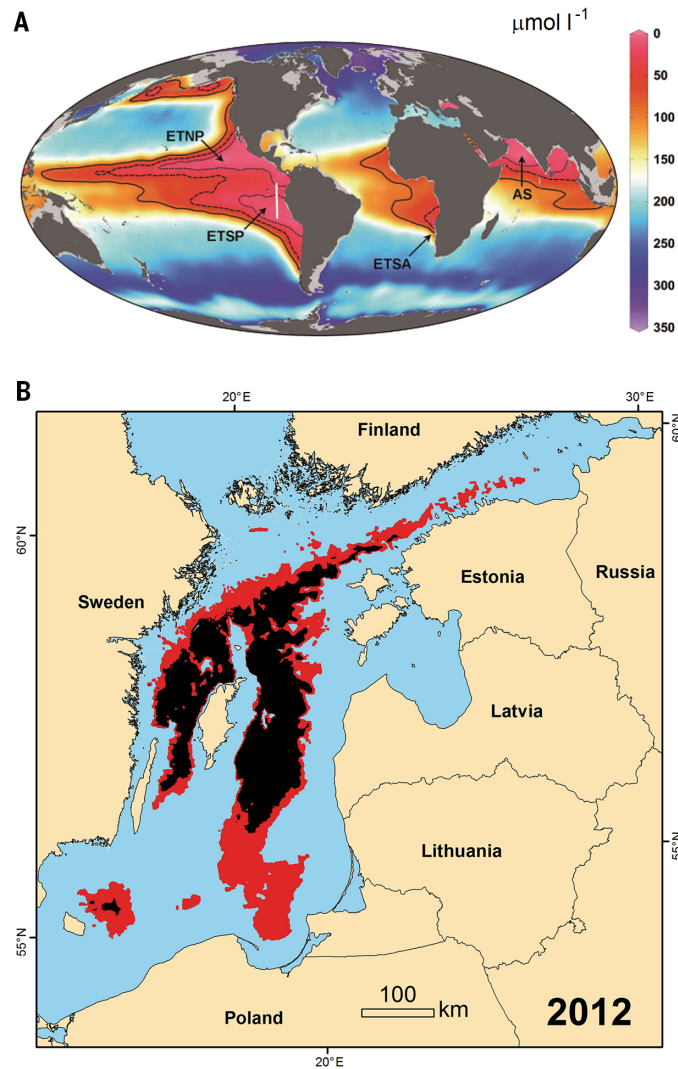


Fig. 2. Dissolved oxygen concentrations in the open ocean and the Baltic Sea. (A) Oxygen levels at a depth of 300 m in the open ocean. Major eastern boundary and Arabian Sea upwelling zones, where oxygen concentrations are lowest, are shown in magenta, but low oxygen levels can be detected in areas other than these major OMZs. At this depth, large areas of global ocean water have O₂ concentrations <100 μmol liter⁻¹ (outlined and indicated in red). ETNP, eastern tropical North Pacific; ETSP, eastern tropical South Pacific; ETSA, eastern tropical South Atlantic; AS, Arabian Sea. [Max Planck Institute for Marine Microbiology, based on data from the World Ocean Atlas 2009] (B) Oxygen levels at the bottom of the Baltic Sea during 2012 (59). In recent years, low-oxygen areas have expanded to 60,000 km² as a result of limited exchange, high anthropogenic nutrient loads, and warming waters (59) (red, O₂ concentration ≤ 63 μmol liter⁻¹ [2 mg liter⁻¹]; black, anoxia). [Reproduced from (59)]

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 levels 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 effects 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 tens to hundreds of kilometers per decade, shifts into deeper waters, and local extinctions (63, 86). Models project that warming combined with even modest O_2 declines ($<10 \mu\text{mol kg}^{-1}$) can cause

declines in important fishery species that are sensitive to low oxygen levels (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 CO_2 . Temporal and spatial variations in oxygen in subpycnocline and shallow eutrophic waters are accompanied by correlated fluctuations in CO_2 . 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 CO_2 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 in which acidification exacerbates the effects of low oxygen are currently predictable (83).

Other covarying 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 a habitat that remains well oxygenated, at least partially offsetting lost production within a 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 20th 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 fishery landings decline. In addition, individual species dependent on a degraded habitat may decline, whereas other species able to use more highly oxygenated habitats within the same system thrive (52).

