Ocean Deoxygenation: A Primer

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Earth's ocean is losing oxygen; since the mid-20th century, 1%–2% of the global ocean oxygen inventory has been lost, and over 700 coastal sites have reported new or worsening low-oxygen conditions. This "ocean deoxygenation" is increasing and of great concern because of the potential magnitude of adverse changes to both global and local marine ecosystems. Oxygen is fundamental for life and biogeochemical processes in the ocean. In coastal and shelf regions and semi-enclosed seas, over-fertilization of waters largely from agriculture, sewage, and airborne sources creates algal blooms that die and decay, consuming oxygen. Globally, climate warming both exacerbates the problems from eutrophication and reduces the introduction of oxygen to the interior of the ocean. We discuss mechanisms, scale, assessments, projections, and impacts, including impacts to human well-being, at the individual, community, and ecosystem levels. Deoxygenation together with other stressors presents a major environmental challenge to sustainability and human use of the ocean.

The Ocean Is Losing Its Breath

Human pressure on Earth is increasing as human populations and the scale of their impacts continue to expand. We highlight here the global loss of dissolved oxygen in Earth's ocean—called ocean deoxygenation, which is occurring globally in coastal waters, semi-enclosed seas, and the open ocean. Since the mid-20th century, the oceans are estimated to have lost about 1%–2% of their oxygen inventory, and over 700 coastal systems have reported low oxygen levels.

In estuaries and coastal seas adjacent to continents, over-fertilization of water primarily from agriculture, sewage, and the burning of fossil fuels has historically been the most important driver. These low-oxygen areas are sometimes referred to as "dead zones," although even where macrofauna are excluded they host a rich microbial assemblage and are sites of important biogeochemical processes.

In addition, climate warming is an increasingly important factor driving the decline in dissolved oxygen in the world's oceans, estuaries, and seas, although this has received little recognition until recently. It is difficult to understand the lack of appreciation of deoxygenation as a climate issue. Given that societies have lived with sewage- and fertilizer-driven oxygen loss for over a century, it has most likely been treated as "just another" conventional water-quality problem. However, it is increasingly becoming clear to scientists studying ocean oxygen that nutrient and eutrophication effects are further exacerbated by warming, and vast areas of low oxygen in the open ocean that are not driven by excess nutrients are expanding. In the open ocean, the most severely oxygen-depleted waters are typically several hundred meters below the ocean surface and might not reach the sea bottom. These are called oxygen minimum zones or OMZs. A combination of winds and ocean circulation can bring the deep, low-oxygen waters toward the surface and closer to shore in a process called upwelling. OMZs, as well as less severely oxygen-depleted waters, are expanding as the ocean warms, and in some regions of the world, upwelling is bringing more severely oxygen-depleted water toward the shore.

What Is Deoxygenation, and How Is It Defined?

"Hypoxia" is defined as a state of low oxygen at which physiological and ecological processes are impaired. Hypoxia is often operationally defined as 2 mg/L O_2, equivalent to 1.4 mL/L or 63 μmol/L. In reality, there is wide variation among species and processes in oxygen requirements, and defining hypoxia as a single oxygen level is problematic. Although there are organisms (including some fish species) that have adapted to life in very low oxygen, many cannot tolerate even 2 mg/L hypoxia for long periods of time without experiencing some negative effects. In fact, many fishes and invertebrates display hypoxia symptoms at much higher levels of dissolved oxygen.

"Anoxia" is defined as the absence of oxygen or, in an operational sense, oxygen concentrations that are too low to be measured with available technology. In some contexts, such as the Baltic Sea, anoxia is even indicated in negative units because additional oxygen would be necessary to satisfy the oxidation demand of the transformation of hydrogen sulfide to sulfate under these chemically reducing conditions.

What Causes Deoxygenation?

As mentioned above, excess nutrient inputs from land-based sources can drive hypoxia. Large watersheds such as the Mississippi River, which drains 41% of the contiguous United States, deliver vast amounts of nutrients to the northern Gulf of Mexico and other coastal ecosystems. These nutrients fuel blooms of algae that eventually die off and decay. Microbes that utilize aerobic (oxygen-dependent) respiration and break down the algae consume oxygen during that decomposition. Hypoxia occurs when the rate of oxygen consumption exceeds its replenishment through photosynthesis and mixing of the water column.

