benchmarks too, allowing the fate of N to be traced from human sources into natural terrestrial ecosystems, the air we breathe and the water we drink. ❒

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Author contributions

B.Z.H. designed the research and wrote the manuscript; A.R.M. and E.B. provided comments and edits. B.Z.H. and E.B. developed the nitrogen isotope model. A.R.M. prepared the figures and ran the CLM model against nitrogen isotopic benchmarks.

COMMENTARY:

Linking coasts and seas to address ocean deoxygenation

Lisa A. Levin and Denise L. Breitburg

Accelerated oxygen loss in both coastal and open oceans is generating complex biological responses; future understanding and management will require holistic integration of currently fragmented oxygen observation and research programmes.

Deoxygenation of the ocean is one of the major manifestations of global change. It accompanies ocean warming and ocean acidification as one of three primary ocean consequences of rising atmospheric CO_2. For the past half century, the study of oxygen stress (hypoxia) — its occurrence, causes and implications for life in the ocean — has been an active area of research. But there have been two separate schools of study, one that addresses eutrophication-induced hypoxia in coastal ecosystems and another that examines naturally occurring oceanic hypoxic zones (including oxygen minimum and limiting zones, and their shoaling into coastal habitats). Each has developed with somewhat different emphases and tools, and largely in isolation of the other. Even within oceanic or coastal realms, geographically based management and funding sources have led to more geographically segregated interactions than might be ideal to stimulate advances in understanding, management and adaptation.

Declines in oxygen have accelerated in recent decades in both realms, as highlighted by Fifth Assessment Report of the IPCC in 2013[1]. The number of eutrophication-induced hypoxic sites reported in the coastal zone has increased by an order of magnitude since the 1960s[2]. At the same time, open-ocean deoxygenation is resulting from a warming ocean, increased stratification and changing circulation[3]. Time-series data reveal an extensive oxygen decline in the northeast Pacific (for example, ref. 4), and a significant expansion of oxygen minimum zones in the tropical and subtropical ocean over the past half century[5].

Coastal and open-ocean hypoxia are largely treated as distinct — spatially and in causality. Adaptation and management discussions generally occur separately. But it is now clear that these phenomena are not distinct and in fact are highly interconnected. Carbon dioxide-induced climate change is increasing the extent and severity of both forms of hypoxia. And we are learning that nutrient enrichment, typically associated with coastal hypoxia, can also worsen oceanic hypoxia by increasing surface-layer production that ultimately fuels microbial respiration at depth. Intensified wind-driven upwelling, related to atmospheric warming and its effect on the depth of waters with low oxygen and low pH, is bathing continental shelves in hypoxic, carbonate-undersaturated waters along the US west coast and in other regions[6], while other areas such as the coasts of Mexico and countries bordering the Bay of Bengal are becoming increasingly vulnerable[7]. Added nutrients and reduced oxygen in upwelling source waters create seasonal dead zones on the inner Oregon Shelf[8]. Excess nutrients from land can stimulate further biogeochemical activity and tip even open-ocean systems into anoxia. At the same