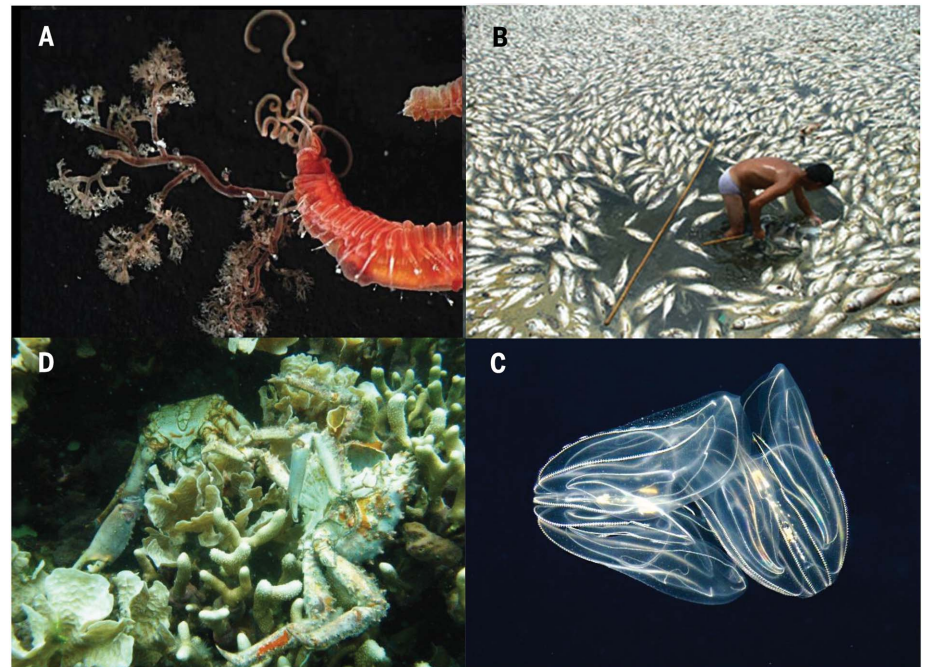


Fig. 3. Life and death at low oxygen levels. (A) Animals using low-oxygen habitats exhibit a range of physiological, morphological, and behavioral adaptations. For example, terbellid worms (*Neoamphitrite* sp., Annelida) with large branchiae and high hemoglobin levels can survive in the extremely low oxygen levels found at 400 m depth in the Costa Rica Canyon. (B) Fish kills 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 the 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 in coral reefs than previously assumed.

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 influence 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 sulfide, 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 methanotro-

phic activity limits its release to the atmosphere (95). Hypoxia increases conversion of As(V) to the more toxic As(III) (96). Cadmium, copper, and zinc form sulfide precipitates in the presence of anoxic or extremely oxygen-deficient waters and sulfides (97). This process may affect the global distribution of trace metals, some of which serve as micronutrients for plankton growth, but the importance of such controls is yet to be fully evaluated.

Where oxygen levels are extremely low or absent, anaerobic remineralization 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 to 80 Tg year⁻¹ from the water column and 130 to 270 Tg year⁻¹ from sediments (100). Analysis and modeling of global benthic data also indicate that denitrification in sediments underlying high-nutrient and low-oxygen areas (such as OMZs) removes around three times as much nitrogen per unit of carbon deposited as sediments underlying highly oxygenated water and accounts for ~10% (i.e., 15 Tg year⁻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, comparable 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 N_2O emission to the atmosphere, and expansion of these systems may substantially enhance oceanic N_2O emissions (95). Record air-sea N_2O fluxes have recently been observed above the OMZ in the eastern tropical South Pacific (106).

