

Oceanographic and Biological Effects of Shoaling of the Oxygen Minimum Zone

William F. Gilly,¹ J. Michael Beman,² Steven Y. Litvin,¹ and Bruce H. Robison³

¹Hopkins Marine Station, Stanford University, Pacific Grove, California 93950; email: lignje@stanford.edu, litvin@stanford.edu

²School of Natural Sciences and Sierra Nevada Research Institute, University of California, Merced, California 95343; email: mbeman@ucmerced.edu

³Monterey Bay Aquarium Research Institute, Moss Landing, California 95039; email: robr@mbari.org

Annu. Rev. Mar. Sci. 2013. 5:393–420

First published online as a Review in Advance on September 17, 2012

The *Annual Review of Marine Science* is online at marine.annualreviews.org

This article's doi:
10.1146/annurev-marine-120710-100849

Copyright © 2013 by Annual Reviews.
All rights reserved

Keywords

hypoxia, ecology, oceans, microbial, mesopelagic, fisheries

Abstract

Long-term declines in oxygen concentrations are evident throughout much of the ocean interior and are particularly acute in midwater oxygen minimum zones (OMZs). These regions are defined by extremely low oxygen concentrations ($<20\text{--}45\ \mu\text{mol kg}^{-1}$), cover wide expanses of the ocean, and are associated with productive oceanic and coastal regions. OMZs have expanded over the past 50 years, and this expansion is predicted to continue as the climate warms worldwide. Shoaling of the upper boundaries of the OMZs accompanies OMZ expansion, and decreased oxygen at shallower depths can affect all marine organisms through multiple direct and indirect mechanisms. Effects include altered microbial processes that produce and consume key nutrients and gases, changes in predator-prey dynamics, and shifts in the abundance and accessibility of commercially fished species. Although many species will be negatively affected by these effects, others may expand their range or exploit new niches. OMZ shoaling is thus likely to have major and far-reaching consequences.

Euphotic zone: the depth range in the water column where sufficient light penetrates to support photosynthesis by phytoplankton; vision by midwater animals generally extends to greater depths

Microbial respiration: consumption of organic matter and oxygen and release of CO₂ by microorganisms, including photosynthetic phytoplankton that respire at night

Oxygen minimum zone (OMZ): a midwater depth range where the oxygen concentration is <20 μmol kg⁻¹ in the Pacific and Indian Oceans or <45 μmol kg⁻¹ in the Atlantic Ocean

Anaerobic microbial processes: reactions using oxidized compounds other than O₂ (e.g., nitrate or sulfate) as an electron acceptor, allowing microbes to persist in the absence of O₂

Oxygen limited zone (OLZ): the region immediately above or below an OMZ with an oxygen concentration of <60 μmol kg⁻¹ in the Pacific and Indian Oceans or <90 μmol kg⁻¹ in the Atlantic Ocean

INTRODUCTION

Oxygen plays a key role in structuring marine ecosystems and controls the spatial and temporal distribution of essentially all marine organisms, from microbes to zooplankton, squid, fish, and (indirectly) marine mammals. Along with light, temperature, salinity, and dissolved nutrients, the concentration of dissolved oxygen in the ocean varies greatly with depth. Sunlight heats the epipelagic (surface) layer of the ocean and drives photosynthesis by phytoplankton (primary production), leading to thermal stratification and the export of production from the euphotic zone to depth. Below the euphotic zone, microbial respiration consumes oxygen, causing oxygen to decline. However, in certain areas where surface production is elevated and the deep circulation of oxygen-rich water derived from polar regions is sluggish, microbial respiration consumes substantial quantities of oxygen that are only slowly replenished, forming steady-state low-oxygen zones in the water column. In such areas, oxygen falls to very low values and then rises again as depth increases; these areas are called oxygen minimum zones (OMZs) (Wyrтки 1962, Fiedler & Talley 2006, Pennington et al. 2007, Karstensen et al. 2008, Fuenzalida et al. 2009, Paulmier & Ruiz-Pino 2009, Keeling et al. 2010, Stramma et al. 2010).

OMZs: WHAT ARE THEY?

An all-encompassing definition of an OMZ based on absolute oxygen concentrations is not realistic, because no single oxygen concentration defines a universal level of hypoxic stress for marine organisms (Seibel 2011). OMZs in the eastern Pacific, the primary focus of this review, are characterized by an oxygen saturation level that is <~10% of that at the sea surface. This corresponds to an oxygen concentration of <20 μmol kg⁻¹ (0.5 ml liter⁻¹ or 0.7 mg liter⁻¹) (Levin 2003b, Helly & Levin 2004, Paulmier & Ruiz-Pino 2009), a value close to that where anaerobic microbial processes become dominant (5–20 μmol kg⁻¹) (Karstensen et al. 2008, A.F. Hofmann et al. 2011). Oxygen levels this low are severely hypoxic for most familiar large organisms, and metazoans inhabiting such strong OMZs show a variety of adaptations to hypoxia (Childress 1995, Childress & Seibel 1998, Drazen & Seibel 2007, Seibel 2011).

Although this definition of an OMZ based on microbial activity is nonarbitrary and useful in the eastern Pacific and Indian Oceans (**Figure 1**), it is not universally applicable. Well-defined OMZs exist in the eastern Atlantic (Stramma et al. 2008a,b, 2010), but the oxygen concentration in the core of the strongest Atlantic OMZ is >20 μmol kg⁻¹, which is significantly higher than those in the Pacific and Indian Ocean OMZs, where the oxygen level can approach zero (Karstensen et al. 2008, Canfield et al. 2010). This complicates identifying a specific oxygen boundary for Atlantic OMZs, but a concentration of <45 μmol kg⁻¹ has been proposed to define OMZs in this region (Karstensen et al. 2008).

These definitions of an OMZ are consistent with physiological data indicating that an oxygen concentration range of 60–120 μmol kg⁻¹ is seriously hypoxic for many marine organisms (Diaz & Rosenberg 1995, Miller et al. 2002, Vaquer-Sunyer & Duarte 2008; tolerances of OMZ-associated species are discussed in Ekau et al. 2010). The lower end of this range leads to hypoxic stress for many marine organisms (Seibel 2011) and has often been used to define hypoxic habitats at depth (Whitney et al. 2007, Bograd et al. 2008, Ekau et al. 2010, Keeling et al. 2010). For the Pacific and Indian Oceans, we therefore use an oxygen concentration of <60 μmol kg⁻¹ to define the hypoxic regions above and below an OMZ's vertical boundaries as oxygen limited zones (OLZs) (**Figure 2a**) (Gilly et al. 2012). These regions are sometimes called oxyclines, but this term is obviously imprecise. An oxygen concentration of <90 μmol kg⁻¹ has been proposed to define analogous OLZs in the eastern Atlantic Ocean (Karstensen et al. 2008).

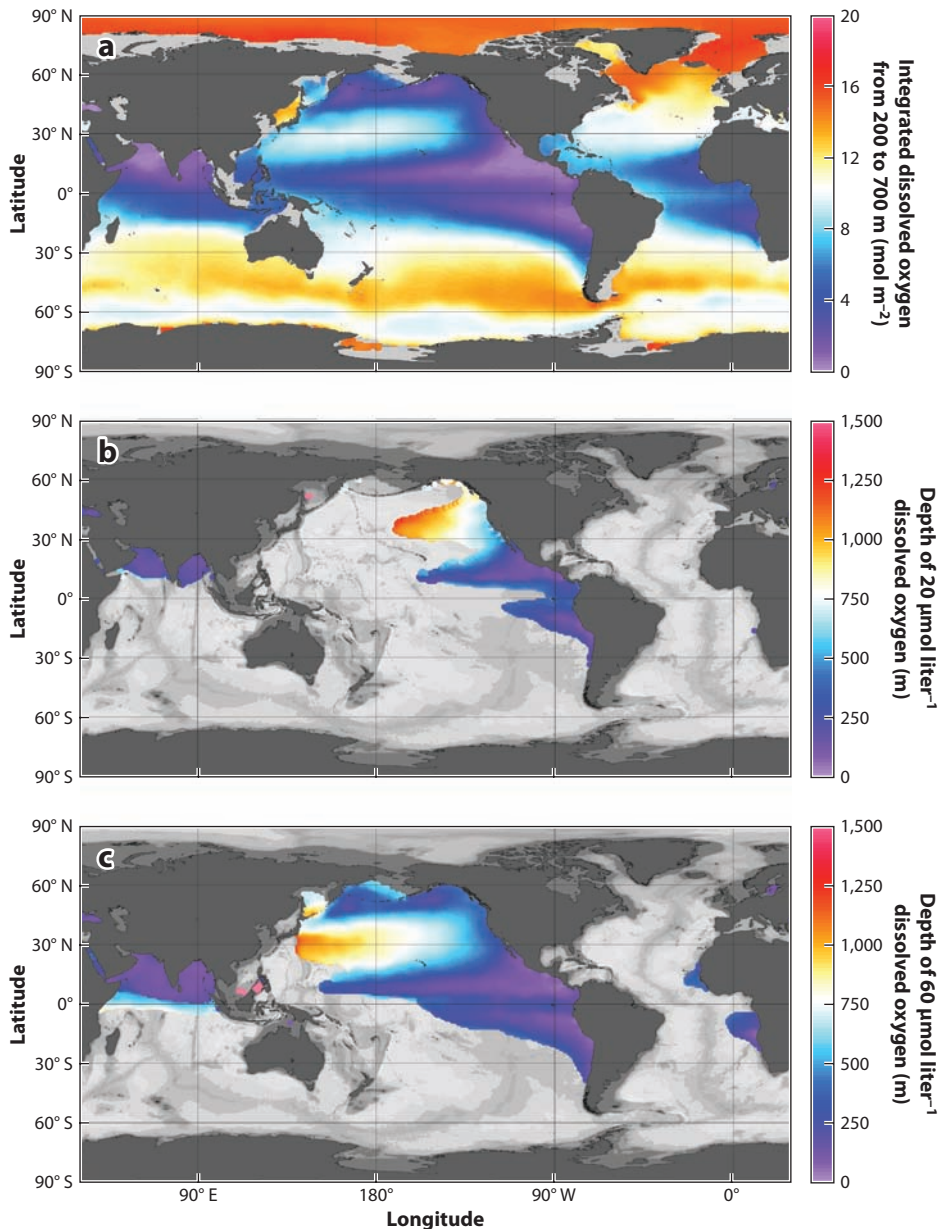


Figure 1

Oceanic oxygen minimum zones (OMZs). (a) Integrated dissolved oxygen concentrations from 200 to 700 m depth in the water column (Garcia et al. 2006). Purple areas are regions with strong OMZs. Only the Pacific and Indian Oceans have areas with values of <2 mol m⁻². (b) Depths of the 20 $\mu\text{mol liter}^{-1}$ oxygen isopleths that define the upper boundaries of the strong OMZs in the eastern Pacific and Indian Oceans. Oxygen concentrations in the gray areas are >20 $\mu\text{mol liter}^{-1}$. (c) Depths of the 60 $\mu\text{mol liter}^{-1}$ oxygen isopleths that we use to define the upper boundaries of the oxygen limited zones (OLZs), hypoxic areas above the OMZs proper. Oxygen concentrations in the gray areas are >60 $\mu\text{mol liter}^{-1}$. The units of $\mu\text{mol liter}^{-1}$ and $\mu\text{mol kg}^{-1}$ are not the same, but they are interchangeable for our purposes here.

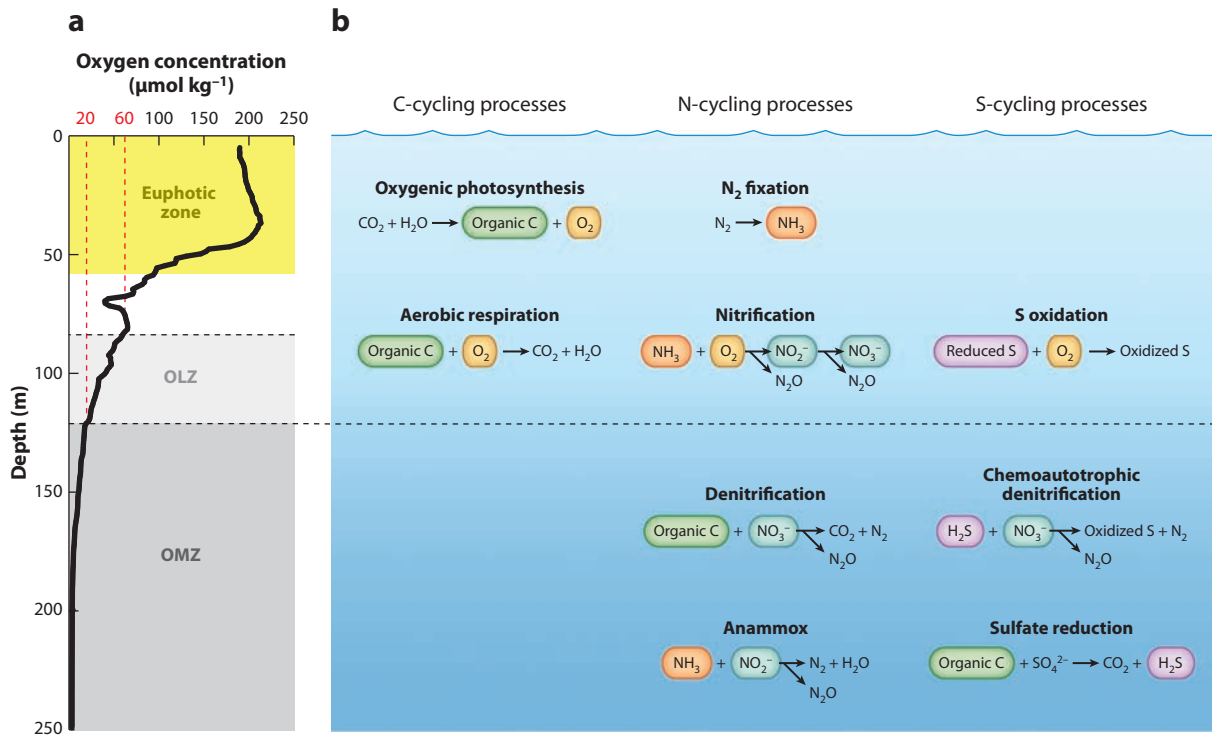


Figure 2

Microbial biogeochemical processes active in oxygen minimum zones (OMZs) and the oxygenated ocean. (a) Characteristic depth profile for dissolved oxygen in the eastern tropical North Pacific (Beman et al. 2012), indicating the depths of the euphotic zone (yellow), oxygen limited zone (OLZ; light gray), and OMZ (dark gray) as defined in this review. (b) Schematic of C-, N-, and S-cycling processes in the ocean. The colors of reactants and products indicate potential coupling and competition among different processes. Within the N cycle, microbial N_2 fixation converts N_2 gas into usable forms of N; in this case we depict ammonia (NH_3), which exists in a pH-sensitive equilibrium with ammonium (NH_4^+) in the ocean. Nitrification is the overall oxidation of ammonia to nitrate (NO_3^-), but it occurs in the distinct steps of the oxidation of ammonia to nitrite (NO_2^-) and the oxidation of nitrite to nitrate. Denitrification and anaerobic ammonium oxidation (anammox) use nitrate or nitrite to oxidize organic C (denitrification), ammonium (anammox), or sulfide (chemoautotrophic denitrification) in an OMZ, eventually producing N_2 gas. Ammonia oxidation, denitrification, and anammox are all known to produce nitrous oxide (N_2O), and ammonia oxidizers do so via two pathways indicated in the panel (note that nitrite oxidizers are not known to produce N_2O). Redox couples for the illustrated reactions are approximate, as exact values depend on the coupling of individual reactions (Falkowski et al. 2008) and the chemical compositions of different substrates (Lam & Kuypers 2011). Panel b is based on information in Francis et al. (2007), Falkowski et al. (2008), Lam & Kuypers (2011), and Wright et al. (2012).

