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# Manifestation, Drivers, and Emergence of Open Ocean Deoxygenation

Lisa A. Levin

Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography,  
University of California, San Diego, La Jolla, California 92093-0218, USA;  
email: llevin@ucsd.edu

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## Keywords

climate change, hypoxia, nutrients, open ocean, oxygen minimum zone, paleo-record, stratification, upwelling, variability, oxygen

## Abstract

Oxygen loss in the ocean, termed deoxygenation, is a major consequence of climate change and is exacerbated by other aspects of global change. An average global loss of 2% or more has been recorded in the open ocean over the past 50–100 years, but with greater oxygen declines in intermediate waters (100–600 m) of the North Pacific, the East Pacific, tropical waters, and the Southern Ocean. Although ocean warming contributions to oxygen declines through a reduction in oxygen solubility and stratification effects on ventilation are reasonably well understood, it has been a major challenge to identify drivers and modifying factors that explain different regional patterns, especially in the tropical oceans. Changes in respiration, circulation (including upwelling), nutrient inputs, and possibly methane release contribute to oxygen loss, often indirectly through stimulation of biological production and biological consumption. Microbes mediate many feedbacks in oxygen minimum zones that can either exacerbate or ameliorate deoxygenation via interacting nitrogen, sulfur, and carbon cycles. The paleo-record reflects drivers of and feedbacks to deoxygenation that have played out through the Phanerozoic on centennial, millennial, and hundred-million-year timescales. Natural oxygen variability has made it difficult to detect the emergence of a climate-forced signal of oxygen loss, but new modeling efforts now project emergence to occur in many areas in 15–25 years. Continued global

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deoxygenation is projected for the next 100 or more years under most emissions scenarios, but with regional heterogeneity. Notably, even small changes in oxygenation can have significant biological effects. New efforts to systematically observe oxygen changes throughout the open ocean are needed to help address gaps in understanding of ocean deoxygenation patterns and drivers.

## INTRODUCTION

Most life in the open ocean requires oxygen to breathe, and even marine plants and phytoplankton, which produce oxygen, also respire it. Oxygen played a key role in the early evolution of life during the Great Oxidation Event (2.4 Bya) and arguably in the radiation of life forms during the Ediacaran and Cambrian explosion (540 Mya) (Lyons et al. 2014). Aerobic (air-breathing) life in the ocean creates food (fish and shellfish), supports livelihoods (fishing, recreation, and tourism), provides habitats that support these services (e.g., coral reefs), and recycles nutrients that facilitate primary production. Low-oxygen regions in the ocean play major roles in biogeochemical cycling, accounting for a large fraction of nitrogen loss, and as areas of focused carbon fixation, sulfur transformation, and metal release. Why then is oxygen loss, potentially one of the most significant consequences of climate change, less likely to be recognized as such than warming and ocean acidification by scientists working outside the climate arena, policy makers, educators, and the public? A recent analysis of how 161 Nationally Determined Contributions (NDCs), pledges made under the Paris Agreement, reflected ocean issues revealed only a single mention of ocean deoxygenation; by contrast, 77 NDCs discussed warming, and 14 NDCs discussed ocean acidification (Gallo et al. 2017). Part of the reason for this lack of attention to ocean deoxygenation is that oxygen is highly dynamic, its link to climate change is complex and sometimes indirect, and the mechanisms controlling oxygen in the open ocean are not fully understood.

What follows is an effort to review the manifestations of deoxygenation over time, with emphasis on the last half century and the current understanding of the complex interacting causes of open ocean deoxygenation, including feedbacks, projections for the future, and the emergence of the anthropogenically forced deoxygenation signal. The extent to which the ocean is oxygenated varies greatly in both space and time. There are vast areas with little or no oxygen, and oxygen concentrations are declining in some of these areas, but the same ocean basin or water depths may host other regions that are well oxygenated and/or exhibit increasing concentrations. Similarly, there are regions with severe oxygen limitation in some seasons or millennia and plenty of oxygen in others. A clear understanding of the drivers and patterns of oxygenation is needed to inform modeling of biogeochemical cycles in the ocean and future projections of oxygen change. These, in turn, will facilitate ecosystem-level assessment of deoxygenation consequences and the integration of oxygen trends into resource management actions, including spatial planning, fisheries regulation, and impact assessments.

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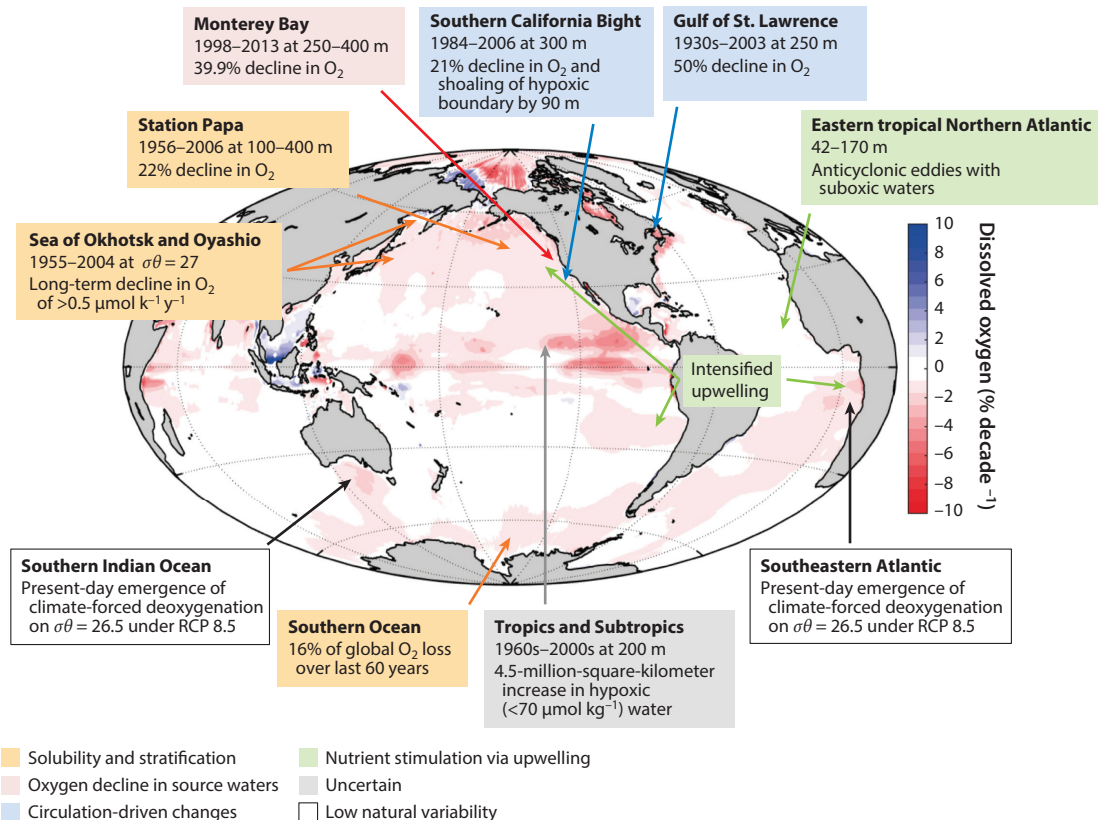
**Open ocean:** ocean waters that are offshore (more than 10–25 km from shore) or heavily influenced by oceanic circulation, including some shelf and gulf waters

**Ocean deoxygenation:** the loss of oxygen caused by anthropogenic influences, including excess CO<sub>2</sub> emissions and nutrient inputs

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## MANIFESTATION OF DEOXYGENATION

Although observational evidence for twentieth-century open ocean deoxygenation had been reported by 2001 (e.g., Ono et al. 2001 and citations in Keeling & Garcia 2002), it is really in the last decade that long-term observations have been integrated into regional and global syntheses of deoxygenation, raising awareness of the phenomenon. The picture that has emerged over the past decade is one of both intense regional oxygen loss and global loss overall, particularly at



**Figure 1**

Representative long-term records of open ocean deoxygenation in intermediate waters superimposed on full ocean percentage change in dissolved oxygen per decade since 1960. The color of each text box reflects potential primary drivers: orange, solubility and stratification; red, oxygen decline in source waters; blue, circulation-driven changes; green, nutrient stimulation via upwelling; gray, uncertain causes; white, low natural variability that reduces the time of emergence. Abbreviations:  $\sigma_\theta$ , density surface; RCP, representative concentration pathway. Base map adapted from Schmidtke et al. (2017) with permission.

intermediate- and mode-water depths of 100–1,000 m (**Figure 1**). Some of this oxygen decline is superimposed on areas already naturally low in oxygen, and thus even small changes may be of biogeochemical and ecological significance. This section reviews evidence for ocean oxygen loss, with emphasis on regional trends and insights from studies emerging since Keeling et al.'s (2010) review of ocean deoxygenation.