Although our understanding of the relationships among oxygen, remineralization of bioavailable N, and production of N_2O has greatly increased, the consequences of a shift in these relationships in a warming world with increased O_2 -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 time scales if nitrogen losses are not compensated for by increases in nitrogen

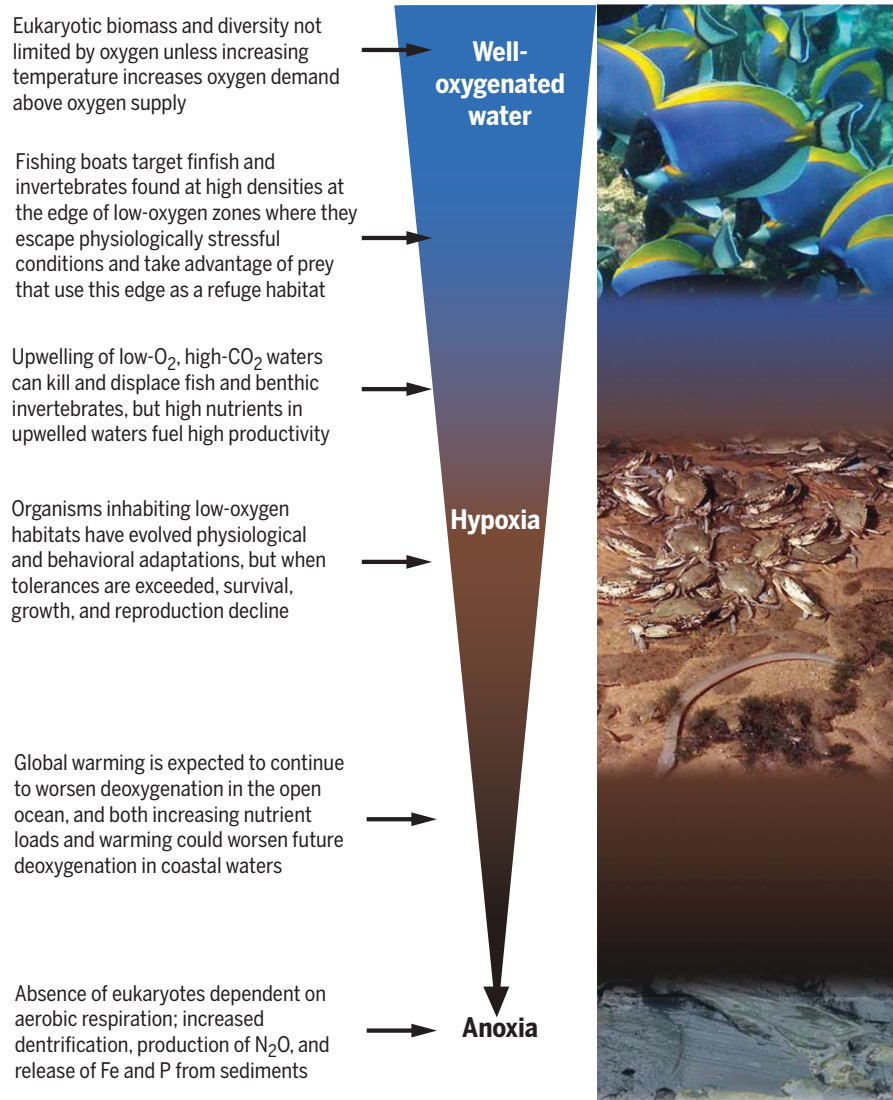


Fig. 4. Oxygen exerts a strong control over biological and biogeochemical processes in the open ocean and coastal waters. Whether oxygen patterns change over space, as with increasing depth, or over time, as the effects of nutrients and warming become more pronounced, animal diversity, biomass, and productivity decline with decreasing levels of oxygen. At the edge of low-oxygen zones, where nutrients are high and predators and their prey are concentrated into an oxygenated habitat, productivity can be very high, but even brief exposures to low oxygen levels can have strong negative effects. **(Top)** Well-oxygenated coral reef with abundant fish and invertebrate assemblages. **(Middle)** Low-oxygen event in Mobile Bay, United States, in which crabs and fish crowd into extreme shallows where oxygen levels are highest. **(Bottom)** Anoxic mud devoid of macrofauna.

fixation (107). However, the feedbacks that link nitrogen loss and nitrogen fixation remain enigmatic (101). The direction and magnitude of change in the N_2O budget and air-sea N_2O flux are also unclear because increased stratification could reduce the amount of N_2O 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 such as the Baltic Sea, 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 effects 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 toward 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 CO_2 -driven global warming—such as atmospheric nutrient deposition and decadal- to multidecadal-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 three-dimensional 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 the 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 insight into 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 STOX (switchable trace amount oxygen) 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 facilitate the implementation of regional and global oxygen observatories targeted toward the much-improved monitoring and, eventually, modeling and management of deoxygenation. For coastal waters, it is also important to develop sensors that are affordable for use in low-income developing countries (LIDCs) and that 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 Earth's climate.