Climate change is amplifying the problem of deoxygenation as a result of the effects on the physical properties of water and on the respiration rates of microbes and animals. Oxygen is not easily dissolved in water, which holds less oxygen as it warms. Warmer water is also less dense than colder water and tends to stratify above colder water layers. In areas such as parts of the Arctic and Antarctic, glacial meltwater from non-saline snow and ice is less dense than seawater and contributes to surface water layers as well. The net effect of stratification is to reduce the mixing of bottom and surface waters such that bottom waters are not re-aerated sufficiently (Figure 1).

Additionally, certain biogeochemical feedbacks can worsen deoxygenation. Examples include so-called legacy phosphorus that is buried in sediments from past algal bloom die-offs. Under anoxic conditions, the phosphorus is released and can become available in the water column as an input to algal blooms, stimulating the cycle again. Similarly, anoxia can promote the formation of nitrous oxide (N_2O), and acidifying dead organic matter can stimulate the formation of methane, which can ultimately be released to the atmosphere. Both are powerful greenhouse gases equivalent to many times the heat-trapping ability of carbon dioxide. The contribution of oceans to global methane emissions is small, however, and the net flux of N_2O from the ocean to the atmosphere is poorly characterized but could be important.

The Scale of the Problem

Prior to 1960, around 45 sites were known to have episodic or chronic hypoxia. According to Robert Diaz and colleagues, the rate of new sites that have reported hypoxia has roughly doubled each decade since the 1960s (Figure 2). Today, there are over 700 sites of eutrophication-induced hypoxia, of which some are responding to mitigation and restoration measures. However, there is clearly under-reporting of hypoxia in many parts of the world, particularly in tropical regions and nations with developing and less developed economies. On the basis of population densities and land uses, Diaz and colleagues estimate that the number of hypoxic zones might actually stand at 1,000. OMZs are described in terms of area or volume. Currently the extent is 8% of the world's ocean area.

Although a 1%–2% drop in oxygen content of the world's oceans might not seem like very much, it is not evenly distributed, and many of the regions that have lost oxygen have been among the most productive areas for fish and shellfish. These include regions such as the northern Gulf of Mexico, the upwelling regions off California and the Pacific Northwest, the Chesapeake Bay, and the Baltic, Black, Bohai, Yellow, and Mediterranean Seas. In addition, the percent change in oxygen in some regions exceeds the global average by an order of magnitude or more. The alarming extent of deoxygenated zones is a cause for great concern, and dealing with the problem constitutes a grand environmental challenge.

Assessing Global Deoxygenation

Getting a handle on deoxygenation requires the use of Earth system models and extensive monitoring networks to provide data for those models. The models track the sources and sinks of oxygen as well as the mixing of water masses, governed by ocean-atmosphere interactions. Sources include oxygen diffusing in from the atmosphere and, importantly, oxygen produced by photosynthesis in surface waters. Oxygen from its origin in surface layers must be transported into deeper layers. Sinks include oxygen consumption (respiration) by organisms, decay of organic matter, and burial as carbonates and other oxides. A large amount of uncertainty is evident in model projections; for example, Oschlies and colleagues found that models of oxygen change in the tropics predict only half of the oxygen loss observed from data collection. Nevertheless, models forced with greenhouse gas inputs from Intergovernmental Panel on Climate Change projections point to substantial increases in oxygen loss throughout the 21st century, even under optimistic scenarios of greenhouse gas reduction. Much of the loss will be at mid- and high latitudes, and some models project some recovery in OMZs as a result of lower ocean primary production as climate change progresses, resulting in lower ecosystem respiration.