Oxygen concentration is expressed in many different units, depending on the discipline, and sometimes partial pressure is considered. Discussions below largely present units used in the original reports (with some conversions provided), but see the sidebar titled Oxygen Concentration Units for conversion details.

## Long-Term Global Studies

Fifty-year oxygen records at tropical locations in the eastern Pacific and Atlantic Oceans have revealed expanding oxygen minimum zones (OMZs), with declines of  $0.09$ – $0.34 \mu\text{mol kg}^{-1} \text{y}^{-1}$  at 300–700 m (Stramma et al. 2008). An expanded synthesis of tropical and subtropical oxygen

**Oxygen minimum zone (OMZ):** defined here as a region of the ocean where the  $O_2$  concentration is  $<22 \mu\text{mol kg}^{-1}$ , usually within depths of 100–1,200 m

## OXYGEN CONCENTRATION UNITS

Different types of scientists use different oxygen units. For ease of conversion:

$$1.4 \text{ mg L}^{-1} = 1.0 \text{ mL L}^{-1} = 44.4 \text{ } \mu\text{mol L}^{-1} \text{ O}_2,$$

$$1 \text{ } \mu\text{mol L}^{-1} = 0.9737 \text{ } \mu\text{mol kg}^{-1} \text{ at a seawater density of } 1.027 \text{ g cm}^{-3}.$$

Notably, the partial pressure of oxygen ( $p\text{O}_2$ , the portion of the pressure exerted by gas in seawater that is attributable to oxygen) is expressed in kilopascals and may be more helpful in understanding biological responses to oxygen stress. At 100% saturation,  $p\text{O}_2 = 21 \text{ kPa} = 280 \text{ } \mu\text{M}$  at  $10^\circ\text{C}$ .

records by Stramma et al. (2010) demonstrated a widespread oxygen decline between 200 and 700 m, with the area having  $<70 \text{ } \mu\text{mol kg}^{-1} \text{ O}_2$  expanding by 4.5 million square kilometers at a depth of 200 m based on records initiated in 1960–1974 and ending in 1990–2008. An update to this work that extended beyond the tropics (between  $50^\circ\text{S}$  and  $50^\circ\text{N}$ ) yielded a global mean loss of oxygen from 1960 to 2010 of  $0.066 \text{ } \mu\text{mol kg}^{-1} \text{ y}^{-1}$  at 300 m (Stramma et al. 2012). Finally, a recent whole-ocean synthesis of global oxygen loss over the past 50 years from the surface to the deep ocean revealed a global ocean oxygen loss of 2% ( $4.8 \pm 2.1 \text{ Pmol}$  or  $\sim 0.072 \text{ } \mu\text{mol kg}^{-1} \text{ y}^{-1}$ ) (Schmidtke et al. 2017).

Another large-scale but more temporally and depth-focused analysis of hydrographic records documented global average oxygen losses of  $0.93 \pm 0.23 \text{ } \mu\text{mol L}^{-1} \text{ y}^{-1}$  ( $0.55 \pm 0.13 \times 10^{14} \text{ mol y}^{-1}$ ) from 1970 to 1990 at depths of 100–1,000 m (Helm et al. 2011). The largest declines occurred poleward of  $40^\circ$  latitude, but increases were also observed in subtropical gyres ( $15\text{--}30^\circ$ ) at intermediate depths (Helm et al. 2011). Gilbert et al. (2010) combined published data and unpublished hydrographic records to compare the oxygen loss in coastal and nearshore waters (30–100 km from shore) with that in open ocean waters ( $>100 \text{ km}$  from shore) from 1951 to 2000. They found that during the first half of that period, in the upper 300 m, both the median rates of oxygen change ( $-0.28 \text{ } \mu\text{mol L}^{-1} \text{ y}^{-1}$  in coastal and nearshore waters versus  $0.02 \text{ } \mu\text{mol L}^{-1} \text{ y}^{-1}$  in open ocean waters) and the percentage of studies showing oxygen loss (64% versus 49%) were greater inshore than offshore. This study yielded a greater proportion of negative trends in oxygen in the 1976–2000 period than in the 1951–1975 period. However, these authors also noted a significant overall publishing bias toward reporting negative over positive or neutral trends based on a comparison between median published oxygen trends and median trends calculated from raw oxygen data (Gilbert et al. 2010), highlighting the value of open access to ocean hydrologic records.

Deoxygenation is often studied as a regional or local phenomenon, in part because some regions have experienced pronounced declines in oxygenation. Monitoring programs have provided evidence for ocean deoxygenation over the past 30–50 years in mode and intermediate waters in the western Pacific, northeastern Pacific, California Current System, North Atlantic, northern tropical Indian Ocean, and Southern Ocean (**Figure 1**).

### Northeastern Pacific Ocean

Among the first and longest oxygen time series, a 50-year record at Station Papa (1956–2006) in the northeastern Pacific revealed that oxygen had declined by 22% at water depths of 100–400 m (Whitney et al. 2007). This study documented oxygen loss of  $0.4\text{--}0.7 \text{ } \mu\text{mol kg}^{-1} \text{ y}^{-1}$  on density

( $\text{kg m}^{-3}$ ) surfaces ( $\sigma\theta$ ) of 26.3–27.0 and a shoaling of the hypoxic boundary ( $60 \mu\text{mol kg}^{-1}$ ) from 400 to 300 m. The 26.5 or 26.6  $\sigma\theta$  density surface exhibits the maximum oxygen decline in the North Pacific (Emerson et al. 2004, Mecking et al. 2008) both at Station Papa ( $-0.7 \mu\text{mol kg}^{-1} \text{y}^{-1}$ ; Whitney et al. 2007) and on the Newport Hydrographic Line off Oregon ( $-0.9 \mu\text{mol kg}^{-1} \text{y}^{-1}$ ; Pierce et al. 2012), potentially linked to variation in ventilation (outcropping at the surface) in the western Pacific. In Canadian waters southwest of Vancouver Island, oxygen concentration declined by  $0.83 \mu\text{mol kg}^{-1} \text{y}^{-1}$  from 1979 to 2011 (Crawford & Peña 2013). Off Oregon, there was a significant shoaling of the  $20 \mu\text{mol kg}^{-1}$  surface by 69 m, and a region of decreasing oxygen ( $-0.7 \pm 0.2 \mu\text{mol kg}^{-1} \text{y}^{-1}$ ) was observed over the upper slope at depths of 150–200 m (Pierce et al. 2012).

The upper 500 m of the California Current System has been well monitored for oxygen. Using California Cooperative Oceanic Fisheries Investigations (CalCOFI) data, Bograd et al. (2008) reported large declines in dissolved oxygen (up to  $2.1 \mu\text{mol kg}^{-1} \text{y}^{-1}$ ) in the southern California Current from 1984 to 2006, a mean decrease of 21% below the thermocline at 300 m, and shoaling of the hypoxic boundary ( $60 \mu\text{mol kg}^{-1}$ ) by up to 90 m within portions of the southern California Current System. However, McClatchie et al. (2010) pointed out that the secular trend in hypoxia in southern California over the last 57 years is not monotonic and that low oxygen levels were also measured in the late 1950s to early 1960s. Additional analyses of post-2006 data showed continued oxygen decline in the region, commensurate with increases in nitrogen and phosphorus (Bograd et al. 2015). Similar results by Ren (2016) for a transect in Monterey Bay, California, showed that oxygen decreased between 250 and 400 m over 16 years (1998–2013), with a dramatic 39.9% decline ( $1.92 \mu\text{mol kg}^{-1} \text{y}^{-1}$ ) observed at  $\sigma\theta = 26.7$ . In contrast to the strong oxygen declines at undercurrent depths in the southern California Current System, there is no long-term trend for oxygen loss in the upper California Current at  $\sigma\theta = 25.8$  (Bograd et al. 2015, Ren 2016).

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**Hypoxia:** a shortage of oxygen for life processes, often defined as an  $\text{O}_2$  concentration of  $<63 \mu\text{mol kg}^{-1}$  ( $<2 \text{ mg L}^{-1}$  or  $<1.4 \text{ mL L}^{-1}$ )

**Anoxia:** the absence of measurable oxygen

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## Equatorial Pacific Ocean

The equatorial Pacific has a large area of naturally occurring low oxygen at intermediate depths (Paulmier et al. 2008) and is the region with the greatest oxygen loss recorded in the last half century (21.9% of total,  $210 \pm 125 \text{ Tmol decade}^{-1}$ ; Schmidtke et al. 2017). This loss was first highlighted by Stramma et al. (2008), who demonstrated that tropical OMZs had expanded and intensified in both the Pacific and Atlantic. Data from four locations in the eastern equatorial Pacific, central equatorial Pacific, eastern tropical South Atlantic, and equatorial Atlantic revealed average oxygen losses of  $0.13\text{--}0.34 \mu\text{mol kg}^{-1} \text{y}^{-1}$  since 1960. Trends in waters with the lowest oxygen levels may differ from those in the rest of the OMZ. Deutsch et al. (2014) noted, based on a geochemical proxy for denitrification, that although anoxia has increased in the North Pacific since the 1990s, the trend for much of the twentieth century was for a shrinking anoxic zone.