Scaling to predict effects on food webs and fisheries is confounded by compensatory mechanisms; examples include increased production of planktonic prey under high nutrient loads and increased encounter rates between predators and their prey when 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 the loss of habitat as species nearer their carrying capacity. In these cases, habitats suitable for feeding and other life functions may remain sufficient, even when 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, as well as new and increasingly sophisticated analyses and modeling tools that address spatial processes (120), temporal fluctuations (121, 122), and the role of co-occurring stressors. Consideration of the effects of early hypoxia exposure on later life stages after organisms migrate to more highly oxygenated habitats can indicate the large spatial scales over which even spatially limited hypoxia can have impacts (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 affect local economies and food security. Place-based, artisanal fisheries with little capacity to relocate as local

Deoxygenation management and policy strategies

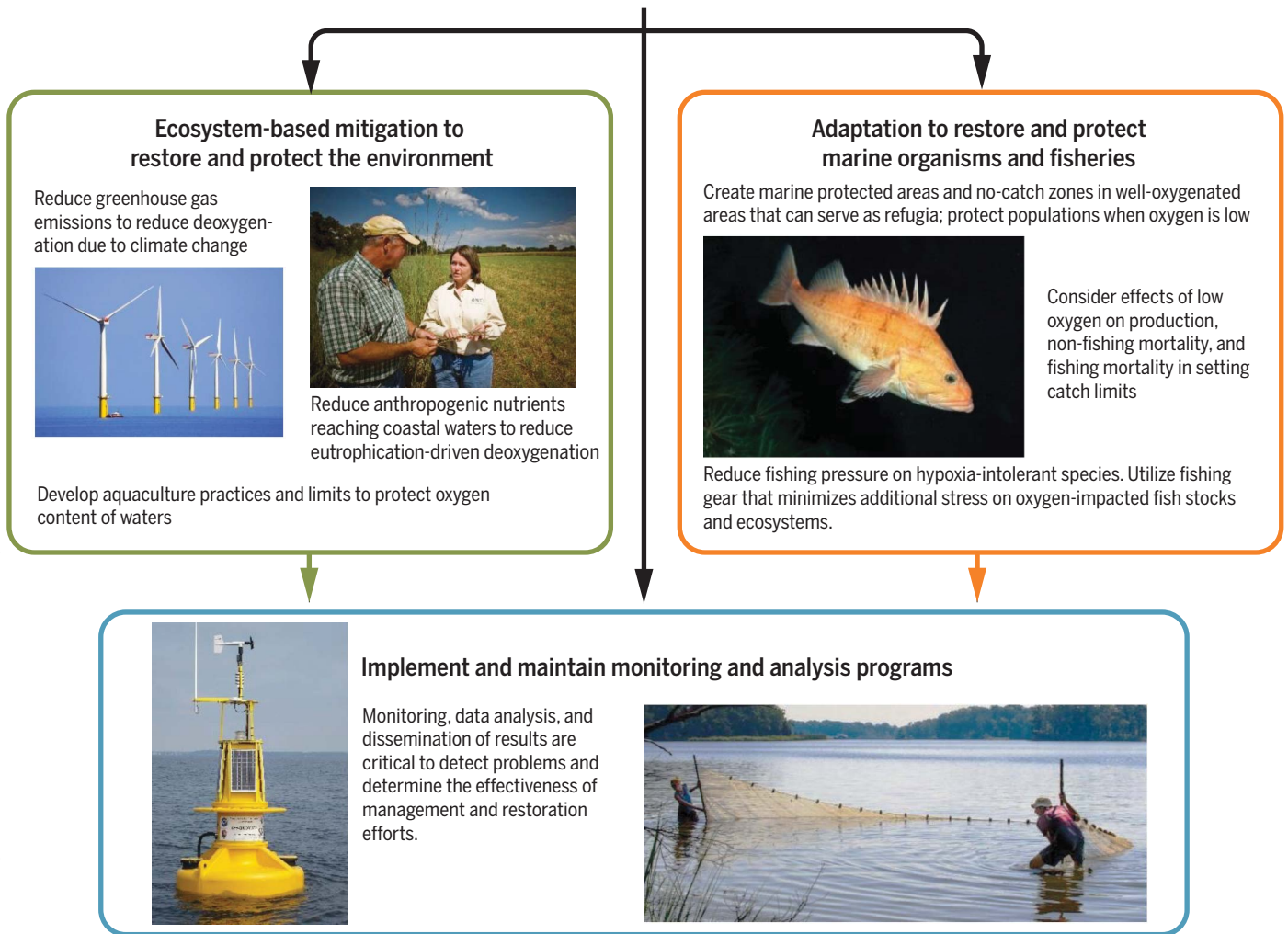


Fig. 5. Strategies for deoxygenation management and policy-making. (Left) Multiple management actions can help to mitigate deoxygenation. Key among these are reductions in (i) anthropogenic nutrient inputs from land, which will reduce algal blooms and subsequent oxygen drawdown; (ii) greenhouse gas emissions, which will slow warming; and (iii) waste production from aquaculture, which will contribute to oxygen consumption. (Right) Adaptive measures 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. (Bottom) 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.

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 LIDCs. Fish kills in aquaculture pens (125) can compromise livelihoods and can directly harm human health when low incomes and food insecurity lead to consumption of fish killed by low-oxygen conditions (126). Coral reefs contrib-

ute to food security and 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 the 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 emissions of N₂O (129) and may decrease nitrogen loads to waterways. Eliminating emissions from combustion of fossil fuels can reduce greenhouse gas production and may result in decreased atmospheric deposition