Effects on Marine Organisms

Low dissolved oxygen compromises many, but not all, biological functions and life forms. Insufficient oxygen can reduce growth, reproduction, and survival; make animals more susceptible to disease and to predation by more hypoxia-tolerant species; and alter distributions. Although some organisms can utilize anaerobic respiration, in which an element other than oxygen is the terminal electron acceptor, the lack of oxygen has strong effects on energetics. Aerobic metabolism is far more efficient than anaerobic respiration at producing energy from organic matter. A molecule of glucose yields 39 ATP molecules aerobically but only about three ATP molecules under anaerobic metabolism. Thus, as oxygen declines, a cascade of physiological responses occurs. The "scope for metabolic activity" (the difference in metabolic rate of active and inactive organisms) declines and can be exacerbated by changes in other stressors, such as an increase in temperature or changes in salinity. Physiologists measure the partial pressure of oxygen (P_{O_2}) to track oxygen consumption and requirements for metabolism. The level at which an organism can no longer maintain aerobic metabolism is called the critical partial pressure (P_{crit}), at which point the organism might not be able to survive in the environment for long periods of low oxygen. Taken at a species or community level, this means that community composition (i.e., the mix of species) and species interactions will change as different species' tolerances are approached or exceeded. Thus, individual responses can scale up to changes in community structure and ecosystem function. Recently, Wishner and colleagues showed that some zooplankton species in the eastern tropical North Pacific OMZ are living very close to their physiological limits; thus, even small changes that lower P_{O_2} could have large consequences.

Effects on Marine Ecosystems

The ecosystem effects of deoxygenation are varied and depend on the mix of species, relative tolerances, and species interactions, in addition to the magnitude, frequency, and duration of hypoxia events. Mobile organisms tend to flee low oxygen, and this can involve small or large movements depending on the

