

The Ocean is Losing its Breath

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The decrease in oxygen content (deoxygenation) of coastal and oceanic waters worldwide has worsened in recent decades. The main causes are climate change (warmer water holds less oxygen and causes increased stratification, which reduces ventilation, *i.e.* oxygen replenishment of the ocean interior and estuaries), and measurably higher nutrient concentrations (eutrophication) due to intensified human activities affecting coastal areas. Open-ocean deoxygenation, warming and ocean acidification are all driven by increased atmospheric carbon dioxide (CO₂); they constitute multiple stressors for marine ecosystems, the socio-economic consequences of which are only just beginning to be appreciated.

The problem of decreasing oxygen content (deoxygenation) of coastal and oceanic waters worldwide has worsened in recent decades, primarily as a result of climate change and nutrient inputs from human sources, such as agriculture and sewage. Deoxygenation of marine waters is predicted to further worsen with continued increases in global temperatures and human population size, with widespread consequences. Oxygen is a fundamental requirement for all aerobic life, from the intertidal to the greatest depths of the ocean. Oxygen is critical to the health of the planet, playing a direct role in the biogeochemical cycling of carbon, nitrogen, and many other key elements. The scale of deoxygenation ranges from small coastal and estuarine regions to vast areas of the interior open ocean, termed oxygen minimum and limiting zones. The effects of local deoxygenation can be translated to larger scales through the migration of organisms and the ecological, economic and societal consequences of lost fisheries and aquaculture production in affected habitats. Ocean deoxygenation was discussed in the latest IPCC report (2014), but the global nature of this emerging threat to the ocean has been not been fully acknowledged or incorporated into planning by policymakers and stakeholders at the global level. Deoxygenation related to agriculture and human waste has generally been managed on

a local or regional level, and low oxygen in deeper and upwelled water, historically viewed as a largely natural phenomenon, is only now recognized as a consequence of CO₂-induced climate change.

SCIENTIFIC BACKGROUND

The ocean is a major actor in mediating global oxygen cycling. Photosynthesis by marine algae produces oxygen, providing at least 50 % of the oxygen we breathe; at the same time, the ocean experiences a continuous loss of oxygen in its water column and sediments through respiration and equilibration of surface waters with the atmosphere. This oxygen loss is exacerbated by anthropogenic nutrient enrichment of coastal and open ocean waters and by changes to the Earth's climate caused by increasing atmospheric carbon dioxide.

Hypoxic to anoxic and even sulfidic conditions have been reported for various aquatic systems, from lakes, estuaries and coastal areas to off-shore regions of the ocean, where oxygen re-supply does not compensate for its consumption (IPCC, 2014). A threshold value for hypoxia often used for estuaries and shallow coastal waters is 60 μ mol kg⁻¹ (approximately 1.5 ml l⁻¹ or 2 mg l⁻¹) (Gray *et al.*, 2002), and areas with oxygen concentrations below this level are



commonly referred to as 'dead zones'. However, tolerance to hypoxia varies greatly among marine taxa; some species require oxygen concentrations far higher than 60 µmol kg⁻¹ for unimpaired recruitment and growth, while others are adapted for life in low oxygen conditions. In general, mobile fish and crustaceans tend to be the most sensitive (Vaquer-Sunyer & Duarte, 2008). Larger animals usually become increasingly scarce as oxygen concentration falls below 60 µmol kg⁻¹ and are ultimately lost from the system.

In the coastal ocean, the number of reported dead zones has increased exponentially since the 1960s with more than 479 systems now reporting oxygen concentrations below 60 µmol kg⁻¹ during some part of the year (Fig. 1, e.g. Baltic, Black, Kattegat Sea, Gulf of Mexico, East China Sea) (Diaz & Rosenberg, 2008) . Some of this increase can be attributed to improved observation and monitoring strategies, as well as increased awareness of the problem, but much is the result of accelerated and inefficient use of chemical fertilizers, and pollution due to increasing human populations. Changing climate is also exacerbating coastal and estuarine hypoxia. In estuarine, shelf and upper slope areas, where the bottom is populated by ecologically and economically valuable benthic species, the occurrence of hypoxic/ anoxic conditions can cause catastrophic biological losses. Some of the most severe examples of hypoxia in estuaries occurred historically and still occur in systems where raw sewage from large population centres is released directly into waterways. This also represents an important confluence of concerns over human and environmental health that extends beyond food-security concerns related to the potential effects of hypoxia on fisheries and aquaculture.