## Northwestern Pacific Ocean

As early as 2001, Ono et al. (2001) documented increasing phosphate and apparent oxygen utilization ( $0.9 \mu\text{mol kg}^{-1} \text{y}^{-1}$ ) between 1968 and 2001 on the  $\sigma\theta = 26.7\text{--}27.2$  surfaces in the Oyashio region. These are similar to changes reported in the eastern Pacific, the latter with a 7-year time lag (Whitney et al. 2007). Significant oxygen loss of  $>0.50 \text{ mL L}^{-1}$  ( $22 \mu\text{mol kg}^{-1}$ ) was reported over 49 years (1955–2004) at the  $\sigma\theta = 27$  surface in the Sea of Okhotsk and Oyashio regions, yielding loss rates of  $0.45 \mu\text{mol kg}^{-1} \text{y}^{-1}$  (Nakanowatari et al. 2007). Based on Japan Meteorological Society monitoring of  $137^\circ\text{E}$  in the western Pacific, Takatani et al. (2012) showed oxygen declines,

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**Oxygen solubility:**

the ability of oxygen gas to dissolve in seawater; it declines at higher temperature and salinity but increases at greater pressure

**Suboxic zone:**

a region of the ocean where the  $O_2$  concentration is  $<5 \mu\text{mol kg}^{-1}$  ( $<0.16 \text{ mg L}^{-1}$  or  $<0.11 \text{ mL L}^{-1}$ ) but  $>0 \mu\text{mol kg}^{-1}$ ; such conditions are conducive to denitrification and anaerobic ammonium oxidation

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particularly in the subtropics, from 1985 to 2010, where the changes were  $-0.28$ ,  $-0.36$ , and  $-0.23 \mu\text{mol kg}^{-1} \text{ y}^{-1}$  in the North Pacific Subtropical Mode Water, North Pacific Intermediate Water, and oxygen minimum layer, respectively. Sasano et al. (2015) analyzed repeat hydrographic data from  $165^\circ\text{E}$  in the western North Pacific from 1987 to 2011. They attributed oxygen changes of  $-0.44$  to  $-0.45 \mu\text{mol kg}^{-1} \text{ y}^{-1}$  to deepening isopycnals and declining oxygen solubility in the North Pacific Subtropical Mode Water and to increased apparent oxygen utilization in the North Pacific Intermediate Water. Lesser changes of  $-0.22 \mu\text{mol kg}^{-1} \text{ y}^{-1}$  in the subtropical OMZ were attributed to westward transport of low-oxygen water, whereas an increase of  $0.36 \mu\text{mol kg}^{-1} \text{ y}^{-1}$  was reported in the OMZ.

## Atlantic Ocean

As with Pacific Ocean oxygen concentrations, the long-term oxygen trends in the Atlantic exhibit considerable variation in intensity and even greater variability in direction. A 72-year record in the St. Lawrence Estuary shows a near halving of oxygen saturation in bottom waters (250 m) from the 1930s to 2003 (Gilbert et al. 2005). In repeat sections along  $7.5^\circ\text{N}$  and  $11^\circ\text{N}$  in the tropical North Atlantic, deoxygenation has occurred at a rate of  $0.5 \mu\text{mol kg}^{-1} \text{ y}^{-1}$  over the last 20 years in the core of the OMZ, but oxygen increased in the central water layer above (Stramma et al. 2009). Brandt et al. (2012) documented reduced ventilation and oxygen loss of  $15 \mu\text{mol kg}^{-1}$  from 1999 to 2008 ( $1.67 \mu\text{mol kg}^{-1} \text{ y}^{-1}$ ) at 400 m in the tropical North Atlantic from  $28.58^\circ\text{W}$  to  $23.8^\circ\text{W}$ . As in the western Pacific, from 1960 to 2009, the North Atlantic exhibited significant declines in oxygen (34–47 Tmol) in its upper ( $\sigma_\theta = 30.2\text{--}31.3$ ), mode ( $\sigma_\theta = 31.3\text{--}31.8$ ), and intermediate waters ( $\sigma_\theta = 31.8\text{--}32.3$ ), with an average loss of  $0.098 \pm 0.045 \mu\text{mol kg}^{-1} \text{ y}^{-1}$  over 49 years in these water masses. Oxygen increases of  $0.073 \pm 0.076 \mu\text{mol kg}^{-1} \text{ y}^{-1}$  (46–47 Tmol) observed in its lower intermediate water ( $\sigma_\theta = 32.3\text{--}32.4$ ) and Labrador Sea waters ( $\sigma_\theta = 32.4\text{--}32.45$ ) were not statistically significant (Stendardo & Gruber 2012).

From the 1990s to 2013, oxygen loss in the upper 300 m of the Atlantic subtropical waters was documented by time-series measurements at the Bermuda Atlantic Time-Series Study site ( $-0.71 \mu\text{mol kg}^{-1} \text{ y}^{-1}$ ), the Carbon Retention in a Colored Ocean (CARIACO) site ( $-0.28 \mu\text{mol kg}^{-1} \text{ y}^{-1}$ ), and Hydrostation S ( $-0.37 \mu\text{mol kg}^{-1} \text{ y}^{-1}$ ). Repeat hydrography yielded similar oxygen losses from the 1980s to 2013 of  $0.58 \mu\text{mol kg}^{-1} \text{ y}^{-1}$  and  $0.68 \mu\text{mol kg}^{-1} \text{ y}^{-1}$  in the Caribbean Sea and western subtropical North Atlantic, respectively (Montes et al. 2016). The oxygen declines appear to be linked to reduced wind-driven mixing and slowed subtropical underwater formation associated with a positive Atlantic Multidecadal Oscillation. No oxygen loss was documented during this period in the eastern subtropical Atlantic off the Canary Islands ( $29.2^\circ\text{N}$ ,  $15.5^\circ\text{W}$ ) based on European Station for Time-Series in the Ocean (ESTOC) (Canary Islands) or ship time series (Montes et al. 2016).

Although Atlantic oxygen levels are relatively high (most oxygen minimum records are above  $40 \mu\text{mol kg}^{-1}$ ), Karstensen et al. (2015) reported finding zones of much greater oxygen depletion ( $<2 \mu\text{mol kg}^{-1}$ ) in propagating anticyclonic mode-water eddies. These suboxic zones are generated by intense respiration and isolation and can propagate at  $4.5 \text{ km d}^{-1}$  toward the open ocean from the east. Whether their incidence is changing with ocean warming is unclear.

## Indian Ocean

Limited long-term records in the Indian Ocean suggest that oxygen is declining in the northern tropical Indian Ocean but increasing in the southern Indian Ocean (McDonagh et al. 2005, Stramma et al. 2010). Naqvi et al. (2006) compiled data from the west India shelf and slope and



showed that oxygen concentrations were lower in 1997–2004 than in 1971–1975, although there was tremendous seasonal variability superimposed on this.

## Southern Ocean and Antarctica


Oxygen loss from the Southern Ocean was investigated as early as 2000, with the recognition that the water masses (Antarctic Intermediate Water and Circumpolar Deep Water) interact strongly with surface waters and the atmosphere and are affected by circulation (Matear et al. 2000). Approximately 25% of the global oxygen loss documented at intermediate depths from 1970 to 1992 occurred in the Southern Ocean (Helm et al. 2011). Over a longer period, Southern Ocean oxygen loss is regionally the third largest (after the equatorial Pacific and North Pacific), accounting for nearly 16% of global oxygen loss in the last 50 years ( $-152 \pm 47$  Tmol decade<sup>-1</sup>,  $\sim 0.06$   $\mu\text{mol kg}^{-1} \text{ y}^{-1}$ ; Schmidtko et al. 2017).

## Are Levels of Recent Oxygen Loss Noteworthy?

The rates of oxygen loss over the last 50–60 years reported here now include oxygen time series that extend into the present decade (2008–2017), which hosts 7 of the 10 hottest years on record (2009, 2010, 2012, 2013, 2014, 2015, and 2016). We can ask how these rates of oxygen loss compare with those reported previously and with rates inferred for past deoxygenation events on geological timescales. Regionally, rates of oxygen loss reported are greatest for bathyal depths between 100 and 1,200 m. Discussion is focused on these depths, which host key vertical carbon and nitrogen fluxes and transformations, massive daily animal migrations, and naturally occurring oxygen minima. The regional O<sub>2</sub> loss rates reported in post-2010 publications ( $0.10$ – $1.92$   $\mu\text{mol kg}^{-1} \text{ y}^{-1}$ ) are similar to the average regional maximum rates ( $0.11$ – $1.65$   $\mu\text{mol kg}^{-1} \text{ y}^{-1}$ ) reported previously by Keeling et al. (2010, their table 3) but higher than those documented by Schmidtko et al. (2017) for 0–1,200 m ( $0.004$ – $0.118$   $\mu\text{mol kg}^{-1} \text{ y}^{-1}$ ) (**Supplemental Table 1**). Although these values appear very small when presented as loss per year, they represent substantial declines in oxygenation (e.g., 5 to  $>75$   $\mu\text{mol kg}^{-1}$ ) over a half-century observation period. These are of course superimposed on natural, multidecadal or longer climate cycles, but a downward secular trend in the last half century is clear (e.g., Whitney et al. 2007, McClatchie et al. 2010).