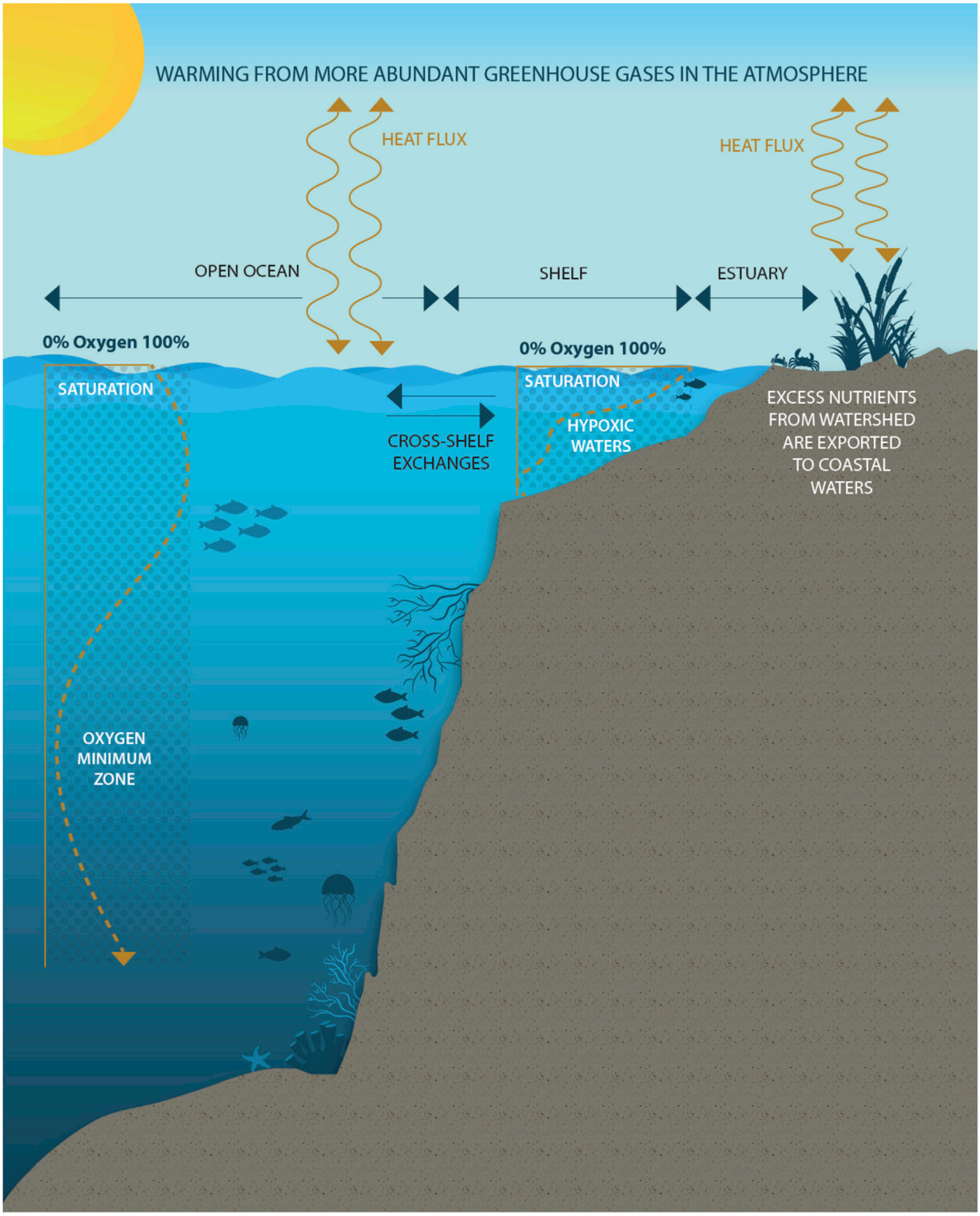

Figure 1. Schematic Showing Drivers, Processes, and Consequences of Deoxygenation
Source: Global Ocean Oxygen Network (2018).

event. Organisms that cannot avoid low levels of oxygen, including those in mariculture sites, can become lethargic or die. Increasingly, hypoxic bottom areas become devoid of invertebrates and fish. Microbial communities can persist or develop and can re-route the flows of elements, such as carbon and nitrogen, in the system.

Mobile organisms that move away from hypoxia can concentrate in better oxygenated habitats. For example, sharks and tunas, which have high metabolic rates, are being found increasingly at shallower depths given that deeper waters are subject to oxygen depletion. Loss of oxygenated habitat, called habitat compression, can alter the encounters and interactions of

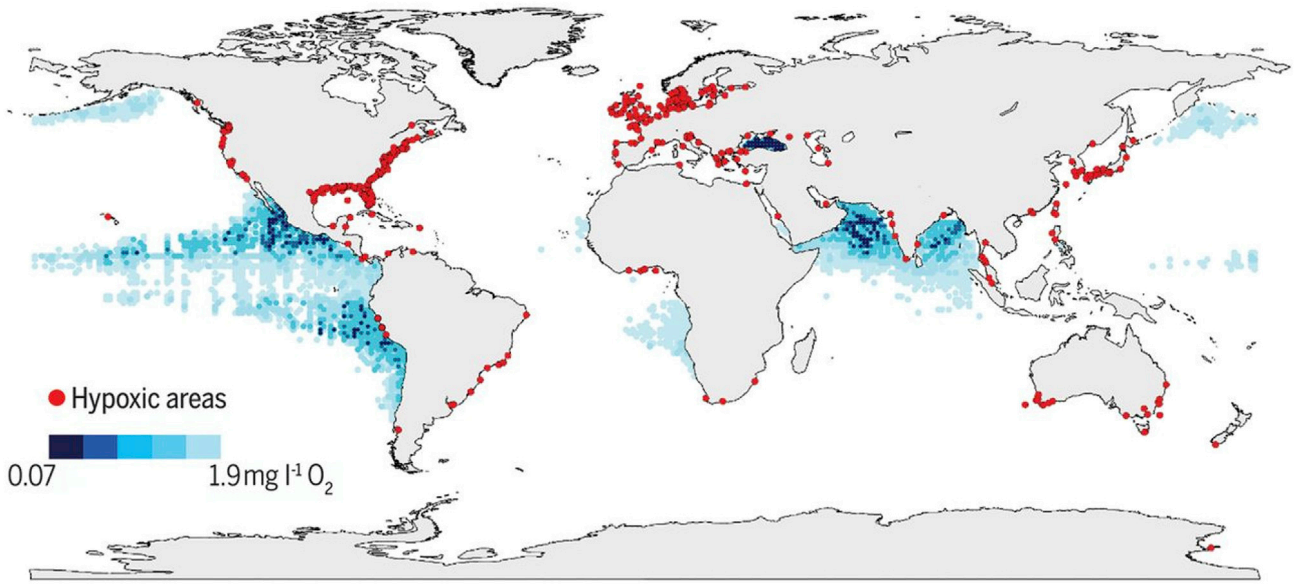

Figure 2. Global Distribution of Deoxygenation in the Coastal and Global Ocean
Source: Breitburg et al. (2018).

predators and prey species. This means that forcing organisms together into a compressed habitat can reconfigure food webs.