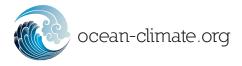
In the open ocean, eastern boundary upwelling systems (EBUSs) are characterized by high primary and export production that, in combination with weak ventilation, cause natural oxygen depletion and the development of midwater oxygen minimum zones (Fig. 2, OMZs). These are defined as areas where subthermocline dissolved oxygen levels are 20 μ mol kg⁻¹ (< 0.5 ml l⁻¹), although many species experience limitation at higher oxygen values (Gilly *et al.*, 2013). For example, large billfish experience oxygen shortage at < 150 μ mol kg⁻¹ (3.5 ml l⁻¹;





Prince & Goodyear, 2006). OMZs play critical roles in atmospheric chemistry and climate through emission of active trace gases (Law *et al.*, 2013) and they affect nearly all aspects of ecosystem structure and function in the water and on the sea floor (Levin, 2003; Levin *et al.*, 2009). OMZs are highly dynamic over glacial-interglacial periods (Moffitt *et al.*, 2015), but they appear to be expanding in tropical and subtropical regions and the NE Pacific as a result of climate change (Stramma *et al.*, 2010).

Ocean warming contributes to deoxygenation in several ways: warmer water holds less oxygen due to temperature regulation of oxygen solubility. Ocean warming increases density stratification through changes in temperature and salinity (through ice melt and precipitation). Greater stratification reduces ventilation (oxygen replenishment) of both the ocean interior (Keeling et al., 2010, Stramma et al., 2008a, 2008b, 2010) and estuaries (Altieri and Gedan, 2014). Warming also increases organism metabolic demands and remineralization rates, drawing down oxygen levels. In the open ocean, particularly the North Pacific, atmospheric inputs of nitrogen and iron are enhancing primary production; sinking and microbial decay ultimately consumes additional oxygen (Ito et al., 2016). Along eastern boundary continental margins, atmospheric warming creates land-sea temperature differentials that can intensify upwelling, leading to greater nutrient inputs (and associated production and biogeochemical drawdown) as well as upward advection of low-oxygen waters (Bakun, 1990, 2015; Sydeman et al., 2014, Wang et al., 2015). Another source of oxygen consumption in deep margin waters may come from warming-induced dissociation of



buried, frozen methane in gas hydrates (Phrampus and Hornbach, 2012). Aerobic oxidation of the methane in the water column will further deplete midwater oxygen levels (Boetius and Wenzhoffer, 2013). There are several areas where climate-altered circulation patterns can intensify hypoxia, by strengthening low oxygen undercurrents or weakening oxygen-carrying currents, (Gilbert et al., 2005, Bograd et al., 2015, Nam et al., 2015), In contrast, predictions of greater incidence and intensity of cyclones and hurricanes will induce mixing, which can ameliorate hypoxia locally (Rabalais et al., 2009). Warming may also extend periods of seasonal hypoxia or lead to earlier onset, and potentially greater incidence of Harmful Algal Blooms (HABS) which also consume oxygen as they decay (Wells et al., 2015).

Several climate changes can exacerbate nutrient inputs, contributing to hypoxia. Indirectly rising sea-level may eliminate wetlands, which remove nutrients from waters flowing to the coastal ocean. Beyond warming, elevated CO_2 levels can alter plant pore function on land, increasing water use efficiency and leaving 3-6% more water runoff, which accumulates nutrients before entering the ocean (Reay *et al.*, 2009). Increasing precipitation can contribute to hypoxia through intensified nutrient runoff, snow melt, soil erosion, and greater stratification (http://nca2014.globalchange.gov).

The latest research results suggest that the potential expansion of coastal hypoxia and OMZs could have large effects on, e.g., fisheries species through habitat compression, altered food webs, and modified species interactions, including with fishermen. Contraction of habitat and of species' ranges are predicted to result from the combined effects of warming and deoxygenation on the metabolic index of fish and invertebrates (Deutsch et al., 205). Even at non-lethal levels, exposure to low dissolved oxygen concentrations can result in reduced growth and reproduction, body size, as well as altered behaviours and distributions of marine species (Cheung et al., 2013). This means that ocean deoxygenation will increasingly stress aquatic ecosystems nearshore and in deeper oceanic habitats. The expansion of hypoxic and anoxic zones will affect the biogeochemical and ecological status and functioning of marine and freshwater ecosystems, as well as the delivery of ecosystem services. As the ocean loses its breath locally the global ecosystem service of providing an environment conducive to life is hampered.