Even relatively rapid deoxygenation events in the paleo-record generally play out over tens of thousands of years (e.g., Brenneke et al. 2011, Ostrander et al. 2017), yielding much lower rates of ocean deoxygenation than have been reported for the modern ocean. There are instances of rapid local deoxygenation in the recent past, however, yielding O<sub>2</sub> loss rates comparable to or slightly lower than those observed today. Moffitt et al. (2015a) reported abrupt (130–170 years) changes in sediment fauna of the Santa Barbara Basin, reflecting O<sub>2</sub> shifts from  $>66$  to  $<22$   $\mu\text{mol kg}^{-1}$  in the last interglacial period [Termination 1A (14.7 kya) and Termination 1B (11.7 kya)].

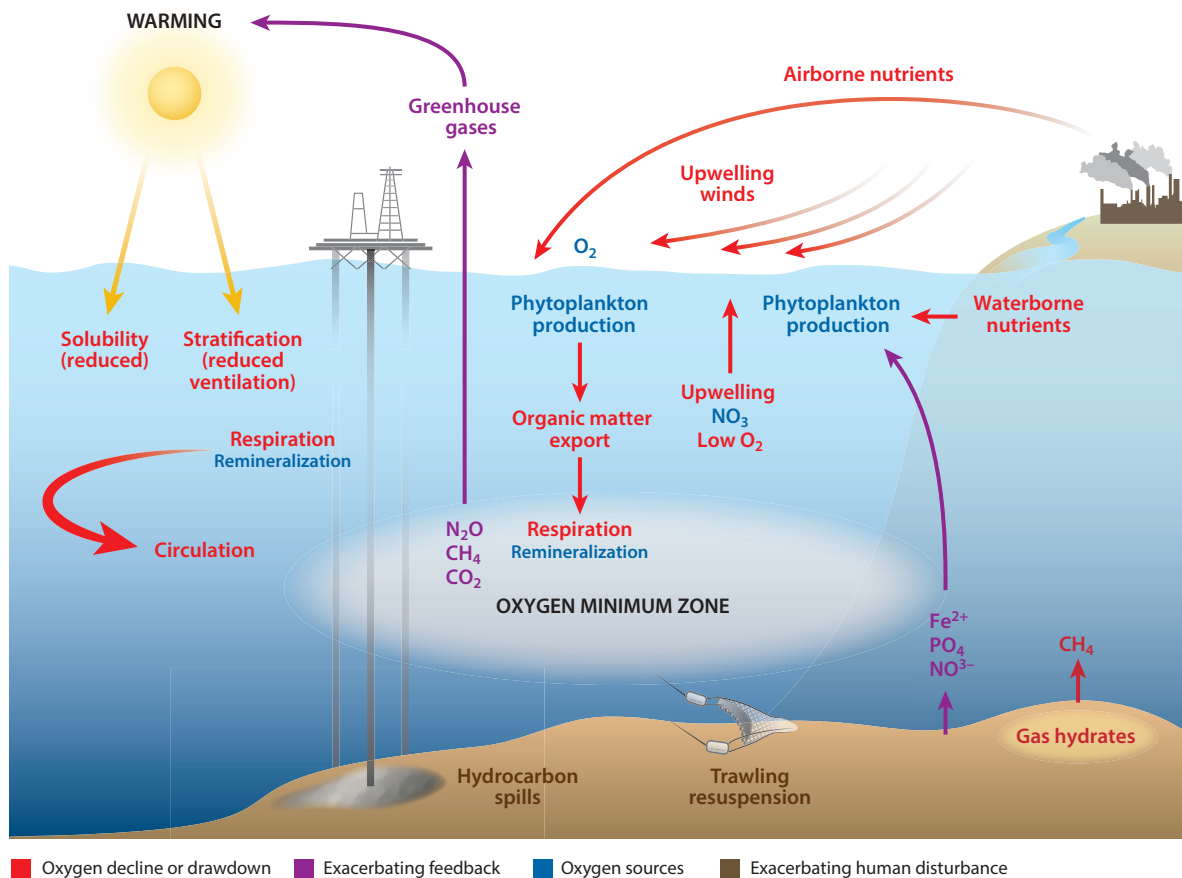
In both the modern and fossil record, it is evident that small changes in oxygenation can have major biological impacts if they carry a system across key thresholds (Vaquer-Sunyer & Duarte 2008). The intermediate-depth waters experiencing the greatest rates of O<sub>2</sub> loss already host oxygen minima and sit at biological tipping points for both animals and microbes. On the Pakistan margin, a 5- $\mu\text{mol}$  oxygen decline from 10  $\mu\text{mol L}^{-1}$  O<sub>2</sub> at 1,100 m to 5  $\mu\text{mol L}^{-1}$  O<sub>2</sub> at 700 m generates a shift from diverse macro-infaunal assemblages (and fully bioturbated sediments) to an assemblage dominated by one macrofaunal species (and fully laminated sediments) (Levin et al. 2009). Meta-analysis of cross-margin macrofaunal communities beneath upwelling regions by Sperling et al. (2016) documented major biodiversity thresholds, with a precipitous drop in biodiversity below 7–8  $\mu\text{mol L}^{-1}$  O<sub>2</sub> in the East Pacific and below 20  $\mu\text{mol L}^{-1}$  O<sub>2</sub> in the Indian

 Supplemental Material

Ocean. Warming waters and declining oxygen levels will increase the vulnerability of many habitats between 500 and 1,000 m to macrofaunal biodiversity loss in the East Pacific (Sperling et al. 2016). Oxygen thresholds are higher for fishes; off California, Namibia, and Chile, demersal fish exhibit large drops in diversity at  $O_2$  levels below  $60 \mu\text{mol kg}^{-1}$  and especially below  $22 \mu\text{mol kg}^{-1}$  (Gallo & Levin 2016), but large, active billfish in the upper ocean have thresholds closer to  $150 \mu\text{mol kg}^{-1}$  (Stramma et al. 2011).

## COMPLEX INTERACTING CAUSES OF DEOXYGENATION

There are multiple causes of and influences on ocean deoxygenation (**Figure 2**). Many of these stem from ocean warming, notably solubility, stratification, respiration, and resulting biogeochemical feedbacks. There are also many other contributors to oxygen loss—changes in circulation (including upwelling), nutrient inputs, and hydrocarbon release—that may well be linked to warming, but the connections are less certain. These are discussed below and summarized in **Figure 2**.



**Figure 2**

Drivers and processes affecting open ocean deoxygenation. Red indicates phenomena contributing to oxygen decline or drawdown, blue indicates oxygen sources, purple indicates feedbacks, and brown indicates examples of direct human disturbance that can exacerbate ocean deoxygenation.



## Warming Effects

The link between open ocean oxygen loss and climate change (global warming) is undeniable, owing to the laws of physics, which affect solubility and stratification. Most global oxygen inventories have attributed the lion's share of oxygen loss to these two phenomena (e.g., Keeling et al. 2010, Helm et al. 2011, Schmidtko et al. 2017), although other factors may be contributing.

**Solubility.** Oxygen solubility in seawater is controlled by temperature, salinity, and pressure. The temperature dependence of oxygen solubility is usually explained using Le Chatelier's principle, which states that a system placed under stress (e.g., excess heat) will have an equilibrium shift to relieve that stress—i.e., dissolution will occur to remove the added heat:




Warming seawater will shift the equilibrium to the left such that less oxygen dissolves at a higher temperature. At saturation, a shift from 4°C to 6°C can yield a loss of 14.7  $\mu\text{mol kg}^{-1}$  (Brewer & Peltzer 2016) (**Supplemental Figure 1**). CO<sub>2</sub>-induced atmospheric warming has been extensively mitigated by massive ocean heat uptake (Glecker et al. 2016); the resulting ocean warming contributes to observed ocean deoxygenation through solubility effects in seawater. Several studies have estimated that solubility accounts for approximately 15–16% of global oxygen loss (Helm et al. 2011, Schmidtko et al. 2017), but a much larger fraction in the upper ocean. Warming-induced changes in oxygen solubility have generated approximately 130 Tmol of the observed oxygen loss since 1960, with most of this focused in the upper 1,000 m, where solubility accounts for approximately 50% of the loss (Schmidtko et al. 2017).