OMZs: WHY ARE THEY IMPORTANT?

Naturally occurring OMZ/OLZ environments are not localized “dead zones” like those associated with eutrophication in coastal waters, including the Gulf of Mexico (Rabalais et al. 2002, Diaz & Rosenberg 2008, Turner et al. 2008); instead, they are permanent midwater features associated with broad, productive expanses of the ocean. The world’s largest OMZ is found in the eastern Pacific beneath the high surface production characteristic of the upwelling-driven Peru (Humboldt) and California Current systems and their equatorial convergence zone. The upper boundary region of all OMZs and their overlying OLZs play an important ecological role in these systems, because vast amounts of micronekton, particularly krill and myctophid fishes, take refuge from visually oriented predators in this hypoxic region during daytime. These small organisms

Micronekton: small, actively swimming organisms that are larger than zooplankton (e.g., small crustaceans, fish, and molluscs)

compress into discrete layers that can be detected acoustically using sonar, and a deep scattering layer (DSL) often lies in the OLZs or near the upper (and lower) boundary of an OMZ (Cornejo & Koppelman 2006, Bertrand et al. 2010, Koslow et al. 2011, Klevjer et al. 2012). Dense aggregations of mesopelagic organisms in these DSLs provide a rich daytime foraging ground for a wide variety of deep-diving pelagic predators in the eastern Pacific, including swordfish (Carey & Robison 1981, Dewar et al. 2011), tunas (Schaefer & Fuller 2010, Schaefer et al. 2011), sharks (Nakano et al. 2003, Jorgensen et al. 2009, Nasby-Lucas et al. 2011), squid (Gilly et al. 2006, 2012; J.S. Stewart et al. 2012), elephant seals (Le Boeuf et al. 2000, DeLong & Stewart 2006), and sperm whales (Davis et al. 2007). At night, much of the DSL community migrates into near-surface waters to feed on plankton and, in turn, provides forage for nocturnal pelagic predators. The DSLs are a vital and dynamic component of productive, upwelling-driven ecosystems with pronounced OMZs. Together, the DSLs and OMZs provide a structural framework for trophic interactions and food webs that connect the mesopelagic and epipelagic environments (Robison 2009).

Productive pelagic zones above strong OMZs in eastern-boundary-current upwelling systems (the Peru and California Current systems in the Pacific and the Benguela and Canary Islands systems in the Atlantic) also support a major fraction of the world's capture fisheries. United Nations Food and Agricultural Organization (FAO) fishing zones that include much of the Peru and California Currents (areas 87 and 77, respectively) constitute 22% of all marine fishing areas, yet they produced 49% of the world's landings of herrings, anchovies, and sardines during 2005–2009 (FAO 2011). These fishes feed on zooplankton, including members of the daytime DSL community. A shallow OMZ in the Peru Current is thought to concentrate the anchoveta—which represents the world's largest single-species fishery—into a narrow surface layer that can be fished more efficiently (Chavez & Messié 2009). This is one reason that the Peru Current produces 10 times more fish than the California Current, despite the comparable levels of primary production in the two systems (Chavez et al. 2008, Brochier et al. 2011). Thus, oxygen in the water column plays an important role in structuring ecosystems and fisheries in the Peru Current (see Fisheries, below).

EXPANSION AND SHOALING OF OMZs

Worldwide shoaling of the upper OMZ boundaries has been documented in all major eastern-boundary-current OMZs over the past several decades (Whitney et al. 2007, Bograd et al. 2008, Stramma et al. 2008b) as well as in strong OMZs (i.e., oxygen concentrations of $<20 \mu\text{mol kg}^{-1}$) in the Bay of Bengal and Arabian Sea (Stramma et al. 2010). In some cases the lower OMZ boundaries have also shifted to greater depths (Stramma et al. 2008b), but this feature has not been monitored as frequently. Shoaling of an OMZ upper boundary (and sinking of the lower boundary) thus increases the OMZ volume in a given area. In some cases the minimum oxygen concentrations in the OMZ cores have also decreased, intensifying the OMZ (Chan et al. 2008, Stramma et al. 2008b). Keeling et al. (2010) have provided detailed tabulations of oxygen declines and volume changes in different OMZs.

OMZ shoaling also translates into horizontal expansion, because the geographical area encompassed by the OMZ upper boundary at a given depth will increase. In the northeastern Pacific, OMZ depth varies with latitude (Helly & Levin 2004), with the upper boundary occurring at 150 m or less in tropical regions as opposed to 500–600 m north of central California (**Figure 3**). The upper boundaries and thicknesses of the OLZs (over the OMZs) also vary greatly, and in tropical regions overlap with the euphotic zone may occur (**Figure 3a**) (Fuenzalida et al. 2009). As discussed below, this overlap has important ecological implications.

On a global scale, the maximum rate of oxygen decrease at a depth of 200 m (generally close to the OLZ upper boundary of $60 \mu\text{mol kg}^{-1}$) since the 1960s has been approximately

Myctophid fishes: immensely abundant and diverse fishes (family Myctophidae) known as lanternfish, which generally undertake diel vertical migrations

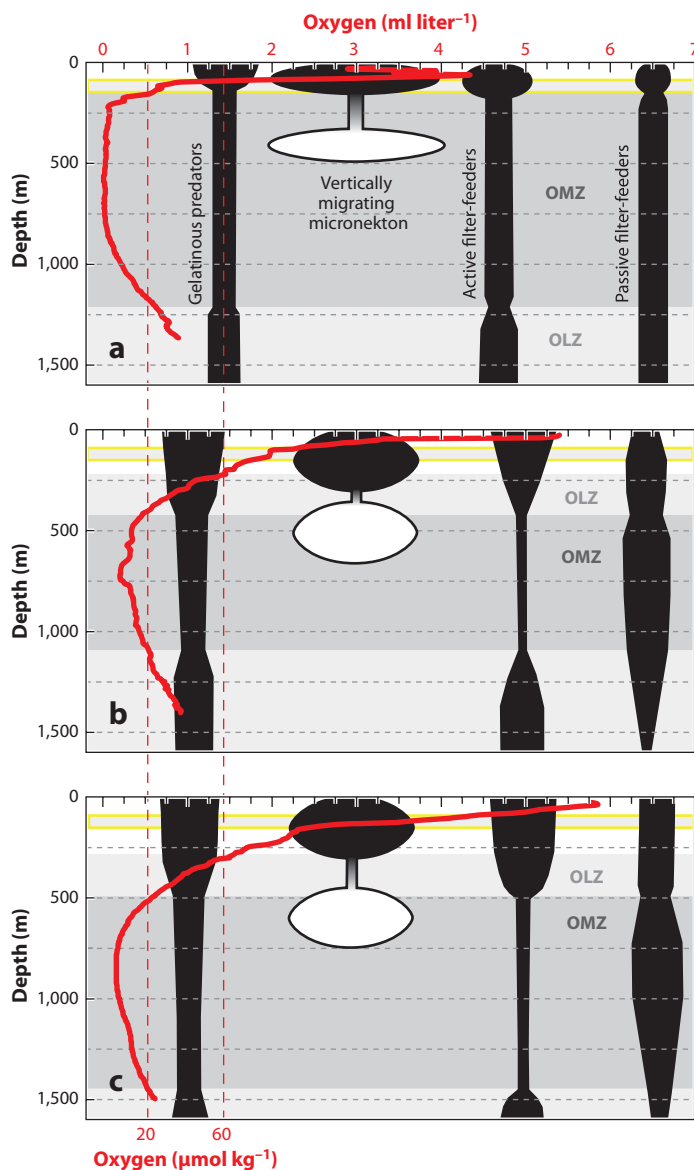
Deep scattering layer (DSL):

a dense collection of micronekton and zooplankton in the water column that can be detected by acoustic backscattering from sonar

Food and Agricultural Organization of the United Nations

(FAO): organization that maintains historical records of worldwide capture fisheries by fishing area, country, species, etc., and issues annual fishery status reports

0.5 $\mu\text{mol kg}^{-1} \text{ year}^{-1}$ over the Atlantic and equatorial eastern Pacific OMZs (Stramma et al. 2010). A similar rate of decrease occurred in the Gulf of Alaska during this time, corresponding to a shoaling of the upper OLZ boundary by ~ 100 m (Whitney et al. 2007). Rates three- to fourfold higher (at 200 m) were observed in a more localized area over a shorter period (1984–2006), with the OLZ upper boundary shoaling 70 m in the southern California Bight (Bograd et al. 2008). In both the southern California Bight (McClatchie et al. 2010) and the Gulf of Alaska (Whitney et al. 2007), the shoaling rate of the upper OMZ boundary (oxygen concentration of 20 $\mu\text{mol kg}^{-1}$) has been smaller than that reported for the OLZ boundary. Whether this is generally true is not clear, but in all cases both OMZ and OLZ upper boundaries are shoaling. Recent work on the Oregon shelf has revealed large differences in the degree of shoaling at a nearshore site (5 nautical miles from the coast) for



different oxygen isopleths since 1960, with the largest change (60 m) occurring in the OMZ upper boundary but almost no change (~5 m) occurring in the upper OLZ boundary (Pierce et al. 2012).

Whether ongoing OMZ/OLZ expansions are monotonic or cyclic is a key question, but in most cases the answer is unclear. In the California Current, decadal variation in the depth of the OLZ upper boundary appears to be linked to the Pacific Decadal Oscillation (PDO) (McClatchie et al. 2010, Deutsch et al. 2011), and a similar coupling is evident in the Gulf of Alaska (Whitney et al. 2007). Given the complexities of multidecadal atmospheric cycles and the long delays in the delivery of source water by currents across ocean basins, our understanding of these dynamics based on empirical data remains limited. Unfortunately, historical oxygen-at-depth measurements do not allow the identification of reliable historical baselines beyond 50–70 years before present. Considerable uncertainty therefore remains in distinguishing long-term trends from multidecadal cycles of OMZ shoaling.

CAUSES OF OMZ EXPANSION

Overall ocean oxygen content (within a 100–1,000 m depth range) is decreasing globally, but at rates ~10% of those cited above for specific OMZ/OLZ environments (Helm et al. 2011, Stramma et al. 2012). This deoxygenation is mechanistically linked to OMZ expansions, because global declines of ocean oxygen will modify the source water that ventilates OMZs from within the water column. These declines and their drivers have been thoroughly reviewed (Keeling et al. 2010). To summarize, large-scale climate change causes the oceans to absorb more heat, resulting in less dissolved oxygen at the surface (decreased solubility) and increased stratification of near-surface waters. This reduces subsurface mixing and transfer of atmospheric oxygen into the water column. Alterations of oceanic circulation patterns can also reduce ventilation from within the water column. These conclusions are based largely on modeling approaches that predict that global oxygen decline will continue in the future (Keeling et al. 2010). Oxygen decline will thus be influenced by a number of processes that will collectively determine the progression of decline in different oceanic regions and link general deoxygenation to OMZ expansion (Stramma et al. 2012).

Although physical influences of climate change and multidecadal oscillations are thought to be the primary drivers of ocean deoxygenation and expanding OMZs, biological mechanisms are also relevant. Primary production is key. Higher surface productivity creates more organic material,

←

Figure 3

Depth, thickness, and intensity of oxygen minimum zones (OMZs) and their inhabitants, which can vary with location. Depth profiles for dissolved oxygen are in red (B.H. Robison, unpublished data). The OMZ (*dark gray*) in each panel is the depth range over which the oxygen concentration is $<20 \mu\text{mol kg}^{-1}$ ($0.5 \text{ ml liter}^{-1}$); the oxygen limited zone (OLZ; *light gray*) is the region above (and below) the OMZ where the oxygen concentration is $>20 \mu\text{mol kg}^{-1}$ and $<60 \mu\text{mol kg}^{-1}$. The black polygons represent the approximate proportional distributions of four mesopelagic faunal groups as surveyed in Monterey Bay Aquarium Research Institute remotely operated vehicle (ROV) operations (B.H. Robison, unpublished data). The daytime distributions of vertically migrating micronekton are in white. (a) Farallon Basin, Gulf of California, 2003: The OMZ starts at ~150 m, and the oxygen level in the OMZ core reaches extremely low values. The OLZ overlying the OMZ (*light gray bordered by yellow*) is extremely narrow and would overlap with the euphotic zone. (b) Monterey Submarine Canyon, California, 2009: The upper OMZ begins at ~450 m; the oxygen level in the OMZ core is greater than that in the Farallon Basin. The OLZ is much broader and would reach slightly deeper than the euphotic zone. The yellow-bordered gray band represents the depth of the OLZ in the Farallon Basin. (c) Astoria Canyon, Oregon, 2006: The OMZ is deeper than that in the Monterey Submarine Canyon; the minimum oxygen level is similar, but the lower boundary is much deeper. The OLZ is also deeper than that in the Monterey Submarine Canyon.

Deoxygenation:

a general decrease in oxygen concentration throughout the water column of the world ocean

Ocean acidification:

decrease in ocean pH caused by the dissolution of human-generated CO₂ emissions in seawater

which is eventually consumed by midwater microbial communities, and increased surface production could thereby stimulate oxygen decline at depth. Primary production may be increasing in large parts of the world ocean (Chavez et al. 2011), but other studies have detected a global decrease in phytoplankton biomass over the past century (Boyce et al. 2010). Regardless of the mean global trend, there are critical differences between specific oceanic regions in regard to changes in primary production. Decreased production in open-ocean oligotrophic regions might lead to a global decrease in overall production (Behrenfeld et al. 2006, Polovina et al. 2008, Doney et al. 2012), whereas production and phytoplankton biomass may be concurrently increasing in productive surface waters overlying OMZs (Gregg et al. 2005, Behrenfeld et al. 2006). These observations are consistent with a strengthening of land-sea temperature gradients and alongshore winds, leading to enhanced coastal upwelling and increased production (Bakun et al. 2010, Doney et al. 2012).