PHOTO: (TOP LEFT) DAVID DIXON/WIKIMEDIA COMMONS; (TOP RIGHT) SMITHSONIAN ENVIRONMENTAL RESEARCH CENTER; (BOTTOM LEFT) NOAA; (BOTTOM RIGHT) SMITHSONIAN ENVIRONMENTAL RESEARCH CENTER; (BOTTOM LEFT) NOAA

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of nitrogen that stimulates primary production in coastal waters (130). Reducing or eliminating greenhouse gas emissions can, more generally, lower 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 (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 nonlinearity of ecological processes, ecosystems may not return to their predisturbed state even if conditions that caused the initial deoxygenation are eased (132).

To maintain the current conditions, per capita reductions in nutrient discharges and greenhouse gas emissions will need to increase as the global population continues to grow. Nevertheless, considerable improvements have been observed in some coastal systems through implementation of a wide range of strategies to reduce the input of nutrients and biomass (133). Some of the most notable improvements have occurred in systems such as the Thames and Delaware River estuaries, where steps to keep raw sewage out of the rivers and, eventually, to treat wastewater substantially decreased biological oxygen demand (133). In the Maryland portion of the Chesapeake Bay, where both point- and nonpoint-source nutrient reduction strategies have been implemented, oxygen concentrations $<0.1 \text{ mg liter}^{-1}$ ($<3 \mu\text{mol kg}^{-1}$) 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 better air quality have played the major role in water quality improvements (135). Additionally, better 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 Intergovernmental Oceanographic Commission (IOC)—UNESCO Global Ocean Oxygen Network ([\[oceans/sections-and-programmes/ocean-sciences/global-ocean-oxygen-network/\]\(http://www.unesco.org/new/en/natural-sciences/oceans/sections-and-programmes/ocean-sciences/global-ocean-oxygen-network/\)\), as well as groups with more limited geographic and disciplinary scope, can help to keep the process updated and to build capacity in parts of the world where](http://www.unesco.org/new/en/natural-sciences/oc-</p>
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improved technology and training are needed. The key to effective management is raised awareness of the phenomenon of deoxygenation, as well as its causes, consequences, and remediation measures.