Deoxygenation does not occur in isolation; marine organisms and ecosystems are affected by a wide range of stressors caused by human activities. Where deoxygenation is driven by climate change, low oxygen occurs together with rising temperatures and acidification. Where nutrients are an important driver, algal blooms occur. Pathogens are transported by shipping and aquaculture, and their transmission and severity of effects can be enhanced when oxygen is low. Because fishing generally reduces population abundance and biomass, exploited species are potentially more susceptible to assaults from additional stressors such as hypoxia. And perhaps most important, oxygen supply to an organism dependent on aerobic respiration determines the energy it has available to protect itself from, and repair damage caused by, other stressors.

Some effects of hypoxia can be masked and appear to be driven by warming. As is the case for other life forms, corals are differentially sensitive to oxygen, temperature, and their interactions. Altieri and colleagues found that coral bleaching events, commonly thought to be caused by warm temperatures, could also be triggered by hypoxia and that some corals are more sensitive to oxygen than to other stressors. Assessing the likelihood of coral susceptibility to hypoxia, these researchers concluded that this is greatly underestimated.

Climate warming has other knock-on effects on hypoxia. In addition to raising metabolic rates and therefore increasing oxygen requirements, an increasing frequency of "ocean heatwaves" has been documented. In coastal areas, this has resulted in die-offs of aquatic macrophytes such as seagrasses. The loss of seagrasses further reduces oxygen production and also lowers habitat quality by removing three-dimensional structures for fishes and other organisms to shelter in.

Effects on Fisheries

It has been difficult to document effects on fisheries, particularly economic effects, because they can be varied and complex (e.g., by interacting with fishing fleet behavior and market demand). Both fish size and quality of harvestable biomass can be affected. In the Gulf of Mexico, the Atlantic croaker, an abundant species that has been documented to suffer reproductive effects and loss of growth as a result of hypoxia exposure, is projected to have a long-term reduction in abundance of 25%. In other Gulf fisheries, such as menhaden or other pelagics, however, little or no effect has been observed.

Fishing behaviors can be affected by hypoxia. Purcell and colleagues found declines in Gulf of Mexico shrimping activity at dissolved oxygen concentrations less than 2 mg/L, and fishers followed the shrimp toward the hypoxia edge where concentrations were higher. When larger shrimp were reduced in abundance by hypoxia, the smaller shrimp that were caught instead fetched lower prices.

Hypoxia can also magnify the impacts of fishing, resulting ultimately in lower catches. In the Hood Canal, a fjord-like estuary in Puget Sound in the northwestern United States, hypoxia caused Dungeness crabs to move up and concentrate in shallower areas, increasing their vulnerability to both legal and illegal fishing and leading to overfishing. Additionally, incidental mortality (bycatch when not targeted) increased when crabs were captured in hypoxic conditions.

In open seas where billfish and tuna habitats are becoming vertically compressed by the expansion of OMZs, some species and stocks can become more concentrated at shallower depths and thus more vulnerable to being caught. The same is true in some periods for fishes (e.g., anchovies, sardines, and grouper) and their fisheries in the eastern boundary upwelling systems, such as off Peru and West Africa. In the case of billfishes, increased catchability when they are forced to "shallow" is not included in stock assessment models and could lead to overly