A long-term increase in production in these upwelling regions must be considered in conjunction with OMZ expansions. Analyses of sediment cores off Peru indicate that during the Little Ice Age (1400–1800 AD), the ocean off Peru was cold, with high subsurface oxygen and low surface nutrients, primary productivity, and fish abundance. At the end of this period, warming conditions led abruptly to an upwelling-driven ecosystem with the low subsurface oxygen and shallow OMZ that today characterize the highly productive Peru Current system (Chavez et al. 2008, 2011). A decrease of bottom-water oxygen over the past 200 years is also suggested by cores in northern Chile (Díaz-Ochoa et al. 2010).

These studies indicate that biological responses to changes in ocean circulation, stratification, and upwelling—ultimately driven by climate change and oscillations—will play a key role in future ocean deoxygenation and OMZ expansion. Other forms of global change, such as ocean acidification (Gao et al. 2012) and reactive nitrogen (N) deposition (Duce et al. 2008), can also alter primary production and potentially influence subsurface oxygen concentrations. More fundamentally, physiological responses to warmer temperatures may lead to enhanced surface production (Behrenfeld 2011) and accelerated respiration of organic material at depth, because heterotrophic microbes may generally be more temperature sensitive than phytoplankton (Wohlers et al. 2009, Sarmiento et al. 2010, Doney et al. 2012). Additional study of these biological drivers of deoxygenation and OMZ expansion is clearly needed.

CONSEQUENCES OF OMZ EXPANSION

Although oceanographic changes accompanying OMZ expansion may be fairly well understood, we are much less certain about how individual species and ecosystems will be affected. Discussion of ecological responses has focused largely on benthic organisms that inhabit continental-shelf environments and hypoxic basins (Levin 2003a,b; Levin et al. 2009), with less attention paid to pelagic organisms (Stramma et al. 2010). Hypoxia is intimately linked to thermal stress (Pörtner & Farrell 2008), and the interaction of these stressors applies to any environment influenced by changing oxygen concentration or temperature. We assume that physical changes in the water column directly associated with OMZ expansion exert their effects primarily through oxygen concentration, but OMZ shoaling is accompanied by small increases in temperature, most notably in the upper OLZ. Temperature-related effects are more important at shallower depths, and because many midwater organisms transiently inhabit the near-surface epipelagic zone at night, the combined effects of decreasing oxygen and increasing temperature on mesopelagic organisms may prove to be more important than we presently suspect.

As has been discussed in depth for a variety of taxa (Ekau et al. 2010), decreased oxygen can affect individual organisms in many ways, including acute physiological impairment, changes in growth and reproductive success, and movement of mobile forms to more favorable oxygen regimes (either

horizontally or vertically). At the ecosystem level, the different tolerances of various species to a changing environment will result in differential success among species and concomitant alterations of community structure and trophic webs. Effects of this latter sort are inherently nonlinear and extremely difficult to predict. We review here what is known about the effects of expanding OMZs on selected nonbenthic taxa, primarily in the eastern Pacific.

Microbial Communities

Microbial communities will be strongly affected by the expansion and shoaling of OMZs; as oxygen declines, more production and energy flow through heterotrophic microbial communities rather than through higher trophic levels (Diaz & Rosenberg 2008, Wright et al. 2012). Three key changes in microbial communities and microbe-mediated biogeochemical cycles are likely to be consequences of OMZ expansion, intensification, and shoaling: alteration of the N cycle, the emergence of sulfur (S) cycling, and the creation of new low-oxygen habitats.

OMZ expansion and alteration of the nitrogen cycle. OMZ expansion and shoaling have the potential to fundamentally alter the N cycle owing to variability in the sensitivity of different N-cycling processes to light, oxygen, pH, and other environmental factors. Several recent reviews have provided excellent coverage of the complex oceanic N cycle (Capone et al. 2008, Lam & Kuypers 2011, Zehr & Kudela 2011). In general, the open-ocean N cycle is characterized by vertical layering (Codispoti & Christensen 1985), with N₂ fixation occurring in the euphotic zone, nitrification at the base of the euphotic zone, and anaerobic N-cycling processes [denitrification and anaerobic ammonium oxidation (anammox)] within OMZs, where they reduce available N to gaseous forms that are unusable by most organisms and eventually lost to the atmosphere (**Figure 2b**).

Recent modeling results for the eastern tropical Pacific indicate that the rate of overall N loss is highly sensitive to the volume of suboxic (oxygen concentration of $<5 \mu\text{mol kg}^{-1}$) water present, which in turn changes much more rapidly than overall ocean oxygen content: Doubling the volume of suboxic water requires only a 1% drop ($\sim 2 \mu\text{M}$) in the mean oxygen of the upper ocean, and the rate of N loss varies fourfold in response to this doubling of suboxic volume (Deutsch et al. 2011). This defines a potentially important negative feedback where OMZ expansion leads to increased rates of anammox and denitrification, which effectively removes large quantities of N from the water column. Because upwelled N can be a limiting nutrient for phytoplankton growth, surface primary production would be reduced. In turn, this would reduce export of organic material to depth, resulting in reduced oxygen consumption via respiration and a braking influence on OMZ expansion (Deutsch et al. 2011).

Denitrification and anammox also produce nitrous oxide (N₂O) (Francis et al. 2007, Kartal et al. 2007) in OMZs, and OMZ expansion is expected to lead to increased production of this ozone-destroying greenhouse gas (Ravishankara et al. 2009, Codispoti 2010). This stems from both additional OMZ volume and enhanced N₂O yield from the aerobic process of nitrification under low oxygen concentrations (Goreau et al. 1980, Frame & Casciotti 2010). Recent findings indicate that the abundant and widespread ammonia-oxidizing archaea (Francis et al. 2007) produce N₂O in the sea (Santoro et al. 2011) and that chemoautotrophic S-oxidizing denitrifiers (see below) also have the genetic capability to produce N₂O (Walsh et al. 2009). OMZs are a significant source of N₂O to the atmosphere—producing about half of all oceanic emissions (Codispoti 2010), which represent at least 20% of total global emissions (Nevison et al. 2003)—but with multiple microbial groups and pathways involved in N₂O production, predicting future emissions from OMZs is presently challenging.

At the same time, OMZ waters also have low pH, because microbial respiration generates carbon dioxide (CO₂) and carbonic acid (H₂CO₃) as it consumes oxygen (Brewer & Peltzer

OCEAN ACIDIFICATION

Ocean acidification refers to the decrease in ocean pH caused by the dissolution of human-generated CO₂ emissions in seawater; this produces a weak acid and has reduced surface ocean pH by ~0.1 units since the Industrial Revolution (Doney et al. 2009). Because microbial respiration consumes oxygen and produces CO₂, pH and oxygen track each other in the ocean (Brewer & Peltzer 2009, Dore et al. 2009), and OMZs are naturally low in pH. OMZ shoaling consequently represents shoaling of low-pH water, but the additional acidity contributed by human-generated CO₂ emissions further reduces pH at shallower depths. This can create corrosive conditions during upwelling events along the west coast of North America (Feely et al. 2008). A rapidly growing body of research has examined the effects of ocean acidification on marine organisms because pH is fundamental for many of them, and a subset of this research has examined the related stressor of ocean warming. However, ocean acidification, deoxygenation, and warming together represent a triple whammy for marine life (Gruber 2011), and the responses of entire communities and ecosystems to such multifactorial environmental changes are extremely difficult to simulate and ultimately to predict (Doney et al. 2012).

2009). Ocean acidification experiments indicate that reduced pH increases N₂-fixation rates and decreases nitrification rates (Hutchins et al. 2009, Beman et al. 2011, Kitidis et al. 2011) (see sidebar Ocean Acidification). N₂ fixers may also be favored by shoaling of OMZ waters, because N is removed by anammox/denitrification in OMZs, producing N deficits relative to other nutrients (Deutsch et al. 2007, White et al. 2007).

OMZ intensification and the emergence of sulfur cycling. A recent study in the Chilean OMZ uncovered a “cryptic sulfur cycle” in which sulfate is reduced to sulfide (HS⁻ or H₂S; **Figure 2b**)—which is toxic to most organisms—and subsequently rapidly oxidized, preventing its accumulation (Canfield et al. 2010). Sulfate reduction is common in marine sediments and within anoxic basins, but the significance of this process in expanding OMZs is currently unknown. Sulfate-reducing bacteria were detected in the Arabian Sea OMZ (Fuchs et al. 2005), but their activity was not established. Plumes of sulfide produced in anoxic sediments off the coast of Namibia were detoxified by S-oxidizing bacteria (Lavik et al. 2009), and many of the same groups were active in the Peru Current OMZ.

These results indicate that high rates of oxidation can control sulfide levels in the ocean (Lavik et al. 2009, Canfield et al. 2010), but the distribution of the involved organisms, their rates of activity, and their sensitivity to oxygen have not been intensively studied—particularly in the context of future OMZ expansion. The S oxidizers ARCTIC96BD-19, SUP05, and *Arcobacter* found in OMZs (Fuchs et al. 2005, Stevens & Ulloa 2008, Lavik et al. 2009, Ma et al. 2009) may present a successional sequence as oxygen concentrations decrease (Wright et al. 2012). The ARCTIC96BD-19 group evidently oxidizes reduced S aerobically (Swan et al. 2011), whereas SUP05 bacteria use nitrate and/or nitrite as an electron acceptor during chemoautotrophic denitrification (Lavik et al. 2009, Walsh et al. 2009, Canfield et al. 2010, Lam & Kuypers 2011). This links N and S cycling, and these bacterial groups may provide a critical ecosystem service in OMZs.

Creation of new low-oxygen habitats at the upper boundaries of shoaling OMZs. Understanding the community ecology of microbes in OMZs will be essential as these regions expand vertically. Hypoxic OMZ/OLZ waters are typically found below the euphotic zone, but OMZs overlap with the euphotic zone in the eastern tropical Pacific, Peru Current, and Indian Ocean

(Figure 3) (Fuenzalida et al. 2009). Obviously the production of oxygen by photosynthesis will preclude major deoxygenation within the upper euphotic (epipelagic) zone, but deeper low-oxygen habitats with available light will likely expand as OMZs shoal, particularly in the California Current system (see below). This will have key effects on C, N, and S cycling, but the ultimate biogeochemical outcome is difficult to predict, because many interacting microbial groups and processes are likely to be affected.

For instance, although the cyanobacterium *Prochlorococcus* is widespread in tropical oceans and accounts for a large percentage of global primary production, specific strains inhabit the OMZs listed above, where they appear to outcompete eukaryotic phytoplankton under low oxygen concentrations (Goerick et al. 2000, Lavin et al. 2010). OMZ shoaling into the euphotic zone may expand this niche.

OMZ shoaling may also alter N cycling through light and oxygen limitation of nitrification, though some of the microorganisms involved appear to be less sensitive than previously thought (Church et al. 2010, Santoro et al. 2010, Kalvelage et al. 2011, Beman et al. 2012). Determining thresholds of sensitivity to light and oxygen will be important, because nitrification supplies oxidized N to anaerobic processes and competes with other organisms for N.

In habitats where both sulfide and light are available, anoxygenic photosynthetic organisms such as the green and purple S bacteria (*Chlorobi* and *Chromatiales*) can form dense plates and oxidize sulfide (Ghosh & Dam 2009). Active sulfate reduction (Canfield et al. 2010) raises the possibility of anoxygenic photosynthesis in the ocean, provided that both sulfide and light are available at the same depth. In the Chilean OMZ, F.J. Stewart et al. (2012) detected transcripts of genes involved in S metabolism from *Chlorobi*, but whether these organisms fix C and oxidize sulfide at appreciable rates, and how widespread this phenomenon might be in other OMZs, are not known.

Altogether, prospective changes in microbial communities driven by OMZ expansion have the potential to alter marine ecosystems and food webs, because they can modify the biogeochemical cycling of key nutrients, substrates, and even toxic compounds.

Mesopelagic Communities

Diminished ambient light is usually used to define the mesopelagic zone, but the OMZ/OLZ environment is not always entirely below the euphotic zone. Instead, we define the upper boundary of the mesopelagic as the $60 \mu\text{mol kg}^{-1}$ oxygen isopleth bounding the OLZ above an OMZ, with the lower boundary being defined by the absence of photons derived from surface illumination. In the northeastern Pacific, including the Gulf of California, the OLZ upper boundary (i.e., the top of the OLZ above the OMZ) corresponds to a depth of $\sim 100\text{--}300$ m, and the lower boundary (i.e., the bottom of the OLZ below the OMZ) corresponds to a depth of $\sim 1,000\text{--}1,500$ m, depending on location (Figure 3). Several relevant reviews of the physiology and ecology of mesopelagic organisms have recently been published (Robison 2009, Ekau et al. 2010, Robison et al. 2010) (see sidebar The Mesopelagic World).

Permanent OMZ residents: habitat expansion. Larger animals that permanently inhabit the California OMZ include species with extremely low metabolic rates, like the slow-moving vampire squid (*Vampyroteuthis infernalis*) (Seibel et al. 1997) and mysid shrimp (*Gnathophausia ingens*), which have enhanced oxygen extraction and transport abilities (Childress 1995). Other common inhabitants include bathylagid owlfishes, the pelagic worm *Poebobius meseres*, filter-feeding tunicates, and a diverse array of abundant cnidarians and ctenophores (Robison 2004).

Data that directly assess changes in abundance or the vertical distributions of such permanent residents in conjunction with OMZ shoaling are not available, but qualitative comparisons of

THE MESOPELAGIC WORLD

This vast midwater region of the oceans was directly explored for the first time in 1930 by William Beebe in his bathysphere:

I was beyond sunlight as far as the human eye could tell, and from here down, for two billion years there had been no day or night . . . until we came to record it. I could now prove without doubt whether continued observations from a window such as this would yield valuable scientific observations, or whether the attainments of these depths must be considered in the light of merely being a stunt, breaking former records. (Beebe 1934, p. 165)

We have since learned a lot about this dark, cold, and hypoxic world. Because of the significant depths involved and the small size and delicate nature of many mesopelagic organisms, ecological studies in this zone have always been challenging. These studies traditionally relied on midwater nets and active acoustics (sonar), but recent applications of ROVs have provided new insights into this important midwater region (Robison et al. 2005, Robison 2009).

daytime remotely operated vehicle (ROV) surveys in locations with large differences in the vertical position and thickness of the OMZ/OLZ have revealed general patterns that might reflect changes in the northern California Current as the OMZ shoals (**Figure 3**). Perhaps the most striking difference was that many nonmigratory active filter-feeders such as salps and larvaceans were crowded into the relatively narrow OLZ in the Gulf of California and were therefore at much shallower depths relative to those in other areas. In contrast, passive detritus feeders like *Poeobius* occurred throughout the mesopelagic water column with minimal vertical zonation in all three locations. Thus, organisms like *Vampyroteuthis* and *Poeobius* will experience a vertical expansion of their habitat, although they will be continuously subjected to lower oxygen concentrations as OMZs intensify. Other species will likely experience a shift in vertical distribution to shallower depths, and an analogous shift to greater depths is expected for those organisms that preferentially inhabit the lower boundary of an OMZ (Childress & Seibel 1998).