**Stratification.** Warming of the surface ocean intensified upper-ocean stratification during the last half of the twentieth century, leading to reduced ventilation of the ocean interior (Keeling et al. 2010). This effect is projected to be greatest at low latitudes based on 10 of the Coupled Model Intercomparison Project Phase 3 (CMIP3) climate models under the Special Report on Emissions Scenarios A2 (SRES-A2) scenario (Capotondi et al. 2012) (**Supplemental Figure 2**). Melting ice caps and glaciers also increase density stratification through changes in salinity, with the greatest effects in the Arctic, North Atlantic, and northeastern Pacific. Short-term climate events that affect temperature and mixing, such as the El Niño–Southern Oscillation, North Atlantic Oscillation, and Antarctic Circumpolar Wave, also alter stratification (Le Quéré et al. 2003). The resulting variability in mixed-layer depths (sometimes by hundreds of meters) affects nutrient supply to the surface and subsequent biomass production by phytoplankton.

One possible consequence of increased stratification and shoaling mixed layers is diminished organic matter export from surface waters and less biogeochemical drawdown of oxygen in the ocean interior, potentially moderating some effects on oxygen of reduced ventilation. Many recent syntheses of oxygen loss have attributed a large fraction of global oxygen loss at intermediate depths to stratification effects (Helm et al. 2011, Talley et al. 2016), but more research is needed to understand how stratification affects oxygen in different regions.

**Respiration.** Naturally occurring oxygen minima are generally formed where remineralization of organic matter occurs in the absence of ventilation or oxygenation; the influence of respiration on oxygen is often greatest in the upper thermocline (Deutsch et al. 2006). Changes in both the supply of organic matter (export production) and the rate of decay can introduce variability in oxygenation. Warming will significantly increase microbial and animal respiration rates and thus can be expected to intensify oxygen drawdown. In the Sargasso Sea, for example, a 2°C increase will increase oxygen

 **Supplemental Material**

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### Upper-ocean stratification:

a density difference between 200 m and the surface

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consumption rates by 29%, and a 3°C increase will increase oxygen consumption rates by 50% (Brewer & Peltzer 2016). Because phytoplankton metabolic and photosynthesis rates can respond differently to warming, it has been proposed that a 5°C rise might shift Arctic phytoplankton from net autotrophy to net heterotrophy, with resulting oxygen loss (Holding et al. 2013). Heterotrophy and oxygen undersaturation have been documented in the Arctic during summer (Vaquer-Sunyer et al. 2013). Temperature-driven increases in remineralization can also yield more nitrate, which, if advected or upwelled into the mixed layer, may further stimulate primary production where carbon is not limiting, with positive feedback to deoxygenation. Surprisingly, temperature and direct CO<sub>2</sub> effects on respiration have received limited attention from Keeling et al. (2010) and subsequent papers explaining ocean deoxygenation, although this is starting to change (Andrews et al. 2017, Brewer & Peltzer 2017). Temperature effects on biogeochemical and biological oxygen losses are complex; they are moderated by the influences of depth, light, and nitrogen, iron, and carbon limitation and remain poorly understood as an explanatory factor for deoxygenation.

Notably, warming increases the threshold oxygen levels required by animals for survival, leading to higher saturation requirements and effectively expanding inhospitable areas (Vaquer-Sunyer & Duarte 2011). A meta-analysis revealed that a 4°C rise in bottom-water temperature (possibly expected by 2100) could reduce survival under hypoxia by 35.6% and raise lethal oxygen thresholds by 25.5% among benthic animals (Vaquer-Sunyer & Duarte 2011). Metabolic rates are also sensitive to oxygen, not just temperature. Thus, although rising temperatures can raise faunal metabolic rates and oxygen demand, oxygen shortages may actually suppress metabolic rates. Many animals use metabolic suppression as one adaptation to live under hypoxia (Seibel 2011). This could counter the effects of thermally enhanced animal respiration, although different organisms may be affected. This potential for counteracting effects of warming on animal respiration can complicate modeling of the biogeochemical and ecological contributions to deoxygenation in places where animal respiration plays a major role.

Elevation of metabolic rates by rising temperature can have other consequences that affect oxygen utilization and production. For example, higher metabolic rates can lead to changes in limiting nutrients for phytoplankton (Dutkiewicz et al. 2013). Net oxygen production by phytoplankton may also be temperature sensitive. Sekerci & Petrovskii (2016) proposed that oxygen production by phytoplankton may diminish if temperatures are too high or too low; however, the thermal adaptive capacity of phytoplankton could moderate these changes (Thomas et al. 2012). There are few species-specific studies of phytoplankton oxygen production as a function of temperature, but given the importance of this process to the Earth system, the potential for this to contribute to deoxygenation bears further investigation.

## Other Influences on Deoxygenation

Beyond the direct effects of warming discussed above, a suite of additional influences on ocean deoxygenation play out on local, regional, and basin-wide scales.

**Circulation changes.** Several large-scale changes in ocean circulation appear to be altering ocean oxygenation. The extent to which some of these changes are driven by climate change is still uncertain, but many may be at least partially linked to CO<sub>2</sub>-driven changes in temperature, pressure, or winds.

The oxygen dynamics of the eastern tropical Pacific is highly sensitive to changes in ocean circulation (Montes et al. 2014). Duteil et al. (2014) proposed that a 30% reduction in wind-driven transport of oxygen from the 1960s to the 1990s by the subtropical-tropical cells accounts

for some of the major oxygen loss in the tropical Pacific, although this trend may be reversing. Warming and shoaling (by 92 m) of the Antarctic Intermediate Water at 500–1,500 m are thought to affect the ventilation of the subtropical and tropical Atlantic (Schmidtko & Johnson 2012), with consequences for the oxygen content and vertical thickness of the eastern tropical Atlantic oxygen minima (Santos et al. 2016). From 1960 to 2015, oxygen in the Antarctic Intermediate Water layer decreased by 10  $\mu\text{mol kg}^{-1}$  in the eastern tropical North Atlantic OMZ and by 8  $\mu\text{mol kg}^{-1}$  in the eastern tropical South Atlantic OMZ (Santos et al. 2016).

In the Atlantic, mesoscale eddies (recognized by dynamic height anomaly and sea surface height) can influence oxygenation. Off Bermuda, there is shoaling of the oxygen minimum induced by cyclonic eddies and deepening induced by anticyclonic eddies (Stevens et al. 2016). In the eastern tropical North Atlantic, as mentioned above, mesoscale dead zone eddies contain shallow suboxic waters with oxygen concentrations as low as 2  $\mu\text{mol kg}^{-1}$  below the mixed layer, at depths of 85–120 m (Karstensen et al. 2015); these waters host unique microbial communities with potential for denitrification (Löscher et al. 2015).

In selected regions, circulation changes underlie long-term oxygen trends. For example, oxygen loss in the Southern California Bight, which has involved a 20–30% decline in outer-shelf oxygenation over the last 30 years, is associated with increased spiciness and strengthening (and shoaling) of the poleward-moving California Undercurrent ( $\sigma_\theta = 26.5$ ), which carries low-oxygen tropical source waters (Meinville & Johnson 2013, Bograd et al. 2015). In the Santa Barbara Basin, diminished flushing, along with recent drops in the oxygen content of the source water (at 475 m), appears to account for declines in oxygenation, increased denitrification, and a 10-fold increase in nitrate (Goerick et al. 2015). The resulting loss of oxygen and increases in nitrogen and phosphorus content in these studies mirror basin-scale patterns in the western and eastern subarctic Pacific (Whitney et al. 2013). More than half of the loss of oxygen saturation in the St. Lawrence Estuary, from 37.7% in the 1930s to 20.7% in 2003, has been attributed to the diminished strength of the well-oxygenated Labrador Current and an increased influence of less well-oxygenated North Atlantic Central Waters (Gilbert et al. 2005).

**Upwelling and winds.** One hypothesized effect of global warming is an increased temperature differential between land and sea, which could intensify upwelling winds in eastern boundary upwelling regions (Bakun 1990). This hypothesis and the interpretation of evidence are controversial and complicated by limited wind data accompanied by methodological changes over time (Rykaczewski et al. 2015). Observed and modeled changes in winds over the past 60 years appear to support the Bakun hypothesis for the Benguela, California, and Humboldt upwelling systems, where winds have intensified, but not for the Iberian and Canary systems (Sydeman et al. 2014). Greater coastal upwelling would introduce more nutrients to lighted surface waters, enhancing export production and its ultimate decay (or consumption), with increased respiration drawing down oxygen. Upwelling can also redistribute low-oxygen waters closer to shore or on the shelf, where they may affect valuable coastal marine resources.