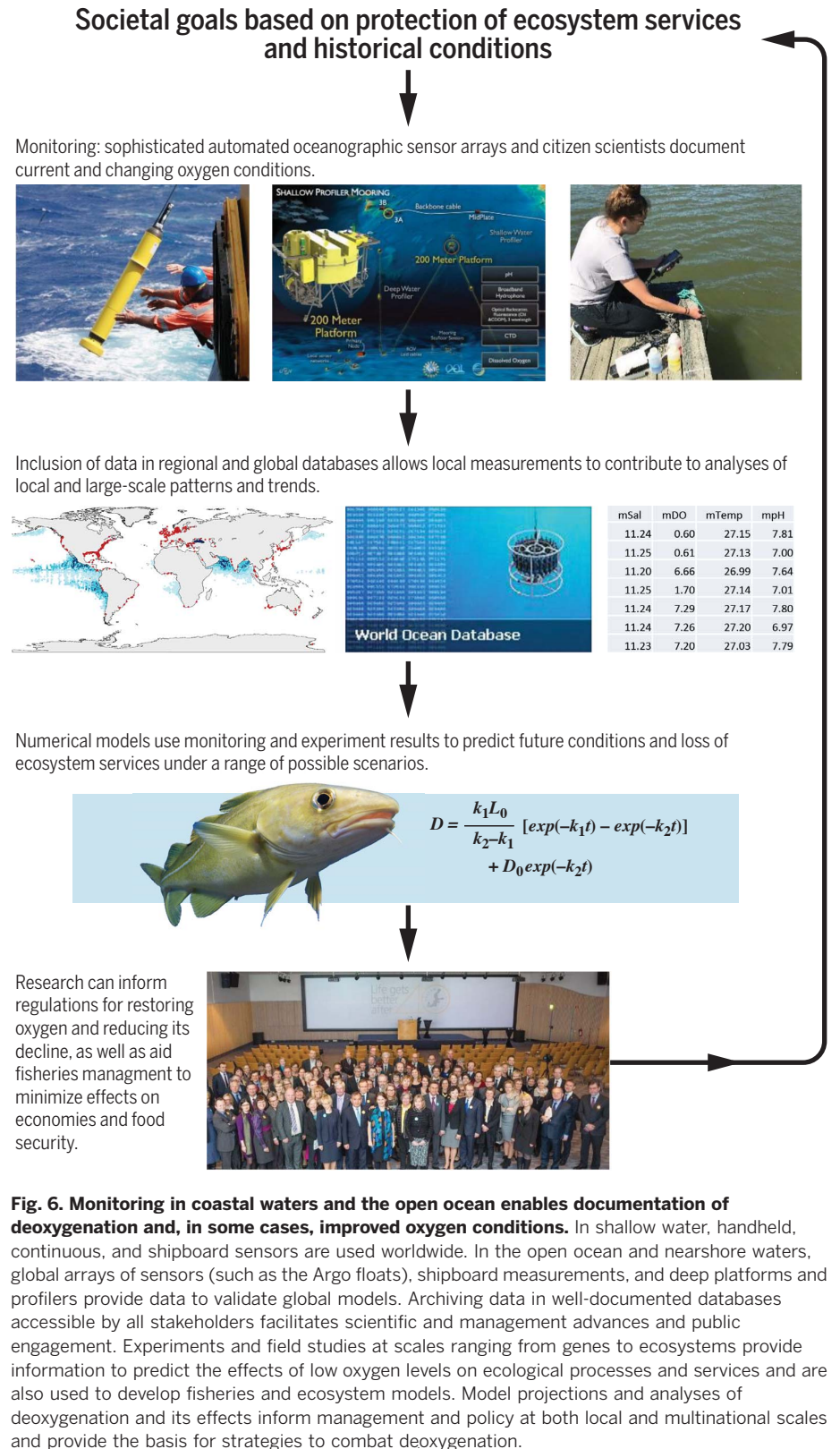


Fig. 6. Monitoring in coastal waters and the open ocean enables documentation of deoxygenation and, in some cases, improved oxygen conditions. In shallow water, handheld, continuous, and shipboard sensors are used worldwide. In the open ocean and nearshore waters, global arrays of sensors (such as the 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 the effects of low oxygen levels on ecological processes and services and are also 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.

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Declining oxygen in the global ocean and coastal waters

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Beneath the waves, oxygen disappears

As plastic waste pollutes the oceans and fish stocks decline, unseen below the surface another problem grows: deoxygenation. Breitburg *et al.* review the evidence for the downward trajectory of oxygen levels in increasing areas of the open ocean and coastal waters. Rising nutrient loads coupled with climate change—each resulting from human activities—are changing ocean biogeochemistry and increasing oxygen consumption. This results in destabilization of sediments and fundamental shifts in the availability of key nutrients. In the short term, some compensatory effects may result in improvements in local fisheries, such as in cases where stocks are squeezed between the surface and elevated oxygen minimum zones. In the longer term, these conditions are unsustainable and may result in ecosystem collapses, which ultimately will cause societal and economic harm.

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