Daytime OMZ residents: habitat compression. Most daytime residents of the upper OMZs (and OLZs) are not permanent and undertake a diel vertical migration to near-surface waters at night. Metabolic suppression, reduced levels of activity, and limited anaerobic metabolism are common mechanisms permitting transient occupation of hypoxic depths by these migrators (Childress & Seibel 1998, Ekau et al. 2010, Seibel 2011). Different species vary widely in their tolerance of hypoxia. For example, in California the shrimp *Sergestes similis* actively forages for copepods and krill in the OLZ (~400 m depth) during the day as well as in near-surface waters at night (Pearcy & Forss 1969; B.H. Robison, unpublished observations), and activity does not appear to decrease under OLZ conditions. In contrast, the physonect siphonophore *Nanomia bijuga*, which is also an active OLZ predator and competes with *Sergestes* for prey (Robison et al. 1998, Robison 2004), shows changes in foraging behavior when it descends into the OMZ, suggesting metabolic suppression. Most myctophid fishes are diel vertical migrators that feed on zooplankton at night (Catul et al. 2011). During the day, myctophids occupy the OLZ and upper OMZ, most likely to avoid visual predators (Childress 1995, Robison 2003). At maximum daytime depths and minimum oxygen concentrations, myctophids often appear to be lethargic (Barham 1971; Seibel 2011; B.H. Robison, unpublished observations), consistent with metabolic suppression.

Shoaling of the OMZ upper boundary will tend to shift the daytime distribution of these vertically migrating organisms to shallower depths, vertically compressing their nighttime habitat

and potentially altering predator-prey relationships with nocturnal predators, particularly fishes. Because the species in question vary greatly in hypoxia tolerance, they will not all shift to the same degree, resulting in fragmentation and reassembly of communities with new patterns of competition and interactions, including daytime predator-prey relationships. In the case of shallow OMZs like those in the Peru and California Current systems, such a shift in the preferred daytime depth of mesopelagic migrators into the lower edge of the euphotic zone could also result in a significant increase in ambient light, making these organisms more susceptible to predators that rely on vision to forage in dim light. This effect has been hypothesized to account for the largely selective decline in the abundance of mesopelagic fish larvae in conjunction with shoaling of the OLZ in the southern California Bight, where ambient light at the OLZ upper boundary may have increased by 2.5–7-fold over the past 20 years (Koslow et al. 2011).

Surface mixed layer: the layer of water at the sea surface that is homogenous owing to thorough mixing by wind and wave action

Pelagic Communities

Shoaling and horizontal expansion of OMZs will change the oxygen landscape for essentially all pelagic taxa that are not strictly limited to the surface mixed layer, where oxygen is in equilibrium with the atmosphere. This section considers the effects of deoxygenation and shoaling OMZs on those organisms that inhabit a broadly defined pelagic zone between the surface mixed layer and the OLZ, including some that transiently enter the OMZ itself.

Decreased pelagic habitat: shifting boundaries and compression. As the OMZ environment shoals, benthic and demersal fishes that inhabit depths near the OLZ upper boundary will be subject to hypoxic stress as oxygen decreases, and such species may shift their vertical distribution to shallower depths. This has been documented for Pacific cod (*Gadus macrocephalus*) on the Japanese continental slope over the past 60 years based on historical records of the deepest commercial landings and oxygen at these depths (Ono 2010, Ono et al. 2010).

A shoaling OMZ will also compress the vertical habitat of pelagic fishes that spend time near the surface and undertake dives to OLZ depths to prey on fish and squid that are part of DSL communities. Blue marlin (*Makaira nigricans*) and mako shark (*Isurus oxyrinchus*) (Vetter et al. 2008) often dive to OLZ depths during daytime, but dives in the eastern tropical Pacific, where a strong OMZ exists, are much shallower than those of conspecifics in the western Atlantic, where there is no OMZ, suggesting a limitation due to hypoxia (Prince & Goodyear 2006). Similar patterns are evident for both marlin and sailfish (*Istiophorus albicans*) in the eastern tropical Atlantic (which has a weak OMZ) compared with those in the western Atlantic (Prince et al. 2010). These observations have given rise to the concept of vertical compression of pelagic habitat (between the surface mixed layer and OLZ) in areas overlying OMZs. In the most thoroughly studied case, chronic OMZ expansion has led to an estimated annual loss of vertical habitat of about 1 m year⁻¹ for blue marlin in the eastern tropical Atlantic, representing an overall habitat loss of 15% between 1960 and 2010 (Stramma et al. 2011). As noted above, many large predators in the eastern Pacific regularly forage at OLZ/upper OMZ depths and are therefore also expected to experience vertical habitat compression as the OMZ shoals in this vast region.

Despite negative aspects of a shrinking environment (see Fisheries, below), the foraging success of large predators in oceanic areas with expanding OMZs may be enhanced, because vertical habitat compression can concentrate prey (Prince & Goodyear 2006, Stramma et al. 2011). Pelagic forage fishes like sardines and anchovies are not hypoxia tolerant (Ekau et al. 2010), and changes in subsurface oxygen may be important in several ways. On the Chilean coast, the apparent periodic shoaling of the upper OLZ favors anchovy populations (over sardines) through decreased subsurface oxygen on the continental shelf and concomitant changes in the composition of vertically

migrating zooplankton (Bertrand et al. 2011) (see Fisheries, below). In the case of the Chilean jack mackerel (*Trachurus murphyi*), daytime depth and schooling behavior are strongly influenced by oxygen at depth, with scattered diffuse schools occupying the OLZ (Bertrand et al. 2006). Shoaling of this environmental feature, which is already shallow in the southeastern Pacific, would tend to shift daytime distribution toward the surface, potentially increasing the susceptibility of this commercially important species to epipelagic predators or commercial fishing operations. Shifts in vertical distributions by predators and prey will certainly have local and regional ecological impacts in areas associated with chronically shoaling OMZs, and interactions with decadal-type shoaling processes will become increasingly important to consider.

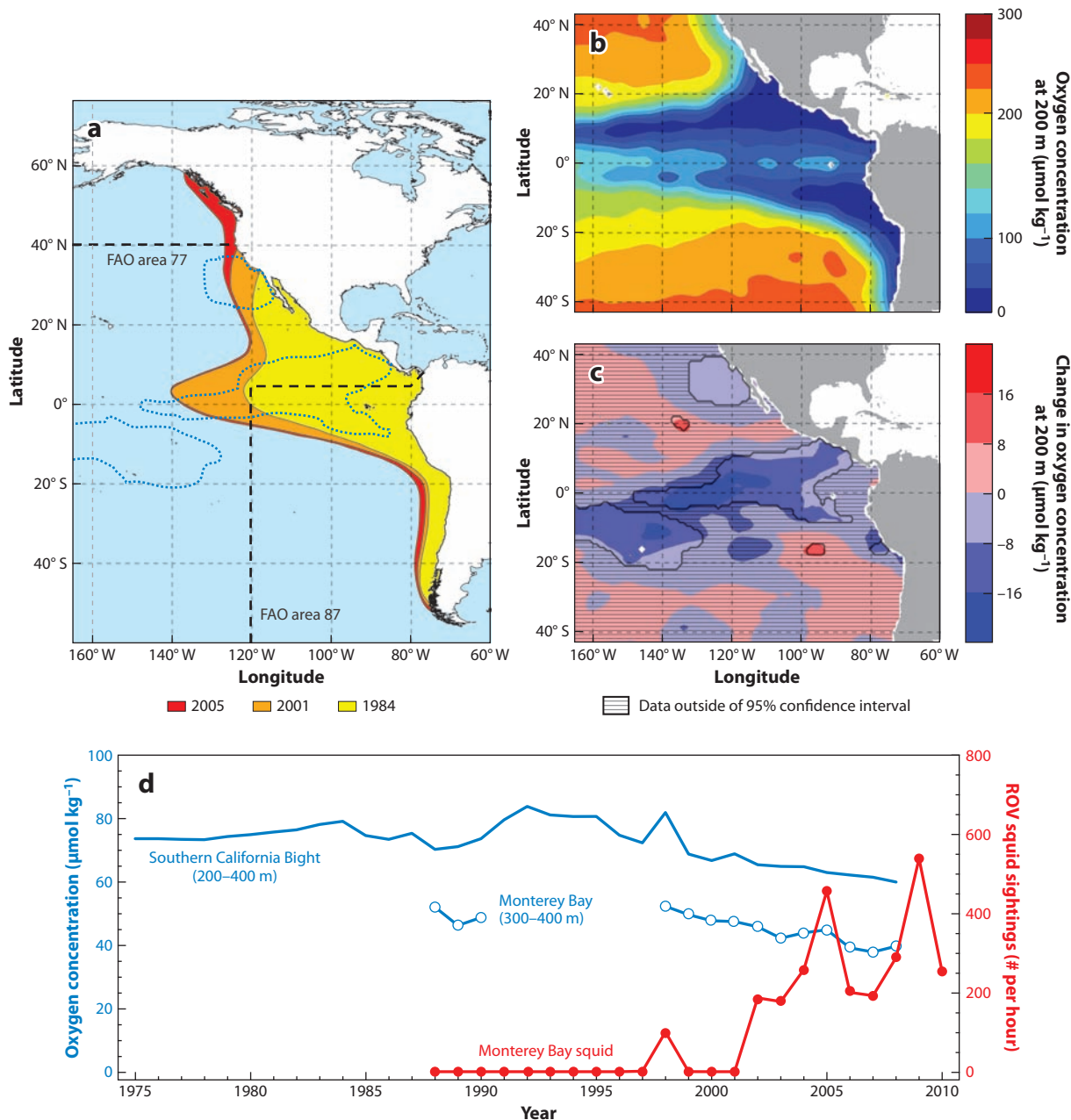
Horizontal expansion of OMZs: range extension. Poleward range shifts of marine species have occurred in conjunction with climate change and warming (Perry et al. 2005, Burrows et al. 2011, Doney et al. 2012), and a similar phenomenon may be expected in conjunction with OMZ shoaling in the northeastern Pacific. Shoaling of the OLZ has been occurring off the California coast during the past 20 years (Bograd et al. 2008), a period in which the Humboldt squid (*Dosidicus gigas*) has expanded its range from a historical northern limit of northern Baja California (1984 range in **Figure 4a**) to southeastern Alaska (2005 range) (Cosgrove 2005, Brodeur et al. 2006, Gilly 2006, Wing 2006, Field et al. 2007). The overall range of *Dosidicus*, an eastern Pacific endemic, corresponds closely to the area encompassed by the OMZ at 200 m depth (**Figure 4b**), and oxygen decreased significantly in the areas where the range expansions were largest—westward at the equator and northward along the Mexican-US Pacific coast (**Figure 4c**). *Dosidicus* arrived in the Monterey Submarine Canyon after the 1997–1998 El Niño, and a persistent presence was established after 2002 (**Figure 4d**) (Zeidberg & Robison 2007), with seasonal excursions as far north as British Columbia (Holmes et al. 2008, Litz et al. 2011, Mazzillo et al. 2011). A similar range expansion during this period also occurred in the Southern Hemisphere (Ibáñez & Cubillos 2007, Alarcón-Muñoz et al. 2008, Keyl et al. 2008).

Comparison of the spatial and temporal relationships between the oxygen decline off California and the rise in squid abundance during this period suggests a relationship between these phenomena, a hypothesis consistent with the known hypoxia tolerance (Gilly et al. 2006), vertical habitat use (Stewart 2012, J.S. Stewart et al. 2012) and diet (Field et al. 2007) of Humboldt squid in the California Current. Based on archival tagging data, this squid regularly inhabits the upper OMZ/OLZ during the day, potentially foraging for DSL organisms (Gilly et al. 2012). A shoaling OMZ/OLZ could benefit the squid through effects on its primary prey, mesopelagic fish, as the OLZ comes to overlap with the lower edge of the euphotic zone (Koslow et al. 2011) or concentrates prey in near-surface regions (see Decreased Pelagic Habitat: Shifting Boundaries and Compression, above).

Figure 4

Humboldt squid range expansion and oxygen decline associated with oxygen minimum zone (OMZ) shoaling. (a) Ranges of squid in 1984 (*yellow*) (Roper et al. 1984), 2001 (*orange*) (Nigmatullin et al. 2001), and 2005 (*red*) (Gilly 2006) (map adapted from Staaf et al. 2011). The boundaries of FAO areas 77 and 87 are indicated by dashed lines. Dotted blue outlines show the areas of significant oxygen decline from panel c. (b) Oxygen concentrations at 200 m depth (data based on Garcia et al. 2006; map adapted from Stramma et al. 2010). (c) Change in oxygen concentration at 200 m depth between 1960–1974 and 1990–2008 (adapted from Stramma et al. 2010). Shaded areas represent data outside of the 95% confidence interval. (d) Oxygen concentrations at 200–400 m depths in the southern California Bight (*blue line*) (data from Koslow et al. 2011) and at 300–400 m depths in Monterey Bay (*blue line with open circles*) (data from MBARI 2008). Both declined over the same period during which squid abundance in Monterey Bay (*red line*) increased. Squid at 200–1,000 m depths were counted from video logs for Monterey Bay Aquarium Research Institute remotely operated vehicle (ROV) dives and normalized by dive time in that depth range for each mission (adapted from Stewart 2012; see also Zeidberg & Robison 2007).

Although this situation might also benefit other pelagic predators that share a vertical distribution with Humboldt squid (Vetter et al. 2008), several adaptations that permit hypoxia tolerance (Rosa & Seibel 2008, 2010; Seibel 2011) and reduced activity levels under OMZ conditions (Gilly et al. 2012) likely give the squid a distinct advantage in using this resource relative to competing predators (J.S. Stewart et al. 2012). Because the OLZ is deeper in the California Current than it is in the Gulf of California, shoaling off California might effectively make the midwater habitat more similar to that in the Gulf of California (Figure 3a,b), where Humboldt squid have been



firmly established since at least the late 1970s, when commercial fishing for this species began in Mexico. In this view, Humboldt squid may simply be expanding into a favorable new midwater habitat in the California Current as it becomes available. Because they are more effective at using this niche, expansion by squid into new areas could potentially displace other predators, as has been hypothesized for the central Gulf of California (Sagarin et al. 2008).