Over larger scales, global syntheses of oxygen data show hypoxic waters have expanded by 4.5 km² at 200m (Stramma *et al.*, 2010) with widespread loss in the southern ocean (Helm *et al.*, 2011), W. Pacific (Takatani *et al.*, 2012), and N. Atlantic (Stendaro and Gruber, 2012). Overall oxygen declines have been greater in the coastal than the open ocean (Gilbert *et al.*, 2010) and often greater inshore than offshore (Bograd *et al.*, 2015).

Model simulations still have difficulties in properly representing oxygen historical data of the last 40 years (Cabré et al., 2015). Clearly we lack a full understanding of the mechanisms controlling oxygen in the ocean interior and on the shelves. Nevertheless, climate model projections predict continued and intensified ocean deoxygenation into the future (e.g. Matear et al., 2000; Bopp et al., 2002, 2013; Oschlies et al., 2008). Recent efforts have modelled deoxygenation against a backdrop of natural variability to predict the time of emergence of the deoxygenation signal in the global oceans (Fig. 3; Long et al., 2016). Hindcasting of these models is supported by the geological record, which illustrates expansive ocean anoxic events that follow climate excursions and glacial interglacial periods (Moffitt et al., 2015).

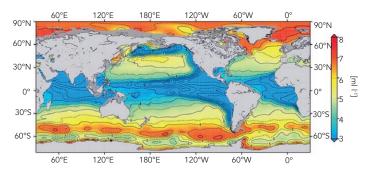


Fig.2 — Annual average oxygen concentration [ml l-1] at 200 m depth (one-degree grid, contour interval 0.5 ml l-1) (World Ocean Atlas 2013, Garcia *et al.*, 2014).



STRATEGIES FOR THE FUTURE

Deoxygenation, along with ocean warming and ocean acidification form a deadly trio of threats to ocean life from shallow water to the deep ocean (Gattusso et al., 2015; Levin and LeBris, 2015). These pressures are of critical importance to marine ecosystems because they are accelerating drastically in a short timeframe (Gruber, 2011; Mora et al., 2013; Bopp et al., 2013). Multiple approaches, including use of natural gradients, 88 historical data, geochemical proxies, and laboratory experiments are needed to better understand how oxygen interacts with other stressors interact to shape ecosystem structure and influence function (Breitburg et al., 2015; Sperling et al., 2016). Future scenarios for oxygen in the coastal areas and the open ocean will largely depend on a combination of drivers related to global environmental change and land-use, including warming, a growing human population, especially along the coasts, and agricultural practices. Under a business as usual scenario, the amount of reactive nitrogen entering the coastal and open ocean is projected to grow by 50 percent by 2050 (Noone et al., 2012), leading to the increased frequency, intensity and duration of hypoxia (Ito et al., 2016). At the same time intensifying upwelling winds (Wang et al., 2015) are projected to bring OMZ waters closer to shore and onto the shelf where they can interact with watershed and coastal sources of hypoxia (Feely et al., 2008, 2010). Integrated action is urgently required to prevent and remediate hypoxia (Levin & Breitburg, 2015).

Much of the information we have about hypoxia is based on scientific activities from researchers in North America, Europe and Asia, but recent findings also indicate that the Peru-Chile margins, West Africa and the northern Indian Ocean and Bay of Bengal are increasingly vulnerable to deoxygenation events on the shelf (Hofmann *et al.*, 2011). Examples illustrating severe hypoxia as a result of this human-induced threat can be found in the past, *e.g.* the estuary of the Thames River in the UK and the Delaware River in the US. This is a serious problem in developing and rapidly industrializing countries, *e.g.* the Pearl River estuary in China. We know very little about oceanographic conditions in the least populated parts of the planet - in the open ocean and oceanic islands - however it is clear that some of these systems are affected as well. A global network would facilitate and improve capabilities for ocean oxygen monitoring and help identify the knowledge gaps in order to direct further research. New collaborative research is needed to expand global coverage of oxygen data, to revise model calculations and standardize applied methods, to improve predictions related to food security and tourism, and to evaluate impacts on non-market ecosystem services such as carbon sequestration, nutrient cycling, biodiversity, and foodweb support. The global extent and threat to human health and marine ecosystem services of ocean deoxygenation are just beginning to be appreciated; the social and economic consequences have yet to be determined but are likely to be significant. Thus, one of the biggest challenges for future scientific actions is to value the impact of ocean deoxygenation. To date, needed monetary assessments taking the market and non-market consequences of decreased oxygen concentration into account are still very scarce, too general (Mora et al., 2013), or are restricted to certain areas in the world, e.g. the Gulf of Mexico (Rabotyagov et al., 2014).