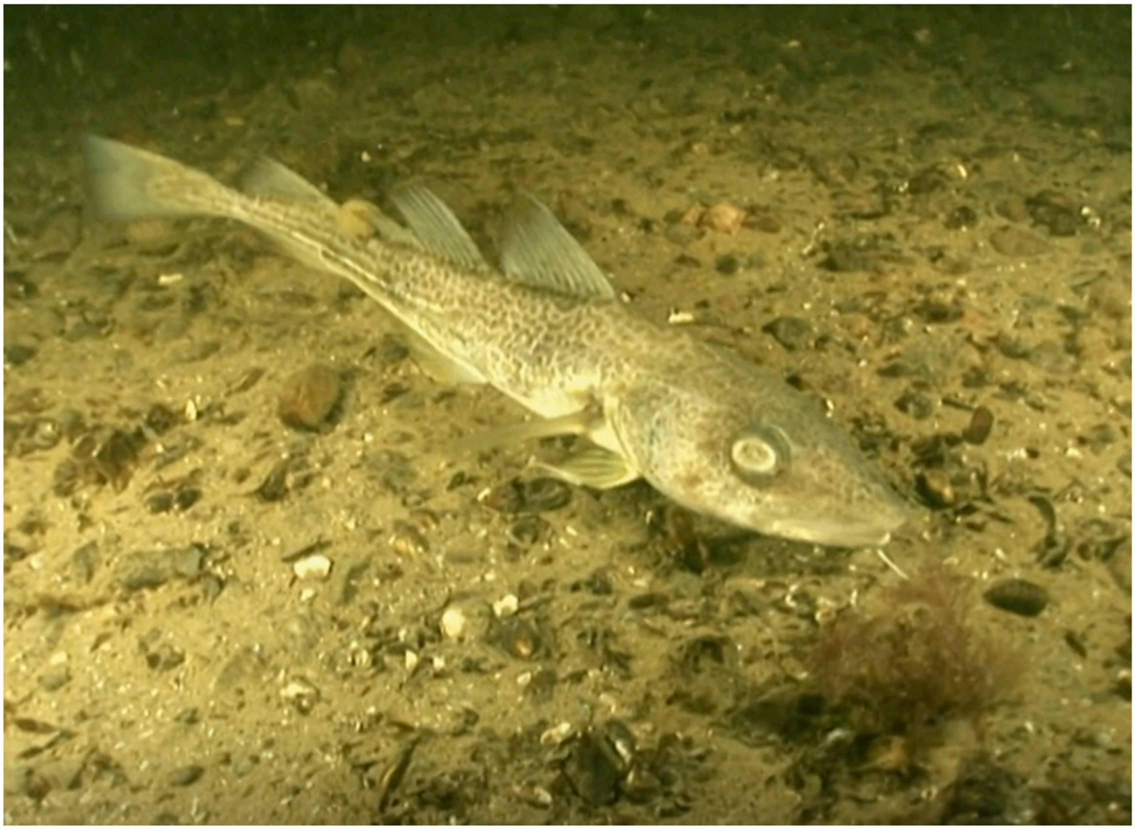

Figure 3. A Starving Baltic Sea Cod, whose Condition Has Been Affected by Extensive Time Spent in Hypoxic Bottom Water
Photo credit: Folke Rydén Productions.

optimistic estimates of abundance and eventually overfishing. In general, including deoxygenation in planning for fishery management is an important component of adaptation.

A case of more extreme fishery impacts is emerging in the Baltic Sea, one of the largest anthropogenic ''dead zones.'' As a semi-enclosed brackish sea surrounded by nine countries, the Baltic has been subjected to high loads of nitrogen and phosphorus for decades, driving eutrophication and hypoxia with enlarging areas over time. Atlantic cod constitute one of the iconic fisheries in the Baltic; for years they have been in decline, and blame has variously been assigned to overfishing, fishery mismanagement, climate-driven shifts in ecosystem regime, and hypoxia. Examining fishery-independent statistics, Casini and colleagues tested a number of factors possibly responsible for the decline and found that hypoxia explained the greatest amount of variation. In a different, novel study, Limburg and Casini applied chemical proxies of hypoxia exposure in the fishes' otoliths (ear stones), which are small, calcified structures that form part of the fish hearing and balance system. The otolith chemistry can be interpreted for evaluating lifetime exposure. The researchers found that highly exposed fish grew less: by 3 years of age, they were 39% smaller (weighing 64% less on average) than healthy cod. The proxy also connects hypoxia exposure directly to the worsened physical condition of the cod, another aspect that has been debated among scientists (Figure 3). The Baltic cod might represent an extreme case of sensitivity to hypoxia. The population is dwindling; given the warming projections that intensify hypoxia, the prognosis for Baltic cod is grim.