Other factors, including long-term warming and overfishing of competing predators, have been discussed in conjunction with the Humboldt squid range expansion (Zeidberg & Robison 2007, Litz et al. 2011, J.S. Stewart et al. 2012). The overfishing hypothesis has been challenged (Vetter et al. 2008, Watters et al. 2008), but a detailed analysis of this important issue remains to be carried out. The correlation between squid abundance off California and temperature anomalies is not strong on a decadal scale (Stewart 2012), and the extreme thermal tolerance of Humboldt squid (Gilly et al. 2006, 2012) suggests that temperature per se is unlikely to drive range expansion directly. Nonetheless, temperature may be an important seasonal driver. Between 2002 and 2009, Humboldt squid engaged in summer foraging migrations along the US Pacific coast to Canadian waters (Litz et al. 2011, Field et al. 2012), with spawning occurring in Mexican waters or far offshore (Staaf et al. 2011). These migrations are similar to those of other species in the California Current, including hake (*Merluccius productus*) (Ressler et al. 2007) (see Fisheries, below), that are driven by seasonal changes in productivity and temperature and are subject to climatic shifts due to El Niño and the PDO (Ware & Thomson 2005, Checkley & Barth 2009).

The maintenance of seasonal migration behavior undoubtedly involves a suite of physical and biological drivers, and anomalies like El Niño can trigger transient alterations of the distribution of squid as well as other pelagic species (Pearcy 2002). But available evidence strongly suggests that OMZ shoaling and multidecadal oscillations work in concert to either favor or discourage longer-term range expansions of Humboldt squid in a given region.

Fisheries

The collective influences of climate change, global deoxygenation, and shoaling OMZs on individual species, populations, and ecosystems will all affect relevant commercial fisheries and economies (Pörtner & Peck 2010, Polovina et al. 2011, Sumaila et al. 2011, Doney et al. 2012). Although the impacts of hypoxia on fisheries in estuaries and marginal seas are becoming better understood (Breitburg et al. 2009), less is known concerning coastal and open-ocean fisheries associated with highly productive, upwelling-driven systems (Stramma et al. 2010, Zhang et al. 2010). Uncertainties about the hypoxia tolerance of individual species, complexities of predator-prey interactions, and environmental drivers underlying range expansions will be compounded by differential susceptibility of taxa to current and future fishing gear and practices (Parrish 1999). Again, both negative and positive effects on individual fisheries can be anticipated (Ekau et al. 2010, Zhang et al. 2010).

Direct influences of low oxygen on the mortality, development, growth, and reproductive success of individuals of a given species will have demographic implications for fisheries (Grantham et al. 2004, Pörtner & Knust 2007, Stramma et al. 2010), but we are unaware of any definitive analyses of this issue for pelagic fisheries. For example, in the northern Benguela system in the eastern Atlantic, OMZ shoaling and increasing hypoxia may impact the development and survival of larval sardines and anchovies, potentially directly affecting stocks of these species and indirectly affecting other commercially important species such as horse mackerel and hake (Ekau & Verheye 2005, Kreiner et al. 2009, Ekau et al. 2010). But many fisheries in this region have also been in decline, with both other environmental factors and overfishing contributing (Boyer et al. 2001, Daskalov et al. 2003, Hutchings et al. 2009, July 2012). In the southern California Bight (California

COUNTING HUMBOLDT SQUID

Quantitative assessment of the Humboldt squid expansion's impact on fisheries owing to direct predation requires biomass estimates for the squid. Acoustic surveys in 2009 off the US-Canadian coast suggested that the biomass of Humboldt squid in the survey area (35°–55° N) was comparable to that of hake (~1.5 million metric tons) (Stewart & Hamel 2010). Surveys off Peru over a comparable area (5°–19° S) in 2007–2008 led to similar biomass estimates for squid and values approximately fivefold larger for their main prey in this region, the mesopelagic lightfish (*Vinciguerra lucetia*) (Rosas-Luis et al. 2011). These combined areas represent approximately one-third of the total coastal range of Humboldt squid, not counting the Gulf of California, and the total biomass of this species is likely to be an order of magnitude larger than current commercial landings (~600,000 tons per year; FAO 2011), making the total level of predation by this voracious squid over its large range staggering.

Current), continued shoaling of the OLZ is expected to affect commercially and recreationally important rockfish (*Sebastes*) species both negatively and positively: The available habitat may be reduced (McClatchie et al. 2010), but the concentration and vulnerability of mesopelagic prey may be increased as DSL communities shift daytime position to depths where there is more light (Koslow et al. 2011).

Humboldt squid fisheries may have benefited in a similar way from OMZ/OLZ shoaling in the eastern Pacific. This fishery was essentially nonexistent 25 years ago but now constitutes the largest invertebrate fishery in the world (630,000 tons in 2009; FAO 2011) (see sidebar Counting Humboldt Squid). The reasons for this explosive rise are not clear, but it is unlikely to simply reflect a change in the level of commercial effort (Rodhouse 2005). Regardless of the causes, the spreading of Humboldt squid into the northern California Current system has affected other commercially important species (Field et al. 2007, 2012), particularly hake (Zeidberg & Robison 2007). Negative impacts on the hake fishery have involved direct predation (Field et al. 2007), alteration of schooling structure (Holmes et al. 2008), and interference with acoustic surveys used to set national quotas (Stewart & Hamel 2010, Thomas et al. 2011). This is a major fishery in the northeastern Pacific with significant economic ramifications—average landings of nearly 500,000 metric tons between 2005 and 2009 were valued in excess of US\$27 million (NOAA 2011). A negative impact on the hake fishery in the Peru Current system has been reported for the same period (Alarcón-Muñoz et al. 2008, Arancibia & Neira 2008).

Vertical habitat compression accompanying OMZ shoaling (see above) is expected to concentrate large predatory fishes in near-surface waters, which may increase vulnerability to commercial exploitation. Stramma et al. (2011) and Prince et al. (2010) hypothesized that this factor explains the higher historical landings of tunas and billfishes from regions of the eastern Atlantic associated with OMZs. These authors stressed the need to consider the influences of midwater oxygen when using catch-per-unit-effort data to infer stock status and manage pelagic fisheries.

OMZ shoaling may also be a key regulator of the Peruvian anchoveta fishery, the world's largest. Bertrand et al. (2011) hypothesized that out-of-phase fluctuations in anchovy and sardine populations over the past several decades (Alheit & Niquen 2004), canonically associated with the PDO (Chavez et al. 2003), are driven primarily by differences in oxygen demand and feeding ecology between the two species in conjunction with variation in oxygen concentration on the continental shelf. In the 1960s and early 1970s, enhanced upwelling of low-oxygen water from the shallow OLZ in this region was correlated with a zooplankton community dominated by larger taxa like euphausiids (Ayón et al. 2011) and with low subsurface oxygen on the shelf and a

compressed depth of the oxygenated surface mixed layer in coastal waters (Bertrand et al. 2011, Chavez et al. 2011). These conditions all favored anchovies on the shelf, with sardines occupying offshore habitats (Espinoza & Bertrand 2008, Bertrand et al. 2010). In the mid-1970s, upwelling and nutrient delivery decreased, resulting in a rise in subsurface oxygen and a shift to smaller zooplankton that are preferred by sardines (Chavez et al. 2011). In the model of Bertrand et al. (2011), the increase in oxygenated surface habitat and shift to more suitable prey for sardines drove the shift in species dominance from anchovies to sardines in the 1980s. In the 1990s, climate conditions reverted to those of the 1960s, favoring a return to anchovy dominance. OLZ shoaling is occurring in the region under discussion, and continued shoaling is likely to continue to impact the sardine/anchovy dynamics in the Peru Current system. A dynamic relationship between OLZ shoaling and the PDO has not been demonstrated in this region, but such a coupling appears to exist in the California Current (see Expansion and Shoaling of OMZs, above).

OMZ SHOALING AND COASTAL UPWELLING IN THE CALIFORNIA CURRENT SYSTEM

OMZ shoaling in the California Current may also be affecting communities on the North American shelf in a way similar to that hypothesized for northern Chile (Bertrand et al. 2011). Persistent wind-driven upwelling on the Oregon coast causes seasonally excessive primary production followed by severely hypoxic episodes and anoxia-driven mass mortalities of invertebrates and fish (Grantham et al. 2004). These events appear to have occurred only since 1999, with 2006 being associated with the most severely hypoxic conditions (Chan et al. 2008), and research trawls have shown a positive correlation between oxygen concentration near the seafloor and catch per unit effort for a variety of demersal fishes and benthic invertebrates (Keller et al. 2010). Similar seasonal hypoxic events occur on the Washington shelf, but they may be more common in the historical record at this location (Connolly et al. 2010). The Columbia River mouth is similarly impacted, and a number of potential physiological and behavioral effects on salmonids and crabs have been discussed (Roegner et al. 2011).

Delivery of hypoxic source water to all of these regions has been linked to offshore upwelling, and as OMZ shoaling progresses offshore, it is likely that episodes of shelf hypoxia will increase (Pierce et al. 2012). Because OMZ/OLZ water also has a low pH, upwelled water in this region is corrosive (Feely et al. 2008), further compounding impacts of seasonal hypoxia in these areas.

Along the northeast coast of the Pacific, the physical mechanisms that couple upwelled hypoxic water in offshore areas to nearshore environments and up into the intertidal areas are not well understood. A decade-long high-frequency time series of oxygen concentration at 17 m depth adjacent to the Monterey Bay Aquarium (Monterey, California) has revealed frequent hypoxic events (and low pH) that can last for hours, during which oxygen concentration can fall to OLZ levels (Booth et al. 2012). Spectral analyses suggest that water movements associated with these events are generated by subsurface internal tides in Monterey Bay as originally proposed by Shea & Broenkow (1982), but oxygen concentration depends strongly on the intensity of seasonal upwelling. Similar events occur in other California locations, but the dynamics vary widely from site to site (G.E. Hofmann et al. 2011, Frieder et al. 2012). As the offshore OLZ shoals in the California Current—for whatever reason—increases in the frequency, duration, intensity, and spatial extent of these hypoxic intrusions seem inevitable, and their consequences are unpredictable. Will they matter? That is the crucial question. Based on the recent lethal hypoxic events in Oregon and seemingly similar oceanographic processes that may occur along much of the US Pacific coast, the answer is almost certainly yes.

CONCLUSION

The responses of pelagic ecosystems and fisheries to OMZ shoaling will occur across all levels of biological organization and will interact with other forms of environmental change, including ocean warming and acidification (Pörtner & Peck 2010, Doney et al. 2012). In reality, it is not productive to discuss one of these variables while ignoring the others, and the axiom that all things are connected continues to confound easy answers. Currently, our limited knowledge of physiological and behavioral responses of key species limits modeling efforts on the effects of declining global oxygen or expanding OMZs on either ecosystems or fisheries. These uncertainties should be addressed through future research directed at quantifying hypoxic stress in an ecologically relevant framework in both field and laboratory studies for a diverse array of susceptible species (Seibel 2011). Systematic monitoring of ocean oxygen at depth in key regions is also critical. These approaches in conjunction with future modeling efforts will move us toward an understanding of the state of pelagic ecosystems and fisheries under future-climate scenarios (Ekau et al. 2010, Ainsworth et al. 2011, Cheung et al. 2011).

SUMMARY POINTS

1. OMZs are found in a number of oceanic regions and vary in depth, horizontal extent, and minimum oxygen concentration. The largest OMZ is in the eastern Pacific. The upper boundaries of OMZs have been shoaling during the past 50 years, and in the northeastern Pacific this change translates into a northward horizontal expansion of the OMZ.
2. OMZ expansion and shoaling may favor anaerobic microbial processes, leading to greater N loss from the sea, increased production of the important trace gas N₂O, and possible production of sulfide.
3. Shoaling of the OMZ upper boundary results in an expansion of hypoxic habitat for permanent OMZ dwellers and a vertical compression of the pelagic habitat above the OMZ. Changes in this latter habitat will impact large pelagic predators like billfishes, tunas, and sharks.
4. The upper regions of the OMZs and all of the hypoxic OLZs immediately above provide daytime habitats for ecologically critical species like krill and myctophid fishes. These organisms directly interact with epipelagic ecosystems through diel vertical migrations, and vertical habitat compression may alter predator-prey interactions by concentrating prey in near-surface waters.
5. OLZ shifting to shallower depths increases exposure of mesopelagic organisms to ambient light at a given oxygen isopleth, potentially increasing daytime foraging pressure by visually oriented predators. This effect may have been important in the recent range expansion of Humboldt squid in the California Current system.
6. OMZ/OLZ expansions will impact commercial oceanic fisheries through a variety of mechanisms, including large-scale changes in suitable pelagic habitats and increased efficiency of surface-deployed fishing gear in vertically compressed pelagic zones.
7. OMZ/OLZ shoaling interacts with coastal fisheries through enhanced delivery of hypoxic water onto continental-shelf habitats in association with upwelling. This mechanism may be a key regulator of the Peruvian anchoveta fishery, the world's largest. It is also associated with seasonal mass mortalities on the Oregon coast.

FUTURE ISSUES

1. How will OMZ expansions interact with other forms of global change in the oceans, including warming, acidification, pollution, and overfishing? Shoaling OMZ water is both hypoxic and corrosive (low pH), so acidification in areas over shoaling OMZ/OLZs will also occur at depth, as well as in surface waters from direct atmospheric absorption of CO₂.
2. How will OMZ expansions alter entire marine ecosystems, including the interactions of organisms (both microbial and metazoan) across multiple trophic levels? Many of these effects will be extremely complex and unpredictable.
3. Do all OMZs respond in similar ways, or are there distinct, system-specific properties that dictate how OMZ expansion and shoaling will proceed? This is of particular interest in regard to severe OMZs in the Indian Ocean that are not eastern-boundary-current systems.
4. Will OMZs continue to expand at relatively rapid rates, or will feedback loops slow or accelerate these changes? Our ability to make meaningful long-term predictions will depend on the geological and paleobiological records, increased long-term monitoring of ocean oxygen in critical areas, and increasingly refined regional modeling approaches.
5. How will OMZ shoaling affect shallow coastal communities on the Pacific coast through upwelling associated with the delivery of hypoxic water onto the continental shelf?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We are grateful for discussions with a number of colleagues who shared their ideas and often unpublished information: Francisco Chavez, Brad Seibel, Julia Stewart, and Lothar Stramma. W.F.G. and J.M.B. were supported by the National Science Foundation (OCE0850839 to W.F.G. and OCE1034943 to J.M.B.), the California Sea Grant and California Ocean Protection Council (R/OPCFISH-06 to W.F.G.), the National Geographic Committee for Research and Exploration (CRE 8458-08 to W.F.G.), and the Hellman Fellows Fund (to J.M.B.). S.Y.L. was supported by the Center for Ocean Solutions, Monterey, California. B.H.R. was supported by the David and Lucile Packard Foundation.