The good news is that when the cause of hypoxia is eutrophication it is possible to recover oxygen levels even in the deadest of dead zones. However, marine sediments introduce a delay in recovery. Due to the

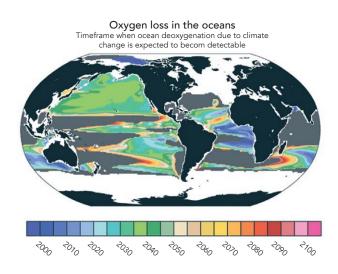
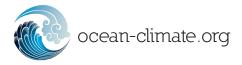


Fig.3 — Time of emergence of the ocean deoxygenation signal against a backdrop of variability (from Long *et al.*, 2016).



non-linearity of marine processes this is difficult to assess and may vary across systems. Moreover, warming will impede the recovery of hypoxic areas, and may require greater reductions in nutrient release to waterways (Capet et al., 2013). Both treatments of human waste and dramatic increases in fertilizer-use efficiency are needed. Institutional capacities for managing waste and nutrients need to be strengthened and installed at the local, national, regional and global levels. New public-private partnerships are also needed across key sectors to stimulate innovation in nutrient reduction and reuse technology. The toolkit for mitigation and adaptation to deoxygenation must be diverse and may include a suite of practices that create a safe space for ecosystems (Scheffer et al., 2015). Among these are water quality management, reduced harvesting or fishery closures during low oxygen seasons, creation of oxygenated refugia or marine protected areas, restoration of circulation or flushing regimes in enclosed water bodies, and control of stress from disease, contaminants, habitat degradation or invasive species. Open-ocean deoxygenation, warming and ocean acidification are all driven by increased atmospheric CO₂. Therefore, the most effective solution to mitigate global environmental change is curbing carbon emissions. It is critical to recognize and understand these climate stressors as cumulative impacts interacting with other human activities, and to manage ocean ecosystems accordingly.

The Ocean's multiple stressor challenge: Elevated temperatures, higher acidity, decreased oxygen

All regions of the ocean are impacted by multiple stressors. The biological response to these is assumed to exhibit a strong variation and complexity. The reduction in local stressors can potentially affect the impact of global drivers. Restricting fisheries can sometimes compensate for mortality and lost production due to hypoxia (Breitburg *et al.*, 2009), but has consequences to human food supplies and economies. In order to manage our ocean sustainably, the impact of multiple stressors has to be considered while calculating and predicting our future marine environment.

While the chemical and physical changes associated with ocean warming, acidification and deoxygenation occur all over the world, the imprint of these global stressors will have a strong regional and local nature. The coalescence of the different global stressors in certain regions is already creating a number of 'hot spots', e.g. the Eastern Boundary Upwelling Regions. In addition to these regional 'hot spots', certain marine ecosystems are highly vulnerable to multiple stressors, e.g. coral reefs. Other examples show that top predators in the marine food web of the Eastern Tropical Pacific, also important for the economic development of certain regions, are impaired by deoxygenation, ocean acidification and temperature increase.

The different levels of response require an assessment, including observations, experiments and forecast models, taking into account the impacts of multiple stressors at the physiological/biogeochemical, the organism, and the ecosystem level.

Following the science, policy has to act to manage the marine resources in light of multiple stressors. Cross-scale governance systems for marine resources need to be developed or implemented. A change of societal behavior should result in reducing local threats, while at the same time a precautionary approach to multiple stressors should be adopted at the global scale. Finally, capacity building is needed in order to transfer the knowledge on data collection, data management and modeling to regions affected by deoxygenation and acidification but where the knowledge and understanding of these processes are still very limited.



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