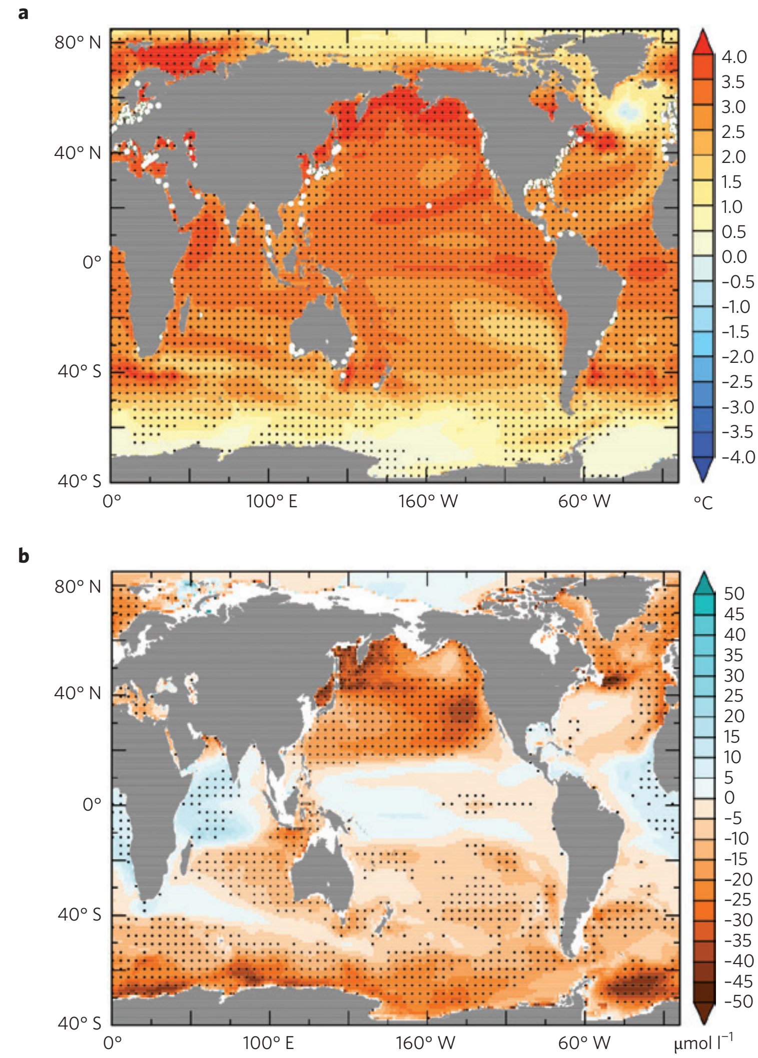

Figure 1 | Both coastal hypoxia and deeper-water deoxygenation are predicted to worsen with increasing global temperatures. **a**, Coastal hypoxia and predicted change in sea surface temperature. Most coastal hypoxia sites (white dots) occur in areas with temperatures predicted to increase by at least 2 °C by the end of this century, a change that is likely to increase the severity and occurrence of oxygen depletion in coastal systems[10]. **b**, Predicted change in oxygen concentration at 200-600 m. Deoxygenation will also become more severe in upper bathyal waters and expand in vertical extent. Maps show end-of-century predictions of the RCP 8.5 'business as usual' models[15]. Panel **a** was generated by combining information from the original publications[10,15] using materials provided by authors. Figure reproduced with permission from ref. 15, © EGU.

time, warmer estuarine and ocean waters carry increasing numbers of eutrophic sites towards hypoxic tipping points and worsen the severity and spatial extent of oxygen depletion in systems historically experiencing hypoxia[9,10]. As a result, continental margins, shelves and estuaries around the world that were previously well-oxygenated now experience hypoxia either seasonally or episodically[10,11].

Declining oxygen content affects virtually all biogeochemical and biological processes within the oceans, either through direct effects on aerobic organisms or indirectly through altered ecological interactions dependent on affected taxa. At the organismal level, insufficient dissolved oxygen can affect growth, reproduction and survival. At higher levels of ecological organization, low dissolved oxygen can affect functional attributes of communities such as productivity, biodiversity, resilience and food-web structure.

Ultimately, these changes caused by deoxygenation can translate into a loss of ecological services on which humans depend. Consequences of worsening hypoxia extend from general issues of ocean health to specific issues of food security, tourism and conservation. On a local scale, fish and shellfish species that support human needs for protein are scarce within hypoxic waters[12] — a problem particularly severe for artisanal fisheries without the mobility to relocate in response to low oxygen events that cause mortality and changes in distributions of fisheries species. Globally, changes in both fish and fisher behaviour in response to hypoxia potentially increase catch rates and deplete stocks[13]. The combined effects of oceanic and coastal hypoxia with warming, acidification, fisheries exploitation and the host of other changes to these systems are largely unknown. Beyond fisheries, hypoxia-altered ecosystems can disrupt habitat support functions, shoreline protections, nutrient cycling, carbon sequestration, recreational activities and more.

What does this mean? There is now an urgent need for unification of expertise directed at advancing knowledge and developing adaptation and mitigation measures relative to oxygen loss in the ocean. A more formal network of oxygen researchers is needed to integrate understanding of coastal and oceanic processes and to focus effort on the common threat of climate change to the oxygen content of all ocean systems. By forming a unified monitoring and research network, scientists can better advance knowledge, and advocate for directing resources to research on deoxygenation and potential mitigation and adaptation measures. In the past decade, practitioners have come together at workshops and symposia, sharing ideas and co-publishing (for example, ref. 14), but much more integration is needed. A communications platform and regular venue for collaborative research that links the communities would aid the formation and productivity of this network. At the international level, coordination could be facilitated by intergovernmental organizations such as the IOC-UNESCO and observing networks such as the Global Ocean Observing System.

A global network of oxygen measurement, monitoring, and analysis that reaches from the upper estuary to the remote open ocean, and from the atmosphere to the deep ocean, will provide the holistic approach needed to address the twenty-first-century changes in ocean oxygen content[15]. Key questions remain about oxygen drivers and the relationship between natural variability and recent trends. These can be answered with strategically placed, timeseries measurements coordinated with other hydrographic data collection. Although such a network could be initiated from existing observation systems (for example the Global Ocean Acidification Observing Network, Argo floats and major time-series stations), additional hypoxia-specific sites will undoubtedly be needed. A global monitoring network will advance mechanistic understanding, inform models and allow for adaptive management of resource extraction, habitat protection and more. This integration of knowledge should extend across time, from anoxic events in the geological past to model predictions in future centuries, using the modern gradients and dynamics as natural laboratories in parallel with manipulative experiments.

A shared observation and data network is critical to enabling broader collaborative, synthetic efforts that can be applied to fisheries and resource management. We now recognize many systems, processes and species that experience deoxygenation influences both from humans on land (through eutrophication) and from the open ocean (through changes to upwelling and the oxygen minimum zone). Fisheries examples include taxa such as salmon with ontogenetic migrations from the watershed or estuary to the open ocean and back. Aquaculture production in fjords, recreational use of coral reefs on human-occupied islands, and biogeochemical cycling of C and N on margins are all examples of issues potentially informed by a broader oxygen network that ties together human and natural drivers. In addition, analyses that span systems with varying relationships between nutrients and hypoxia may better identify effects of hypoxia on the biomass and catch of fisheries species at large spatial scales.

Just as important, a focused effort is needed to communicate to the public, regulators, top politicians and climate negotiators the importance of oxygen in the ocean, the changes that are occurring, the causes and the solutions. Collaboration with organizations expert in translating science to the public and policymakers can help scientists craft their message as well as gain access to important stakeholders. The ocean acidification community has done this well in a remarkably short time; the oxygen community has yet to step forward as a unified voice across all ocean realms. ❐

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