LITERATURE CITED

- Ainsworth CH, Samhuri JF, Busch DS, Cheung WWL, Dunne J, Okey TA. 2011. Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries. *ICES J. Mar. Sci.* 68:1217–29
- Alarcón-Muñoz R, Cubillos L, Gatica C. 2008. Jumbo squid (*Dosidicus gigas*) biomass off central Chile: effects on Chilean hake (*Merluccius gayi*). *CalCOFI Rep.* 49:157–66
- Alheit J, Niquen M. 2004. Regime shifts in the Humboldt Current ecosystem. *Prog. Oceanogr.* 60:201–22
- Arancibia H, Neira S. 2008. Overview of the Chilean Hake (*Merluccius gayi*) stock, a biomass forecast, and the jumbo squid (*Dosidicus gigas*) predator-prey relationship off central Chile (33°S–39°S). *CalCOFI Rep.* 49:104–15

- Ayón P, Swartzman G, Espinoza P, Bertrand A. 2011. Long-term changes in zooplankton size distribution in the Peruvian Humboldt Current System: conditions favouring sardine or anchovy. *Mar. Ecol. Prog. Ser.* 422:211–22
- Bakun A, Field DB, Redondo-Rodriguez A, Weeks SJ. 2010. Greenhouse gas, upwelling-favorable winds, and the future of coastal ocean upwelling ecosystems. *Glob. Change Biol.* 16:1213–28
- Barham EG. 1971. Deep-sea fishes: lethargy and vertical orientation. In *Proceedings of an International Symposium on Biological Sound-Scattering in the Ocean*, ed. GB Farquhar, pp. 100–18. Washington, DC: Maury Cent. Ocean Sci.
- Beebe W. 1934. *Half Mile Down*. New York: Harcourt, Brace and Co. 344 pp.
- Behrenfeld MJ. 2011. Biology: uncertain future for ocean algae. *Nat. Clim. Change* 1:33–34
- Behrenfeld MJ, O'Malley RT, Siegel DA, McClain CR, Sarmiento JL, et al. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444:752–55
- Beman JM, Chow C, King AL, Feng Y, Fuhrman JA, et al. 2011. Global declines in oceanic nitrification rates as a consequence of ocean acidification. *Proc. Natl. Acad. Sci. USA* 108:208–13
- Beman JM, Popp BN, Alford SE. 2012. Quantification of ammonia oxidation rates and ammonia-oxidizing archaea and bacteria at high resolution in the Gulf of California and eastern tropical North Pacific Ocean. *Limnol. Oceanogr.* 57:711–26
- Bertrand A, Ballón M, Chaigneau A. 2010. Acoustic observation of living organisms reveals the upper limit of the oxygen minimum zone. *PLoS ONE* 5:e10330
- Bertrand A, Barbieri MA, Gerlotto F, Leiva F, Córdova J. 2006. Determinism and plasticity of fish schooling behaviour as exemplified by the South Pacific jack mackerel *Trachurus murphyi*. *Mar. Ecol. Prog. Ser.* 311:145–56
- Bertrand A, Chaigneau A, Peraltilla S, Ledesma J, Graco M, et al. 2011. Oxygen: a fundamental property regulating pelagic ecosystem structure in the coastal southeastern tropical Pacific. *PLoS ONE* 6:e29558
- Bograd SJ, Castro CG, DiLorenzo E, Palacios DM, Bailey H, et al. 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. *Geophys. Res. Lett.* 35:L12607
- Booth JAT, McPhee-Shaw EE, Chua P, Kinsley E, Denny M, et al. 2012. Natural intrusions of hypoxic, low pH water into nearshore marine environments on the California coast. *Cont. Shelf Res.* 45:108–15
- Boyce DG, Lewis MR, Worm B. 2010. Global phytoplankton decline over the past century. *Nature* 466:591–96
- Boyer DC, Boyer HJ, Fossen I, Kreiner A. 2001. Changes in abundance of the northern Benguela sardine stock during the decade 1990–2000, with comments on the relative importance of fishing and the environment. *S. Afr. J. Mar. Sci.* 23:67–84
- Breitbart DL, Hondorp DW, Davias L, Diaz RJ. 2009. Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. *Annu. Rev. Mar. Sci.* 1:329–49
- Brewer PG, Peltzer ET. 2009. Limits to marine life. *Science* 324:347–48
- Brochier T, Lett C, Fréon P. 2011. Investigating the “northern Humboldt paradox” from model comparisons of small pelagic fish reproductive strategies in eastern boundary upwelling ecosystems. *Fish Fish.* 12:94–109
- Brodeur RA, Ralston S, Emmett RL, Trudel M, Auth TD, Philips AJ. 2006. Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the northern California Current in 2004 and 2005. *Geophys. Res. Lett.* 33:L22S08
- Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, et al. 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334:652–55
- Canfield DE, Stewart FJ, Thamdrup B, DeBrabandere L, Dalsgaard T, et al. 2010. A cryptic sulfur cycle in oxygen-minimum-zone waters off the Chilean coast. *Science* 330:1375–78
- Capone DG, Bronk D, Mulholland M, Carpenter EJ. 2008. *Nitrogen in the Marine Environment*. San Diego: Academic. 1,757 pp. 2nd ed.
- Carey FG, Robison BH. 1981. Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fish. Bull.* 79:277–92
- Catul V, Gauns M, Karuppusamy PK. 2011. A review on mesopelagic fishes belonging to family Myctophidae. *Rev. Fish Biol. Fish.* 21:339–54
- Chan F, Barth JA, Lubchenco J, Kirincich A, Week H, et al. 2008. Emergence of anoxia in the California Current large marine ecosystem. *Science* 319:920

- Chavez FP, Bertrand A, Guevara-Carrasco R, Soler P, Csirke J. 2008. The northern Humboldt Current System: brief history, present status and a view towards the future. *Prog. Oceanogr.* 79:95–105
- Chavez FP, Messié M. 2009. A comparison of eastern boundary upwelling ecosystems. *Prog. Oceanogr.* 83:80–96
- Chavez FP, Messié M, Pennington JT. 2011. Marine primary production in relation to climate variability and change. *Annu. Rev. Mar. Sci.* 3:227–60
- Chavez FP, Ryan J, Lluch-Cota SE, Niquen M. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299:217–21
- Checkley DM, Barth JA. 2009. Patterns and processes in the California Current System. *Prog. Oceanogr.* 83:49–64
- Cheung WWL, Dunne J, Sarmiento JL, Pauly D. 2011. Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. *ICES J. Mar. Sci.* 68:1008–18
- Childress JJ. 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals? *Trends. Ecol. Evol.* 10:30–36
- Childress JJ, Seibel BA. 1998. Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. *J. Exp. Biol.* 201:1223–32
- Church MJ, Wai B, Karl DM, DeLong EF. 2010. Abundances of crenarchaeal *amoA* genes and transcripts in the Pacific Ocean. *Environ. Microbiol.* 12:679–88
- Codispoti LA. 2010. Interesting times for marine N₂O. *Science* 327:1339–40
- Codispoti LA, Christensen JP. 1985. Nitrification, denitrification and nitrous oxide cycling in the eastern tropical South Pacific Ocean. *Mar. Chem.* 16:277–300
- Connolly TP, Hickey BM, Geier SL, Cochlan WP. 2010. Processes influencing seasonal hypoxia in the northern California Current System. *J. Geophys. Res.* 115:C03021
- Cornejo R, Koppelman R. 2006. Distribution patterns of mesopelagic fishes with special reference to *Vinciguerria lucetia* Garman 1899 (Phosichthyidae: Pisces) in the Humboldt Current Region off Peru. *Mar. Biol.* 149:1519–37
- Cosgrove JA. 2005. The first specimens of Humboldt squid in British Columbia. *PICES Press* 13(2):30–31
- Daskalov GM, Boyer DC, Roux JP. 2003. Relating sardine *Sardinops sagax* abundance to environmental indices in northern Benguela. *Prog. Oceanogr.* 59:257–74
- Davis RW, Jaquet N, Gendron D, Markaida U, Bazzino G, Gilly W. 2007. Diving behavior of sperm whales in relation to the behavior of a major prey-species, the jumbo squid, in the Gulf of California, Mexico. *Mar. Ecol. Prog. Ser.* 333:291–302
- DeLong RL, Stewart BS. 2006. Diving patterns of northern elephant seal bulls. *Mar. Mamm. Sci.* 7:369–84
- Deutsch C, Brix H, Ito T, Frenzel H, Thompson L. 2011. Climate-forced variability of ocean hypoxia. *Science* 333:336–39
- Deutsch C, Sarmiento JL, Sigman DM, Gruber N, Dunne JP. 2007. Spatial coupling of nitrogen inputs and losses in the ocean. *Nature* 445:163–67
- Dewar H, Prince ED, Musyl MK, Brill RW, Sepulveda C, et al. 2011. Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. *Fish. Oceanogr.* 20:219–41
- Diaz RJ, Rosenberg R. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr. Mar. Biol. Annu. Rev.* 33:245–303
- Diaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321:926–29
- Díaz-Ochoa JA, Pantoja S, De Lange GJ, Lange CB, Sánchez GE, et al. 2010. Oxygenation variability off Northern Chile during the last two centuries. *Biogeosci. Discuss.* 7:4987–5009
- Doney SC, Fabry VJ, Feely RA, Kleypas JA. 2009. Ocean acidification: the other CO₂ problem. *Annu. Rev. Mar. Sci.* 1:169–92
- Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, et al. 2012. Climate change impacts on marine ecosystems. *Annu. Rev. Mar. Sci.* 4:11–37
- Dore JE, Lukas R, Sadler DW, Church MJ, Karl DM. 2009. Physical and biogeochemical modulation of ocean acidification in the central North Pacific. *Proc. Natl. Acad. Sci. USA* 106:12235–40

- Drazen JC, Seibel BA. 2007. Depth-related trends in metabolism of benthic and benthopelagic deep-sea fishes. *Limnol. Oceanogr.* 52:2306–16
- Duce RA, LaRoche J, Altieri K, Arrigo KR, Baker AR, et al. 2008. Impacts of atmospheric anthropogenic nitrogen on the open ocean. *Science* 320:893–97
- Ekau W, Auel H, Pörtner H-O, Gilbert D. 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* 7:1669–99
- Ekau W, Verheye HM. 2005. Influence of oceanographic fronts and low oxygen on the distribution of ichthyoplankton in the Benguela and southern Angola currents. *Afr. J. Mar. Sci.* 27:629–39
- Espinoza P, Bertrand A. 2008. Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt Current system. *Prog. Oceanogr.* 79:215–27
- Falkowski PG, Fenchel T, DeLong EF. 2008. The microbial engines that drive Earth's biogeochemical cycles. *Science* 320:1034–49
- FAO (Food Agric. Organ. UN). 2011. Fishery and aquaculture statistics. *FAO Yearb. 2009*, FAO, Rome. <http://www.fao.org/fishery/publications/yearbooks>
- Feely RA, Sabine CL, Hernandez-Ayon JM, Ianson D, Hales B. 2008. Evidence for upwelling of corrosive “acidified” water onto the continental shelf. *Science* 320:1490–92
- Fiedler PC, Talley LD. 2006. Hydrography of the eastern tropical Pacific: a review. *Prog. Oceanogr.* 69:143–80
- Field JC, Baltz K, Phillip A, Walker W. 2007. Range expansion and trophic interactions of the jumbo squid, *Dosidicus gigas*, in the California Current. *CalCOFI Rep.* 48:131–46
- Field JC, Elliger C, Baltz K, Gillespie G, Gilly WF, et al. 2012. Foraging ecology and movement patterns of jumbo squid (*Dosidicus gigas*) in the California current system. *Deep-Sea Res. II*. In press
- Frame CH, Casciotti KL. 2010. Biogeochemical controls and isotopic signatures of nitrous oxide production by a marine ammonia-oxidizing bacterium. *Biogeosciences* 7:2695–709
- Francis CA, Beman JM, Kuypers MMM. 2007. New processes and players in the nitrogen cycle: the microbial ecology of anaerobic and archaeal ammonia oxidation. *ISME J.* 1:19–27
- Frieder CA, Nam SH, Martz TR, Levin LA. 2012. High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. *Biogeosci. Discuss.* 9:4099–132
- Fuchs BM, Woebken D, Zubkov MV, Burkill P, Amann R. 2005. Molecular identification of picoplankton populations in contrasting waters of the Arabian Sea. *Aquat. Microb. Ecol.* 39:145–57
- Fuenzalida R, Schneider W, Garcés-Vargas J, Bravo L, Lange C. 2009. Vertical and horizontal extension of the oxygen minimum zone in the eastern South Pacific Ocean. *Deep-Sea Res. II* 56:992–1003
- Gao K, Xu J, Gao G, Li Y, Hutchins DA, et al. 2012. Rising CO₂ and increased light exposure synergistically reduce marine primary productivity. *Nat. Clim. Change* 2:519–23
- Garcia HE, Locarnini RA, Boyer TP, Antonov JI. 2006. *World Ocean Atlas 2005*. Vol. 3: *Dissolved Oxygen, Apparent Oxygen Utilization, and Oxygen Saturation*. Ed. S Levitus. NOAA Atlas NESDIS 63. Washington, DC: US Gov. Print. Off. 342 pp. http://www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html
- Ghosh W, Dam B. 2009. Biochemistry and molecular biology of lithotrophic sulfur oxidation by taxonomically and ecologically diverse bacteria and archaea. *FEMS Microbiol. Rev.* 33:999–1043
- Gilly WF. 2006. Spreading and stranding of Humboldt squid. In *Ecosyst. Obs. Monterey Bay Natl. Mar. Sanctuary 2005*, pp. 20–22. Monterey, CA: Monterey Bay Natl. Mar. Sanctuary. <http://montereybay.noaa.gov/reports/2005/eco/harvestedsp.html>
- Gilly WF, Markkaida U, Baxter CH, Block BA, Boustany A, et al. 2006. Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Mar. Ecol. Prog. Ser.* 324:1–17
- Gilly WF, Zeidberg LD, Booth JAT, Stewart JS, Marshall G, et al. 2012. Locomotion and behavior of Humboldt squid, *Dosidicus gigas*, in relation to natural hypoxia in the Gulf of California, Mexico. *J. Exp. Biol.* 215:3175–90
- Goericke R, Olson RJ, Shalapyonok A. 2000. A novel niche for *Prochlorococcus* sp. in low-light suboxic environments in the Arabian Sea and the eastern tropical North Pacific. *Deep-Sea Res. I* 47:1183–205
- Goreau TJ, Kaplan WA, Wofsy SC, McElroy MB, Valios FW, Watson SW. 1980. Production of NO₂⁻ and N₂O by nitrifying bacteria at reduced concentrations of oxygen. *Appl. Environ. Microbiol.* 40:526–32
- Grantham B, Chan F, Nielsen K, Fox D, Barth J, et al. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* 429:749–54