One suite of climate models predicts longer and more intense upwelling in the Canary, Benguela, and Humboldt systems by the end of the century, especially at high-latitude, poleward regions of the eastern boundary upwelling systems, but not in the California Current, where other sources of climate variability (the El Niño–Southern Oscillation, Pacific Decadal Oscillation, and North Pacific Gyre Oscillation) likely control upwelling (Wang et al. 2015). However, extreme intensification of upwelling winds may shunt nutrients and particles off of the shelf before they sink and decay, lowering subsurface respiration and in part mitigating coastal hypoxia (Harrison et al. 2016). In addition, warming could counter the effects of upwelling by increasing thermal

stratification, reducing the depth of the mixed layer and reducing the input of nutrients into the euphotic zone, making the ultimate effects of upwelling on oxygenation less certain (García-Reyes et al. 2015). At least one model based on the Geophysical Fluid Dynamics Laboratory's Earth System Model (ESM) 2.1 predicts that decreased ventilation in the North Pacific will increase the supply of nitrate in source waters to the California Current System, leading to further deoxygenation (18%) by 2100 (Rykaczewski & Dunne 2010). Multiple modeling efforts predict poleward intensification of winds in upwelling systems but show that Bakun's mechanism is not the dominant driver (Garreaud & Falvey 2009, Belmadani et al. 2014, Rykaczewski et al. 2015). Rather, poleward shifts in high-pressure zones appear to intensify upwelling winds. In the California Current, for example, upwelling winds at the poleward boundaries (north of San Francisco) are predicted to intensify in spring, whereas winds farther south will weaken.

There may be terrestrial influences on upwelling as well. CO<sub>2</sub>-induced changes in vegetation on land can alter albedo, evaporation, and soil moisture; these have been treated as land-cover-atmosphere feedbacks that can influence wind-stress curl (and upwelling) by augmenting the land-sea temperature differences but altering seasonal effects. In the California Current, the land-cover-atmosphere coupling further intensifies peak and late-season wind-stress curl to the north and decreases it to the south (Diffenbaugh et al. 2004).

**Airborne nutrient inputs.** Nutrient inputs that stimulate primary production are at the heart of both upwelling-driven and eutrophication-driven hypoxia (Levin & Breitburg 2015). Thus, any additional source of limiting nutrients in the open ocean may ultimately enhance production and lead to increased oxygen consumption. Riverine inputs of nutrients from land to the coastal ocean are well recognized to play a role in deoxygenation of coastal waters (Rabalais et al. 2014) (see the sidebar titled Waterborne Nutrients from Land); they are not reviewed here because their effects, which are primarily coastal, have been reviewed elsewhere, and the emphasis of this review is on the open ocean. Atmospheric inputs are harder to quantify, particularly in the remote, nutrient-limited regions of the open ocean. For northeastern Asian marginal seas, Kim et al. (2011) reported increased N:P availability linked to increased atmospheric nitrogen deposition, as well as riverine input over the previous 30 years. Combined models of atmospheric chemistry, ocean circulation, and biogeochemical cycling suggest that anthropogenic atmospheric inputs of iron and fixed nitrogen may help explain oxygen loss in the tropical high-nutrient, low-chlorophyll ocean, where iron is limiting (Ito et al. 2016). Both fuel combustion and increases in dust increase the availability of atmospheric iron. Atmospheric deposition of nitrogen (NO<sub>x</sub> and NH<sub>3</sub>) has tripled since 1860 to 67 Tg N y<sup>-1</sup> and is expected to grow further (Duce et al. 2008). The effect of nutrients may be to stimulate production and CO<sub>2</sub> uptake but also to release additional N<sub>2</sub>O, which could exacerbate warming (and offset the increased CO<sub>2</sub> uptake). The geographic patterns of marine productivity and subsurface O<sub>2</sub> concentration declines (which are greatest in the tropics) differ from the geographic patterns of atmospheric iron and nitrogen deposition, which are greatest in the subtropics, possibly because of ocean transport of nutrients from the subtropics to the tropics (Ito et al. 2016).

Continuous fertilization of the open ocean may eventually lead to phosphorus limitation. However, expanded anoxia of waters overlying the seafloor can enhance phosphorus release from sediments, and land use changes have also increased anthropogenic phosphorus inputs (Watson 2016). These could further stimulate production and enhance carbon burial, possibly leading to reoxygenation over very long (100,000-year) timescales (Watson 2016).

**Hydrocarbon oxidation.** Although the aerobic degradation of modern organic matter is a primary source of biological oxygen consumption in the ocean, the oxidation of newly released

## WATERBORNE NUTRIENTS FROM LAND

Waterborne nitrogen and phosphorus and organic wastes from the watershed are a major source of eutrophication-induced deoxygenation in enclosed bays and coastal waters (Rabalais et al. 2014). They stimulate phytoplankton and algal growth and result in blooms in bays, estuaries, lagoons, and coastal waters that increase biological oxygen demand. As the human population has grown, so has the input of nutrients and the number of coastal and estuarine hypoxic sites reported (Diaz & Rosenberg 2008). These sites are not discussed at length in this review to retain focus on the open ocean. However, in addition to the airborne transfer of nutrients discussed in the main text, terrestrial runoff carrying fertilizer-derived nutrients and organic waste from agricultural, industrial, and domestic sources may influence open ocean ecosystems through riverine inshore-offshore water exchange or by acting on animals that migrate between these settings (Levin & Breitburg 2015). Warming will intensify and extend periods of deoxygenation in the coastal zone (Altieri & Gedan 2015). Climate change might elevate waterborne nutrient fluxes from land through increased efficiency of plant water use, increased precipitation, and wetland loss linked to sea level rise, all of which would lead to more deoxygenation and acidification

hydrocarbons such as methane or oil may also consume substantial quantities of oxygen. Large quantities of gas hydrates (frozen methane) containing 500–2,000 Gt of carbon are buried on continental margins, with stability zones typically between 300 and 1,000 m, where the ambient water temperature is below 4°C and the pressure is over 60 bar (Kvenvolden & Rogers 2005, Wallmann et al. 2012). Where methane seeps upward from beneath the seafloor, it is consumed both anaerobically and aerobically. Bacterially mediated aerobic methane oxidation occurs in benthic bacterial mats and sediments, symbiont-bearing animals (e.g., mussels and tubeworms), and the water column (Hansman et al. 2017). Both methane oxidation and sulfide oxidation, also carried out by bacteria and symbionts, consume oxygen at the seafloor. The aerobic consumption of oxygen at seeps can exceed the anaerobic consumption, especially in diffuse flow settings that support more animals (Boetius & Wenzhöfer 2013). At higher flow rates, methane enters the water, where most will be consumed by methanotrophy (Valentine 2011), and methane-derived dissolved inorganic carbon can exceed that from surface photosynthetic production (Hansman et al. 2017).

As the ocean water overlying continental margins warms, the temperature increase may dissociate gas hydrates, increasing the methane emitted to the hydrosphere from seeps, now estimated at 0.02 Gt C y<sup>-1</sup> (Boetius & Wenzhöfer 2013). Evidence for aerobic methane oxidation in the tropical eastern Pacific was found in waters above a hydrothermal seep (Levin et al. 2012) but not at several other well-known seep sites (Hansman et al. 2017). Shifting of warm currents such as the Gulf Stream may release additional methane (Phrampus & Hornbach 2012). Oxidation of released methane draws down oxygen, but the magnitude of this effect and whether it can contribute significantly to deoxygenation are unknown.

Increasing seepage with stronger bubble plumes could draw nutrient- and hydrocarbon-rich water upward to the pycnocline and stimulate primary production, as observed above seeps in the Gulf of Mexico (D'Souza et al. 2016). Ultimately, microbial and protistan respiration of this production could also draw down oxygen. Increased respiration and oxygen depletion ( $18.9 \pm 3.8$  Gmol), largely driven by methane, was observed after the *Deepwater Horizon* blowout contributed approximately 0.47 Tg of hydrocarbons to the Gulf of Mexico (Du & Kessler 2012). Therefore, accidental release of hydrocarbons can contribute to oxygen loss as well. Other forms of human disturbance, such as bottom trawling (De Leo et al. 2016) and potentially seabed phosphate mining (Levin et al. 2016), which resuspend sediments and organic matter and release pore-water solutes into overlying low-oxygen waters, might also elevate oxygen consumption. It

is unclear whether any of these mechanisms will consume a sufficient amount of oxygen to affect oxygen concentrations locally or regionally; however, further study is warranted.

If newly dissociated methane, which is up to 84 times more potent as a greenhouse gas than CO<sub>2</sub> (IPCC 2013), is not consumed in the ocean, its release to the atmosphere would induce further warming, which will act to enhance oxygen loss through the solubility and stratification mechanisms described above (Prather et al. 2001). Although methane from gas hydrate emissions is currently estimated to contribute 5 Tg C y<sup>-1</sup> to the atmosphere, there are many uncertainties about the timescales over which increased release could play out (they could be very long) and the various chemical processes, such as rising pressure from sea level rise, that may counteract gas hydrate dissociation by warming (O'Connor et al. 2010, Ruppel & Kessler 2017).