Effect of Hypoxia on Ecosystem Services

Ecosystem services are those aspects of nature that support human well-being. These have been described in four main categories: provisioning, regulating, supporting, and cultural and/or aesthetic. To date, very few studies have tried to quantify ecosystem services either at risk from or enhanced by deoxygenation. The most obvious service at risk is the provisioning of fish as food. Documented fish kills from hypoxia or anoxia have driven home the impact. In the Philippines, aquaculture farms lost tons of fish in several hypoxia events. The dead fish released histamines that poisoned many who consumed them. Other forms of aquaculture, including shellfish farming, are also at risk from the combination of low oxygen and low pH.

As discussed in the case study of Baltic Sea cod, one provisioning service that can be assessed, through the combination of datasets such as otolith chemistry and fishery-independent surveys, is the ''foregone biomass'' that does not develop as a result of hypoxia. In other words, what is the amount of marine food biomass that did not occur because of hypoxia? This will take on relevancy as a food-security issue if hypoxia expands, and it also could become a biological endpoint for the management and recovery of hypoxic areas.

Supporting ecosystem services include such ecosystem properties as habitat availability for organisms to carry out their life histories, nutrient cycling, and biodiversity as a proxy of healthy ecosystem functioning. Deoxygenation reduces habitat availability and biodiversity. In Southeast Asia, particularly in the Coral Triangle waters of Indonesia, Malaysia, and the Philippines, high marine biodiversity will potentially be affected by deoxygenation. Similar to the foregone biomass of fish, it should be possible to quantify or index the foregone production of marine invertebrates that support fish and production. The supporting service of biogeochemical cycling could have the adverse effect of favoring greenhouse gas production. Hypoxia's effect on regulating services (i.e., processes that regulate climate, maintain water and air quality, mitigate natural hazards, etc.) is highly uncertain, except for worsening water quality.

As for cultural and/or aesthetic services, deoxygenation might be affecting traditional (indigenous) uses of seafood or other resources associated with the sea. For example, traditional fisheries on coral reefs might be imperiled by hypoxic episodes in some locations. Additionally, recreational uses of the sea could be reduced in response to noxious events such as fish kills or the degradation of underwater habitats. And finally, in some cases low oxygen seascapes could be unaesthetic below the surface, even if amenities on land might still be appealing.

What Can Be Done to Reduce Deoxygenation?

The most important and most difficult step toward reducing deoxygenation is to bring down the global discharge of greenhouse gases. National economies are confronted by political disagreements, which make rapid change very difficult. Yet if this is not accomplished within the next decade, it might be too late, and runaway warming could be inevitable. The modest agreements at the 2019 United Nations Climate Change Conference (COP25) highlight the difficulties of international climate negotiations.

At local and regional scales, however, stakeholders can make substantial improvements toward reducing and managing nutrient inputs to allow eutrophic systems to recover. Decreasing land-based loading and atmospheric sources are very much needed, particularly in Asia. The good news is that action can produce results. A successful case study is Tampa Bay, Florida, which has successfully managed nutrient discharges, protected and restored seagrasses and fringing wetlands, and brought back fish and wildlife. A much larger case of success in nutrient management is the Baltic Sea drainage basin, where the cooperation of the nine surrounding countries has brought down nutrient levels substantially by following an action plan that has implemented sustainable farming practices and improved sewage treatment around the basin. However, legacy phosphorus in the sediments will continue to be recycled for several decades and, combined with climate effects on temperature and rainfall, make improving oxygen content a stubborn problem.

In the end, however, it is likely that many regions globally will be facing the impacts of ocean and coastal deoxygenation. Adaptive planning for assessing and addressing change will be needed. More and better ocean and coastal observation infrastructure is needed, and continued improvement of models that use the data will be necessary for understanding and projecting the magnitude and trends in oxygen in the world's waters.

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