- Gregg WW, Casey NW, McClain CR. 2005. Recent trends in global ocean chlorophyll. *Geophys. Res. Lett.* 32:L03606
- Gruber N. 2011. Warming up, turning sour, losing breath: ocean biogeochemistry under global change. *Philos. Trans. R. Soc. Lond. A* 369:1980–96
- Helly J, Levin L. 2004. Global distribution of naturally occurring marine hypoxia on continental margins. *Deep-Sea Res. I* 51:1159–68
- Helm KP, Bindoff NL, Church JA. 2011. Observed decreases in oxygen content of the global ocean. *Geophys. Res. Lett.* 38:L23602
- Hofmann AF, Peltzer ET, Walz PM, Brewer PG. 2011. Hypoxia by degrees: establishing definitions for a changing ocean. *Deep-Sea Res. I* 58:1212–26
- Hofmann GE, Smith JE, Johnson KS, Send U, Levin LA, et al. 2011. High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PLoS ONE* 6:e28983
- Holmes J, Cooke K, Cronkite G. 2008. Interactions between jumbo squid (*Dosidicus gigas*) and Pacific hake (*Merluccius productus*) in the northern California Current in 2007. *CalCOFI Rep.* 49:129–41
- Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HMS, et al. 2009. The Benguela Current: an ecosystem of four components. *Prog. Oceanogr.* 83:15–32
- Hutchins DA, Mulholland MR, Fu F. 2009. Nutrient cycles and marine microbes in a CO₂-enriched ocean. *Oceanography* 22(4):128–45
- Ibáñez CM, Cubillos LA. 2007. Seasonal variation in the length structure and reproductive condition of the jumbo squid *Dosidicus gigas* (d'Orbigny, 1835) off central-south Chile. *Sci. Mar.* 71:123–28
- Jorgensen SJ, Klimley AP, Muhlia-Melo AF. 2009. Scalloped hammerhead shark *Sphyrna lewini*, utilizes deep-water, hypoxic zone in the Gulf of California. *J. Fish Biol.* 74:1682–87
- Jury MR. 2012. Physical oceanographic influences on central Benguela fish catch. *Earth Interact.* 16:1–16
- Kalvelage T, Jensen M, Contreras S, Revsbech NP, Lam P, et al. 2011. Oxygen sensitivity of anammox and coupled N-cycle processes in oxygen minimum zones. *PLoS ONE* 6:e29299
- Karstensen J, Stramma L, Visbeck M. 2008. Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. *Prog. Oceanogr.* 77:331–50
- Kartal B, Kuypers MMM, Lavik G, Schalk J, Op den Camp HJM, et al. 2007. Anammox bacteria disguised as denitrifiers: nitrate reduction to dinitrogen gas via nitrite and ammonium. *Environ. Microbiol.* 9:635–42
- Keeling RF, Körtzinger A, Gruber N. 2010. Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* 2:199–229
- Keller AA, Simon V, Chan F, Wakefield WW, Clarke ME, et al. 2010. Demersal fish and invertebrate biomass in relation to an offshore hypoxic zone along the US West Coast. *Fish. Oceanogr.* 19:76–87
- Keyl F, Argüelles JR, Wolff M, Yamahiro C. 2008. A hypothesis on range expansion and spatio-temporal shifts in size-at-maturity of jumbo squid (*Dosidicus gigas*) in the eastern Pacific Ocean. *CalCOFI Rep.* 49:119–28
- Kitidis V, Laverock B, McNeill LC, Beesley A, Cummings D, et al. 2011. Impact of ocean acidification on benthic and water column ammonia oxidation. *Geophys. Res. Lett.* 38:L21603
- Klevjer TA, Torres DJ, Kaartvdt S. 2012. Distribution and diel vertical movements of mesopelagic scattering layers in the Red Sea. *Mar. Biol.* 159:1833–41
- Koslow JA, Goericke R, Lara-Lopez A, Watson W. 2011. Impact of declining intermediate-water oxygen on deepwater fishes in the California Current. *Mar. Ecol. Prog. Ser.* 436:207–18
- Kreiner A, Stenevik EK, Ekau W. 2009. Sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* larvae avoid regions with low dissolved oxygen concentration in the northern Benguela Current system. *J. Fish Biol.* 74:270–77
- Lam P, Kuypers MMM. 2011. Microbial nitrogen cycling processes in oxygen minimum zones. *Annu. Rev. Mar. Sci.* 3:317–45
- Lavik G, Stührmann T, Brüchert V, Van der Plas A, Mohrholz V, et al. 2009. Detoxification of sulphidic African shelf waters by blooming chemolithotrophs. *Nature* 457:581–84
- Lavin P, González B, Santibáñez JF, Scanlan DJ, Ulloa O. 2010. Novel lineages of *Prochlorococcus* thrive within the oxygen minimum zone of the eastern tropical South Pacific. *Environ. Microbiol. Rep.* 2:728–38
- Le Boeuf BJ, Crocker DE, Costa DP, Blackwell SB, Webb PM, Houser DS. 2000. Foraging ecology of northern elephant seals. *Ecol. Monogr.* 70:353–82

- Levin LA. 2003a. Deep-ocean life where oxygen is scarce. *Am. Sci.* 90:436–44
- Levin LA. 2003b. Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanogr. Mar. Biol. Annu. Rev.* 41:1–45
- Levin LA, Ekau W, Gooday AJ, Jorissen F, Middelburg JJ, et al. 2009. Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosci. Discuss.* 6:2063–98
- Litz MNC, Phillips AJ, Brodeur RD, Emmett RL. 2011. Seasonal occurrences of Humboldt squid (*Dosidicus gigas*) in the northern California Current system. *CalCOFI Rep.* 52:97–108
- Ma Y, Zeng Y, Jiao N, Shi Y, Hong N. 2009. Vertical distribution and phylogenetic composition of bacteria in the Eastern Tropical North Pacific Ocean. *Microbiol. Res.* 164:624–33
- Mazzillo FFM, Staaf DJ, Field JC, Carter ML, Ohman MD. 2011. A note on the detection of the neurotoxin domoic acid in beach-stranded *Dosidicus gigas* in the Southern California Bight. *CalCOFI Rep.* 52:109–15
- MBARI (Monterey Bay Aquar. Res. Inst.). 2008. State of Monterey Bay 2008. In *Annual Report 2008*, pp. 31–33. Moss Landing, CA: MBARI. http://www.mbari.org/news/publications/ar/2008ann_rpt.pdf
- McClatchie S, Goericke R, Cosgrove R, Auad G, Vetter R. 2010. Oxygen in the Southern California Bight: multidecadal trends and implications for demersal fisheries. *Geophys. Res. Lett.* 37:L19602
- Miller DC, Poucher SL, Coiro L. 2002. Determination of lethal dissolved oxygen levels for selected marine and estuarine fishes, crustaceans, and a bivalve. *Mar. Biol.* 140:287–96
- Nakano H, Matsunaga H, Okamoto H, Okazaki M. 2003. Acoustic tracking of bigeye thresher shark *Alopias superciliosus* in the eastern Pacific Ocean. *Mar. Ecol. Prog. Ser.* 265:255–61
- Nasby-Lucas N, Dewar H, Lam CH, Goldman JK, Domeier ML. 2011. White shark offshore habitat: a behavioral and environmental characterization of the eastern Pacific shared offshore foraging area. *PLoS ONE* 4:e8163
- Nevison C, Butler JH, Elkins JW. 2003. Global distribution of N₂O and the ΔN₂O-AOU yield in the subsurface ocean. *Glob. Biogeochem. Cycles* 17:1119
- Nigmatullin CM, Nesis KN, Arkhipkin AI. 2001. A review on the biology of the jumbo squid *Dosidicus gigas*. *Fish. Res.* 54:9–19
- NOAA (Natl. Oceanogr. Atmos. Adm.). 2011. Fisheries of the United States: 2010. *Curr. Fish. Stat.* 2010, NOAA, Silver Spring, MD. <http://www.st.nmfs.noaa.gov/st1/fus/fus10>
- Ono T. 2010. Oxygen decline in the continental slope waters off-Japan and its potential influence on groundfishes. In *PICES-2010: North Pacific Ecosystems Today, and Challenges in Understanding and Forecasting Change*, p. 17. Sidney, Can.: North Pac. Mar. Sci. Organ. (Abstr.)
- Ono T, Ito M, Hattori T, Narimatsu Y, Kitagawa D. 2010. *Oxygen decline in the continental slope waters off-Japan and its potential influence on groundfishes*. Presented at PICES-2010, Portland, OR, Oct. 22–31. <http://www.pices.int/publications/presentations/PICES-2010/2010-S1/S1-day2/S1-1425-Ono.pdf>
- Parrish JK. 1999. Using behavior and ecology to exploit fishes. *Environ. Biol. Fishes* 55:157–81
- Paulmier A, Ruiz-Pino D. 2009. Oxygen minimum zones (OMZs) in the modern ocean. *Prog. Oceanogr.* 80:113–28
- Pearcy WG. 2002. Marine nekton off Oregon and the 1997–98 El Niño. *Prog. Oceanogr.* 54:399–403
- Pearcy WG, Forss CA. 1969. The oceanic shrimp *Sergestes similis* off the Oregon coast. *Limnol. Oceanogr.* 14:755–65
- Pennington JT, Mahoney KL, Kuwahara VS, Kolber DD, Calienes R, Chavez FP. 2007. Primary production in the eastern tropical Pacific: a review. *Prog. Oceanogr.* 69:285–317
- Perry AL, Low P, Ellis J, Reynolds J. 2005. Climate change and distribution shifts in marine fishes. *Science* 308:1912–15
- Pierce SD, Barth JA, Shearman RK, Erofeev AY. 2012. Declining oxygen in the Northeast Pacific. *J. Phys. Oceanogr.* 42:495–501
- Polovina JJ, Dunne J, Woodworth PA, Howell EA. 2011. Projected expansion of the subtropical biome and contraction of the temperate and equatorial upwelling biomes in the North Pacific under global warming. *ICES J. Mar. Sci.* 68:986–95
- Polovina JJ, Howell EA, Abecassis M. 2008. Ocean's least productive waters are expanding. *Geophys. Res. Lett.* 35:L03618

- Pörtner HO, Farrell AP. 2008. Physiology and climate change. *Science* 322:690–92
- Pörtner HO, Knust R. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315:95–97
- Pörtner HO, Peck MA. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *J. Fish Biol.* 77:1745–79
- Prince ED, Goodyear CP. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. *Fish. Oceanogr.* 15:451–64
- Prince ED, Luo J, Goodyear CP, Hoolihan JP, Snodgrass D, et al. 2010. Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. *Fish. Oceanogr.* 19:448–62
- Rabalais NN, Turner RE, Wiseman WJ. 2002. Gulf of Mexico hypoxia, a.k.a. “The Dead Zone.” *Annu. Rev. Ecol. Syst.* 33:235–63
- Ravishankara AR, Daniel JS, Portmann RW. 2009. Nitrous oxide (N₂O): the dominant ozone-depleting substance emitted in the 21st century. *Science* 326:123–25
- Ressler PH, Holmes JA, Fleischer GW, Thomas RE, Cooke KC. 2007. Pacific hake, *Merluccius productus*, autecology: a timely review. *Mar. Fish. Rev.* 69:1–24
- Robinson C, Steinberg DK, Anderson TR, Aristegui J, Carlson CA, et al. 2010. Mesopelagic zone ecology and biogeochemistry—a synthesis. *Deep-Sea Res. II* 57:1504–18
- Robison BH. 2003. What drives the diel vertical migration of Antarctic midwater fishes? *J. Mar. Biol. Assoc. UK* 83:639–42
- Robison BH. 2004. Deep pelagic biology. *J. Exp. Mar. Biol. Ecol.* 300:253–72
- Robison BH. 2009. Conservation of deep pelagic biodiversity. *Conserv. Biol.* 23:847–58
- Robison BH, Reisenbichler KR, Sherlock RE. 2005. Giant larvacean houses: rapid carbon transport to the deep sea floor. *Science* 308:1609–11
- Robison BH, Reisenbichler KR, Sherlock RE, Silguero JMB, Chavez FP. 1998. Seasonal abundance of the siphonophore, *Nanomia bijuga*, in Monterey Bay. *Deep-Sea Res. II* 45:1741–51
- Rodhouse PG. 2005. World squid resources. In *Review of the State of World Marine Fishery Resources*, FAO Fish. Tech. Pap. 457, pp. 175–86. Rome: Food Agric. Organ. UN
- Roegner GC, Needoba JA, Baptista AM. 2011. Coastal upwelling supplies oxygen-depleted water to the Columbia River estuary. *PLoS ONE* 6:e18672
- Roper CFE, Sweeney MJ, Nauen CE. 1984. *FAO Species Catalogue*. Vol. 3: *Cephalopods of the World: An Annotated and Illustrated Catalogue of Species of Interest to Fisheries*. FAO Fish. Synop. 125. Rome: Food Agric. Organ. UN. 277 pp.
- Rosa R, Seibel BA. 2008. Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *Proc. Natl. Acad. Sci. USA* 105:20776–80
- Rosa R, Seibel BA. 2010. Metabolic physiology of the Humboldt squid, *Dosidicus gigas*: implications for vertical migration in a pronounced oxygen minimum zone. *Prog. Oceanogr.* 86:72–80
- Rosas-Luis R, Tafur-Jimenez R, Alegre-Norza AR, Castillo-Valderrama PR, Cornejo-Urbina RM, et al. 2011. Trophic relationships between the jumbo squid (*Dosidicus gigas*) and the lightfish (*Vinciguerria luetia*) in the Humboldt Current System off Peru. *Sci. Mar.* 75:549–57
- Sagarin RD, Gilly WF, Baxter CH, Burnett N, Christensen J. 2008. Remembering the Gulf: changes to the marine communities of the Sea of Cortez since the Steinbeck and Ricketts expedition of 1940. *Front. Ecol. Environ.* 6:372–79
- Santoro AE, Buchwald C, McIlvin MR, Casciotti KL. 2011. Isotopic signature of N₂O produced by marine ammonia-oxidizing archaea. *Science* 333:1282–85
- Santoro AE, Casciotti KL, Francis CA. 2010. Activity, abundance and diversity of nitrifying archaea and bacteria in the central California Current. *Environ. Microbiol.* 12:1989–2006
- Sarmiento H, Montoya JM, Vázquez-Domínguez E, Vaqué D, Gasol JM. 2010. Warming effects on marine microbial food web processes: How far can we go when it comes to predictions? *Philos. Trans. R. Soc. Lond. B* 365:2137–49
- Schaefer KM, Fuller DW. 2010. Vertical movements, behavior, and habitat of bigeye tuna (*Thunnus obesus*) in the equatorial eastern Pacific Ocean, ascertained from archival tag data. *Mar. Biol.* 157:2625–42