## Biogeochemical and Biological Feedbacks

Oxygen declines can create many biogeochemical, microbial, and primary production feedbacks that will exacerbate, or in some cases ameliorate, ocean deoxygenation (**Figure 2**). Some of these, like methane release from gas hydrates or stimulation of primary production by iron mobilization and phosphorus regeneration, are discussed in sections above and below. Although remobilization of iron can be very important in high-nutrient, low-chlorophyll regions, the extent to which this occurs is highly sensitive to oxygen level and H<sub>2</sub>S production (Scholz et al. 2014).

CO<sub>2</sub> entering the ocean from the atmosphere can, under some circumstances, act as a fertilizer. Although the resulting primary production generates oxygen, once exported it will enhance subsurface O<sub>2</sub> utilization and can contribute to expanded volumes of suboxic waters in OMZs (Oschlies et al. 2008, Tagliabue et al. 2011). At the same time, increased CO<sub>2</sub> content of ocean water may reduce plankton calcification, leading to weakened mineral-ballast fluxes, shallower remineralization, and new areas of oxygen depletion (oxygen holes) at intermediate-water depths (Hofmann & Schellnhuber 2009).

OMZs are also nitrogen hot spots where bioavailable and non-bioavailable forms are transformed through a series of interacting aerobic and anaerobic microbial pathways. Controls on the volume of suboxic waters (<5 μmol kg<sup>-1</sup> O<sub>2</sub>) influence denitrification and loss of fixed nitrogen (up to 50%), which in turn influence nitrite and limits on global productivity (Codispoti et al. 2001, Deutsch et al. 2011). Bianchi et al. (2012) estimated that the removal of fixed nitrogen is 70 ± 50 Tg y<sup>-1</sup> in the open ocean and 198 ± 64 Tg y<sup>-1</sup> in sediments. Ocean deoxygenation may cause an increase in denitrification of approximately 14 Tg N y<sup>-1</sup> per millimole per cubic meter of oxygen decrease (Bianchi et al. 2012). Suboxic zones are key sites for the production of N<sub>2</sub>O, a potent greenhouse gas that may exacerbate warming (Gruber 2008). Global N<sub>2</sub>O production is estimated at 6.2 ± 3.2 Tg y<sup>-1</sup>, but models suggest that this production may not increase with deoxygenation (Bianchi et al. 2012). However, recent observations of unexpectedly high fluxes of N<sub>2</sub>O observed in Peruvian waters suggest that upwelling hot spots may need to be incorporated into models addressing the effects of intensified upwelling impacts on the marine nitrogen cycle response to climate change (Arévalo-Martínez et al. 2015). Methane may also be produced as a result of deoxygenation, but this influence is considered to be relatively minor (Naqvi et al. 2010).

Expanded severe suboxia and anoxia may intensify the production of H<sub>2</sub>S. One effect is to precipitate FeS and reduce the expected release of iron into the water column (Scholz et al. 2014). Another effect is to enhance the formation of bacterial mats, which remove nitrate and promote subsurface sulfate reduction, facilitating further sulfide production (Valentine et al. 2016).

At nanomolar oxygen levels (5–30 nmol kg<sup>-1</sup>) in OMZs, ammonium and nitrate oxidation compete with anaerobic ammonium oxidation and denitrification (Bristow et al. 2016), creating feedbacks to productivity. Biogeochemical response times and resulting changes in fluxes of key




elements such as nitrogen and phosphorus, as well as in C:N and N:P ratios, can be rapid, as illustrated by flushing events in the Santa Barbara Basin (Goericke et al. 2015) and the deep Baltic Sea (Hall et al. 2017). Where OMZs impinge on the seafloor at shallow (shelf) depths, remineralization processes within sediments can have a major feedback to pelagic biogeochemical processes. By coupling water column time-series data to an empirical diagenetic model for the Peru Shelf, Dale et al. (2017) showed key sediment influences on the pelagic nitrogen budget and therefore primary production. For example,  $\text{NH}_4^+$  production by bacterial-mat-forming *Thioploca* may stimulate anaerobic ammonium oxidation, which accounts for much of the nitrogen loss in the eastern tropical South Pacific.

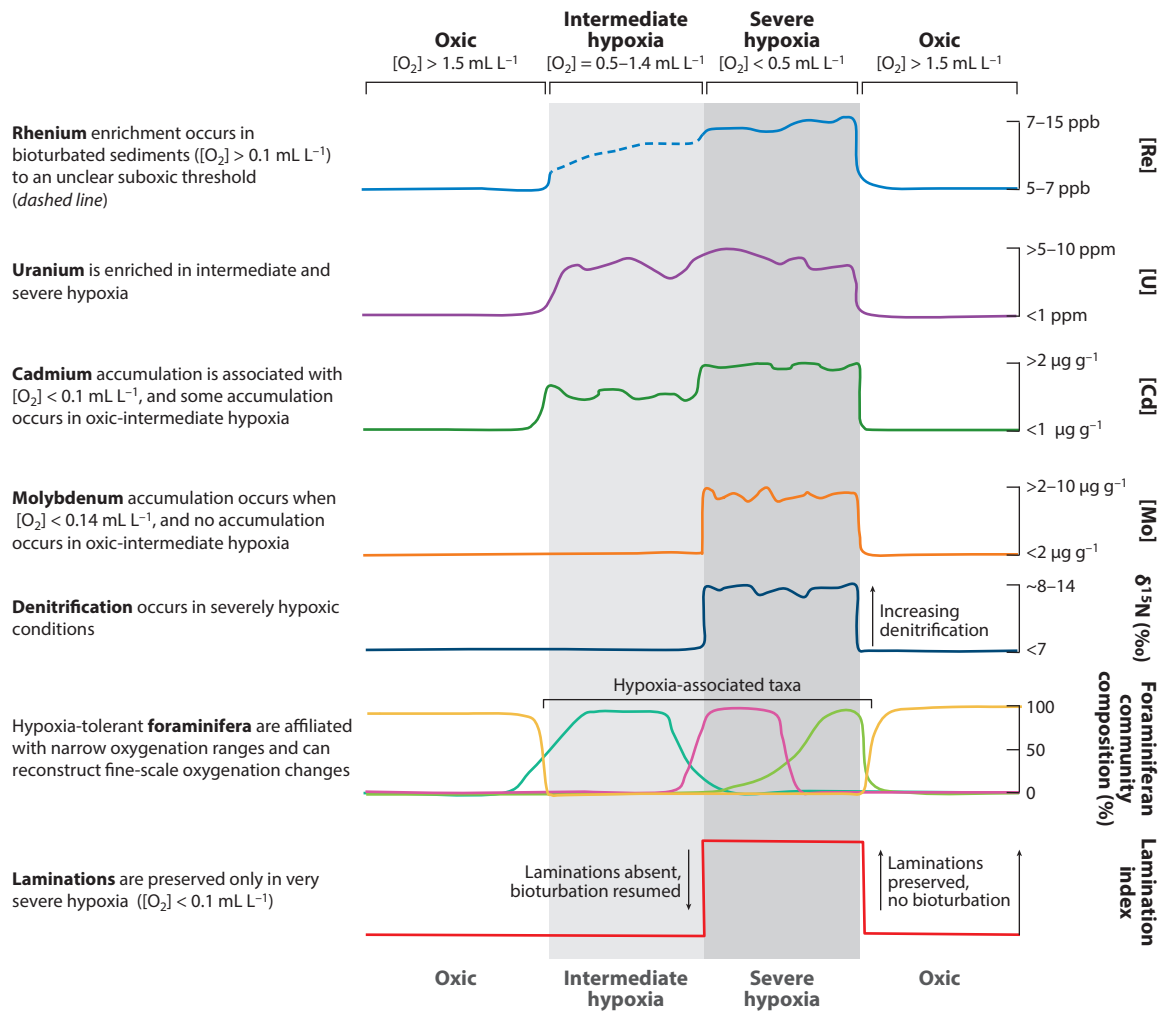
In addition, biological feedbacks involving higher animals may emerge that intensify oxygen depletion. Although many questions remain about the interactions of microbes that function at hypoxic and suboxic oxygen levels and how these affect oxygen consumption (Wright et al. 2012, Bristow et al. 2016), the influence of metazoan animals on oxygenation is rarely considered. Climate- and oxygen-induced shoaling of vast numbers of vertical migrating plankton (Bianchi et al. 2013, Netburn & Koslow 2015) could increase metabolic rates and might intensify oxygen depletion at intermediate depths. Warming effects on large, high-consumption taxa such as billfishes and tunas (Stramma et al. 2011) might elevate or redistribute their oxygen consumption within the water column, but any effects of this are speculative. New information about unexpected extreme metabolic suppression by migrators at depth (Seibel et al. 2016) illustrates the complexity of accurately modeling the biological responses and contributions to deoxygenation. Oxygen-induced changes in biological communities, such as blooms of jellyfish, can lead to carcass accumulation on the seafloor, and their decay increases oxygen consumption locally as well (e.g., Sweetman et al. 2016).