- Schaefer KM, Fuller DW, Block BA. 2011. Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the Pacific Ocean off Baja California, Mexico, determined from archival tag data analyses, including unscented Kalman filtering. *Fish. Res.* 112:22–37
- Seibel BA. 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *J. Exp. Biol.* 214:326–36
- Seibel BA, Thuesen EV, Childress JJ, Gorodezky LA. 1997. Decline in pelagic cephalopod metabolism with habitat depth reflects differences in locomotory efficiency. *Biol. Bull.* 192:262–78
- Shea RE, Broenkow WW. 1982. The role of internal tides in the nutrient enrichment of Monterey Bay. *Estuar. Coast. Shelf Sci.* 15:57–66
- Staa DJ, Zeidberg LD, Gilly WF. 2011. Effects of temperature on embryonic development of the Humboldt squid, *Dosidicus gigas*. *Mar. Ecol. Prog. Ser.* 441:165–75
- Stevens H, Ulloa O. 2008. Bacterial diversity in the oxygen minimum zone of the eastern tropical South Pacific. *Environ. Microbiol.* 10:1244–59
- Stewart FJ, Ulloa O, DeLong EF. 2012. Microbial metatranscriptomics in a permanent marine oxygen minimum zone. *Environ. Microbiol.* 14:23–40
- Stewart JJ, Hamel OS. 2010. Stock assessment of Pacific hake, *Merluccius productus*, (a.k.a. whiting) in U.S. and Canadian waters in 2010. *Rep.*, Northwest Fish. Sci. Cent., Seattle. http://www.pcouncil.org/wp-content/uploads/E3a_ATT2_HAKE_USCAN_NWFSC_MARCH_2010_BB.pdf
- Stewart JS. 2012. *Humboldt squid in the northern California Current system*. PhD thesis. Stanford Univ., Stanford, CA. 193 pp. <http://purl.stanford.edu/pb685tk3754>
- Stewart JS, Field JC, Markaida U, Gilly WF. 2012. Behavioral ecology of jumbo squid (*Dosidicus gigas*) in relation to oxygen minimum zones. *Deep-Sea Res. II*. In press. doi: 10.1016/j.dsr2.2012.06.005
- Stramma L, Brandt P, Schafstall J, Schott F, Fisher J, Körtzinger A. 2008a. Oxygen minimum zone in the North Atlantic south and east of the Cape Verde Islands. *J. Geophys. Res.* 113:C04014
- Stramma L, Johnson GC, Sprintall J, Mohrholz V. 2008b. Expanding oxygen-minimum zones in the tropical oceans. *Science* 320:655–58
- Stramma L, Oschlies A, Schmidtko S. 2012. Anticorrelated observed and modeled trends in dissolved oceanic oxygen over the last 50 years. *Biogeosci. Discuss.* 9:4595–626
- Stramma L, Prince ED, Schmidtko S, Luo J, Hoolihan JP, et al. 2011. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nat. Clim. Change* 2:33–37
- Stramma L, Schmidtko S, Levin LA, Johnson GC. 2010. Ocean oxygen minima expansions and their biological impacts. *Deep-Sea Res. I* 57:587–95
- Sumaila UR, Cheung WWL, Lam VWY, Pauly D, Herrick S. 2011. Climate change impacts on the biophysics and economics of world fisheries. *Nat. Clim. Change* 1:449–56
- Swan BK, Martinez-Gardia M, Preston CM, Sczyrba A, Woyke T, et al. 2011. Potential for chemolithoautotrophy among ubiquitous bacteria lineages in the dark ocean. *Science* 333:1296–300
- Thomas R, Stewart I, Chu D, Pohl J, Cooke K, et al. 2011. Acoustic biomass estimation and uncertainty of Pacific hake and Humboldt squid in the Northern California current in 2009. *J. Acoust. Soc. Am.* 129:2691 (Abstr.)
- Turner RE, Rabalais NN, Justic D. 2008. Gulf of Mexico hypoxia: alternate states and a legacy. *Environ. Sci. Technol.* 42:2323–27
- Vaquer-Sunyer R, Duarte CM. 2008. Thresholds of hypoxia for marine biodiversity. *Proc. Natl. Acad. Sci. USA* 105:15452–57
- Vetter R, Kohin S, Preti A. 2008. Predatory interactions and niche overlap between mako shark, *Isurus paucus*, and jumbo squid, *Dosidicus gigas*, in the California Current. *CalCOFI Rep.* 49:142–56
- Walsh DA, Zaikova E, Howes CG, Song YC, Wright JJ, et al. 2009. Metagenome of a versatile chemolithoautotroph from expanding oceanic dead zones. *Science* 326:578–82
- Ware DM, Thomson RE. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science* 308:1280–84
- Watters GM, Olson RJ, Field JC, Essington TE. 2008. Range expansion of Humboldt squid was not caused by tuna fishing. *Proc. Natl. Acad. Sci. USA* 105:E5
- White AE, Prah FG, Letelier RM, Popp BN. 2007. Summer surface waters in the Gulf of California: prime habitat for biological N₂ fixation. *Glob. Biogeochem. Cycles* 21:GB2017

- Whitney FA, Freeland HJ, Robert M. 2007. Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. *Prog. Oceanogr.* 75:179–99
- Wing BL. 2006. Unusual invertebrates and fish observed in the Gulf of Alaska, 2004–2005. *PICES Press* 14(2):26–28
- Wohlert J, Engel A, Zöllner E, Breithaupt P, Jürgens K, et al. 2009. Changes in biogenic carbon flow in response to sea surface warming. *Proc. Natl. Acad. Sci. USA* 106:7067–72
- Wright JJ, Konwar KM, Hallam SJ. 2012. Microbial ecology of expanding oxygen minimum zones. *Nat. Rev. Microbiol.* 10:381–94
- Wyrtki K. 1962. The oxygen minima in relation to ocean circulation. *Deep-Sea Res.* 9:11–23
- Zehr JP, Kudela RM. 2011. Nitrogen cycle of the open ocean: from genes to ecosystems. *Annu. Rev. Mar. Sci.* 3:197–225
- Zeidberg LD, Robison BH. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proc. Natl. Acad. Sci. USA* 104:12948–50
- Zhang J, Gilbert D, Gooday AJ, Levin L, Naqvi SW, et al. 2010. Natural and human-induced hypoxia and consequences for coastal areas: synthesis and future development. *Biogeosciences* 7:1443–67

RELATED RESOURCES

- Cavalle J. 2008. The human factor: eutrophication, dead zones and the future of our oceans. *Baja Life Online*, EcoWatch 26. <http://www.bajalife.com/ecowatch/ecowatch26.html>
- Cent. Ocean Solut. *Hypoxic zone*. <http://centerforoceansolutions.org/climate/impacts/cumulative-impacts/hypoxic-zone>
- C-MORE (Cent. Microb. Oceanogr. Res. Educ.). <http://cmore.soest.hawaii.edu>
- Gewin V. 2010. Dead in the water. *Nature* 466:812–14. <http://www.nature.com/news/2010/100811/pdf/466812a.pdf>
- Levy S. 2007. Cannery Row revisited. *BioScience* 57:8–13. <http://www.sharonlevy.net/PDFs/BioScience%20Cannery%20Row.pdf>
- Natl. Sci. Found. 2011. *Special report: dead zones*. http://www.nsf.gov/news/special_reports/deadzones
- Olney J. 2011. Dropping ocean oxygen levels concern scientists. *KGO-TV/ABC7 News*, San Francisco, Nov. 21. http://abclocal.go.com/kgo/story?section=news/assignment_7&id=8440749
- PISCO (Partnersh. Interdiscip. Stud. Coast. Oceans). 2011. *Hypoxia*. Aug. 23. <http://www.piscoweb.org/research/science-by-discipline/coastal-oceanography/hypoxia>
- Santoro A. Scientist at work: notes from the field. *N. Y. Times* blog. <http://scientistatwork.blogs.nytimes.com/author/alyson-santoro>
- Velasquez-Manoff M. 2009. Squid invasions signal changes in the Pacific Ocean. *MinnPost*, Dec. 21. <http://www.minnpost.com/scientific-agenda/2009/12/squid-invasions-signal-changes-pacific-ocean>
- Zimmer C. 2010. A looming oxygen crisis and its impact on world's oceans. *Yale Environ.* 360, Aug. 5. http://e360.yale.edu/feature/a_looming_oxygen_crisis_and_its_impact_on_worlds_oceans/2301/



Contents

Reflections About Chance in My Career, and on the Top-Down Regulated World <i>Karl Banse</i>	1
Causes for Contemporary Regional Sea Level Changes <i>Detlef Stammer, Anny Cazenave, Rui M. Ponte, and Mark E. Tamisiea</i>	21
Gravity Flows Associated with Flood Events and Carbon Burial: Taiwan as Instructional Source Area <i>James T. Liu, Shub-Ji Kao, Chih-An Hub, and Chin-Chang Hung</i>	47
A Deep-Time Perspective of Land-Ocean Linkages in the Sedimentary Record <i>Brian W. Romans and Stephan A. Graham</i>	69
Remote Sensing of the Nearshore <i>Rob Holman and Merrick C. Haller</i>	95
High-Frequency Radar Observations of Ocean Surface Currents <i>Jeffrey D. Paduan and Libe Washburn</i>	115
Lagrangian Motion, Coherent Structures, and Lines of Persistent Material Strain <i>R.M. Samelson</i>	137
Deglacial Origin of Barrier Reefs Along Low-Latitude Mixed Siliciclastic and Carbonate Continental Shelf Edges <i>André W. Droxler and Stéphan J. Jorry</i>	165
The Trace Metal Composition of Marine Phytoplankton <i>Benjamin S. Twining and Stephen B. Baines</i>	191
Photophysiological Expressions of Iron Stress in Phytoplankton <i>Michael J. Behrenfeld and Allen J. Milligan</i>	217
Evaluation of In Situ Phytoplankton Growth Rates: A Synthesis of Data from Varied Approaches <i>Edward A. Laws</i>	247

Icebergs as Unique Lagrangian Ecosystems in Polar Seas <i>K.L. Smith Jr., A.D. Sherman, T.J. Shaw, and J. Sprintall</i>	269
Ecosystem Transformations of the Laurentian Great Lake Michigan by Nonindigenous Biological Invaders <i>Russell L. Cubel and Carmen Aguilar</i>	289
Ocean Acidification and Coral Reefs: Effects on Breakdown, Dissolution, and Net Ecosystem Calcification <i>Andreas J. Andersson and Dwight Gledhill</i>	321
Evolutionary Adaptation of Marine Zooplankton to Global Change <i>Hans G. Dam</i>	349
Resilience to Climate Change in Coastal Marine Ecosystems <i>Joanna R. Bernhardt and Heather M. Leslie</i>	371
Oceanographic and Biological Effects of Shoaling of the Oxygen Minimum Zone <i>William F. Gilly, J. Michael Beman, Steven Y. Litvin, and Bruce H. Robison</i>	393
Recalcitrant Dissolved Organic Carbon Fractions <i>Dennis A. Hansell</i>	421
The Global Distribution and Dynamics of Chromophoric Dissolved Organic Matter <i>Norman B. Nelson and David A. Siegel</i>	447
The World Ocean Silica Cycle <i>Paul J. Tréguer and Christina L. De La Rocha</i>	477
Using Triple Isotopes of Dissolved Oxygen to Evaluate Global Marine Productivity <i>L.W. Juranek and P.D. Quay</i>	503
What Is the Metabolic State of the Oligotrophic Ocean? A Debate <i>Hugh W. Ducklow and Scott C. Doney</i>	525
The Oligotrophic Ocean Is Autotrophic <i>Peter J. le B. Williams, Paul D. Quay, Toby K. Westberry, and Michael J. Behrenfeld</i>	535
The Oligotrophic Ocean Is Heterotrophic <i>Carlos M. Duarte, Aurore Regaudie-de-Gioux, Jesús M. Arrieta, Antonio Delgado-Huertas, and Susana Agustí</i>	551

Errata

An online log of corrections to *Annual Review of Marine Science* articles may be found at <http://marine.annualreviews.org/errata.shtml>



ANNUAL REVIEWS

It's about time. Your time. It's time well spent.

New From Annual Reviews:

Annual Review of Statistics and Its Application

Volume 1 • Online January 2014 • <http://statistics.annualreviews.org>

Editor: **Stephen E. Fienberg**, *Carnegie Mellon University*

Associate Editors: **Nancy Reid**, *University of Toronto*

Stephen M. Stigler, *University of Chicago*

The *Annual Review of Statistics and Its Application* aims to inform statisticians and quantitative methodologists, as well as all scientists and users of statistics about major methodological advances and the computational tools that allow for their implementation. It will include developments in the field of statistics, including theoretical statistical underpinnings of new methodology, as well as developments in specific application domains such as biostatistics and bioinformatics, economics, machine learning, psychology, sociology, and aspects of the physical sciences.

Complimentary online access to the first volume will be available until January 2015.

TABLE OF CONTENTS:

- *What Is Statistics?* Stephen E. Fienberg
- *A Systematic Statistical Approach to Evaluating Evidence from Observational Studies*, David Madigan, Paul E. Stang, Jesse A. Berlin, Martijn Schuemie, J. Marc Overhage, Marc A. Suchard, Bill Dumouchel, Abraham G. Hartzema, Patrick B. Ryan
- *The Role of Statistics in the Discovery of a Higgs Boson*, David A. van Dyk
- *Brain Imaging Analysis*, F. DuBois Bowman
- *Statistics and Climate*, Peter Guttorp
- *Climate Simulators and Climate Projections*, Jonathan Rougier, Michael Goldstein
- *Probabilistic Forecasting*, Tilmann Gneiting, Matthias Katzfuss
- *Bayesian Computational Tools*, Christian P. Robert
- *Bayesian Computation Via Markov Chain Monte Carlo*, Radu V. Craiu, Jeffrey S. Rosenthal
- *Build, Compute, Critique, Repeat: Data Analysis with Latent Variable Models*, David M. Blei
- *Structured Regularizers for High-Dimensional Problems: Statistical and Computational Issues*, Martin J. Wainwright
- *High-Dimensional Statistics with a View Toward Applications in Biology*, Peter Bühlmann, Markus Kalisch, Lukas Meier
- *Next-Generation Statistical Genetics: Modeling, Penalization, and Optimization in High-Dimensional Data*, Kenneth Lange, Jeanette C. Papp, Janet S. Sinsheimer, Eric M. Sobel
- *Breaking Bad: Two Decades of Life-Course Data Analysis in Criminology, Developmental Psychology, and Beyond*, Elena A. Erosheva, Ross L. Matsueda, Donatello Telesca
- *Event History Analysis*, Niels Keiding
- *Statistical Evaluation of Forensic DNA Profile Evidence*, Christopher D. Steele, David J. Balding
- *Using League Table Rankings in Public Policy Formation: Statistical Issues*, Harvey Goldstein
- *Statistical Ecology*, Ruth King
- *Estimating the Number of Species in Microbial Diversity Studies*, John Bunge, Amy Willis, Fiona Walsh
- *Dynamic Treatment Regimes*, Bibhas Chakraborty, Susan A. Murphy
- *Statistics and Related Topics in Single-Molecule Biophysics*, Hong Qian, S.C. Kou
- *Statistics and Quantitative Risk Management for Banking and Insurance*, Paul Embrechts, Marius Hofert

Access this and all other Annual Reviews journals via your institution at www.annualreviews.org.

ANNUAL REVIEWS | Connect With Our Experts

Tel: 800.523.8635 (US/CAN) | Tel: 650.493.4400 | Fax: 650.424.0910 | Email: service@annualreviews.org