## INSIGHT FROM THE PAST

Evidence for a link between warming events and ocean deoxygenation, and for the underlying mechanisms, feedbacks, and response times, can be found in the paleo-record of sediments and fossils. A wide range of proxies provide relevant insight about oxygenation (**Figure 3**): redox-sensitive trace metals (e.g., molybdenum, uranium, cadmium, rhenium, manganese, and iron) and sometimes their isotopes, laminations and trace fossils, hypoxia-tolerant (or hypoxia-intolerant) foraminifera, ostracods and molluscs, organic matter  $^{15}\text{N}/^{14}\text{N}$  isotope ratios, carbonate  $^{18}\text{O}/^{16}\text{O}$  ratios (for temperature), and various biomarkers [alkenones, methylation and cyclization of branched tetraethers (MBT-CBT), the tetraether index of 86 carbon atoms ( $\text{TEX}_{86}$ ), and productivity indicators] (Gooday et al. 2009; Lyons et al. 2014; Moffitt et al. 2015a,b; Praetorius et al. 2015).

To better understand the biological sensitivity to oxygen changes, we can look to the Cambrian explosion (~540 Mya). Oxygen has been called the environmental gatekeeper of this period; the increased availability of molecular oxygen removed the barrier to the evolution of large animals and released a host of development regulatory potential that led to the diversification of life forms (Knoll & Carroll 1999) and the evolution of carnivory (Sperling et al. 2013). Multiple deoxygenation or anoxic events have occurred throughout the Phanerozoic, sometimes in conjunction with marine extinctions (**Supplemental Figure 3**), although making a direct link between the two can be difficult. Perhaps the best analog to the coupled warming and deoxygenation occurring today is the Paleocene-Eocene Thermal Maximum (PETM) (56 Mya), when temperatures rapidly rose 5–8°C over tens of thousands of years, with oxygen declining to levels that were likely lower than those of the present (Dickson et al. 2012). Destabilization of gas hydrates provides one explanation for this warming, with relevance for modern conditions. However, during the PETM, the loss of foraminiferal biodiversity in the sediment record preceded the period of least

 **Supplemental Material**



**Figure 3**

Examples of geochemical and biological proxies derived from the sediment record used to infer patterns and mechanisms of deoxygenation. Adapted from Moffitt et al. (2015b) under the Creative Commons Attribution 4.0 International license (<https://creativecommons.org/licenses/by/4.0>).

oxygenation; extinctions could have been induced at higher oxygen levels or linked to warming at the onset of the PETM (McInerney & Wing 2011).

Records off Peru over the past 140,000 years suggest that the iron supply limits production and controls deoxygenation. Iron appears most likely to be released from sediments in a narrow redox window where neither oxygen nor sulfide is present; thus, partial deoxygenation may enhance the iron supply in weaker OMZs. Areas with expanding OMZs and increased sulfide retain iron through iron sulfide precipitation, contributing to greater iron limitation. In areas where oxygen is not as low (e.g., the southeast Atlantic and subarctic Pacific), oxygen declines over shelf sediments could enhance iron release and carbon fixation in surface waters (Scholz et al. 2014), possibly exacerbating deoxygenation.

Glacial sediment records from the Indian and Pacific Oceans reveal Dansgaard-Oeschger fluctuations on millennial timescales of subsurface dissolved oxygen levels and denitrification coherent with North Atlantic temperature oscillations and changes in the meridional overturning circulation. Reduced North Atlantic Deep Water subduction and less heat transport occurred during cold periods, and the reverse occurred in warm periods. Ocean simulations of oxygen and nitrogen cycling during idealized Dansgaard-Oeschger oscillations suggest that buoyancy-driven ocean circulation effects on productivity and subsurface nutrient and oxygen distributions can explain apparent teleconnections between the North Atlantic deepwater subduction and the Indian and Pacific Ocean OMZs (Schmittner et al. 2007).

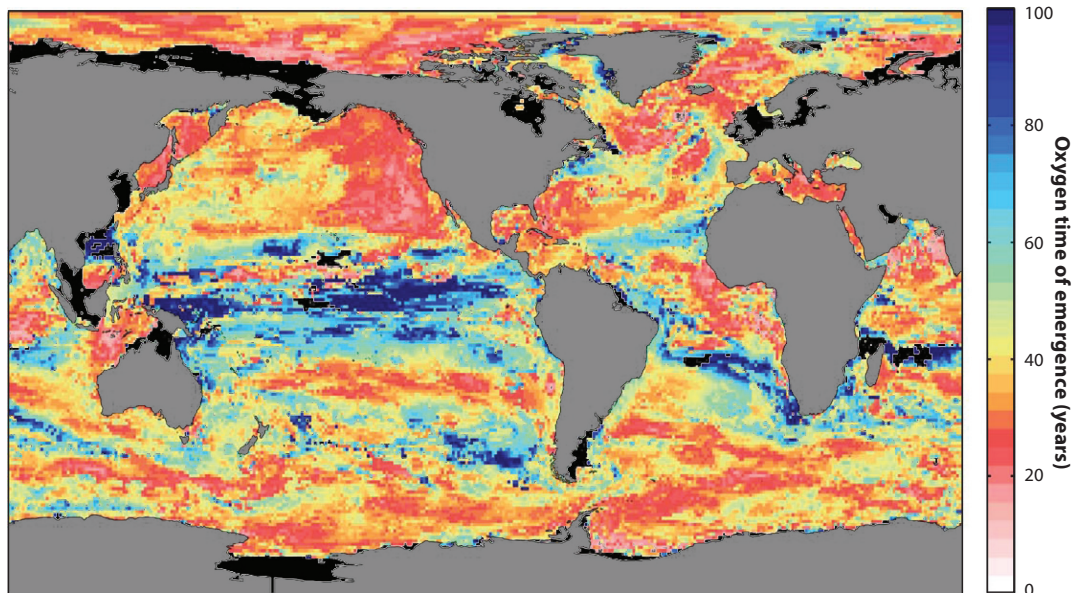
Warming-induced deoxygenation has been reported from recent deglaciation cycles (Praetorius et al. 2015). In the Gulf of Alaska, metal, isotope, diatom, and foraminiferal proxies indicate that two 4–5°C warming events occurred at 14.7–12.9 kya (the Bølling-Allerød interstade) and 11.5–10.5 kya (the Holocene interglacial) that coincided with hypoxia linked to high export production. A positive feedback may have resulted from expansion of the OMZ acting to mobilize iron from shelf sediments. This is hypothesized to have stimulated production in the high-nutrient, low-chlorophyll surface waters and increased carbon export and oxygen demand in underlying waters (Praetorius et al. 2015). Similar feedbacks involving phosphorus regeneration that fueled shelf eutrophication have been suggested for anoxia that ensued during the PETM in the Gulf Coastal Plain (Sluijs et al. 2014). This ultimately enhances carbon burial, forming a negative feedback to warming.

We often seek oxygenation history to understand both modern (Sperling et al. 2016) and paleo-faunal patterns (Sperling et al. 2013). Paleo-scientists in turn use faunal remains to infer deoxygenation events that could cause extinction (Moffitt et al. 2015a,b; Bowyer et al. 2017). Molluscs are highly responsive to oxygenation and have contributed to understanding of the rates of oxygen change and associated biological responses. Anoxia, linked to elevated productivity in the early Jurassic (Toarcian), affected bivalve taxonomic composition and shell size (determined using  $\delta^{13}\text{C}_{\text{org}}$  as a proxy for primary productivity) and molybdenum concentration (which limits  $\text{N}_2$ -fixing primary productivity) (Caswell & Coe 2013). Extremophile taxa, including bivalves with symbiotic, sulfide-oxidizing bacteria and gastropods that graze chemosynthetic bacteria, show sensitivity to abrupt deoxygenation events over the past 3,000–16,000 years (Moffitt et al. 2015a, Myhre et al. 2017).

## NATURAL VARIABILITY AND TIME OF EMERGENCE

Oxygen is a highly dynamic ocean property. However, the extent to which oxygen content in the ocean varies temporally is itself highly variable across space and time. The temporal variability of oxygen may be semidiurnal (e.g., driven by tides), event driven or seasonal (especially in coastal waters subject to wind-driven upwelling or eutrophication), subannual but transient (e.g., driven by mesoscale eddies), interannual (e.g., linked to El Niño–Southern Oscillation cycles), multidecadal and linked to regime shifts (e.g., associated with the North Atlantic Oscillation or Pacific Decadal Oscillation), centennial, or millennial (Whitney et al. 2007, Frölicher et al. 2009, Ito & Deutsch 2010, Levin et al. 2015, Moffitt et al. 2015a, Long et al. 2016). Factors that control temperature variation may also influence oxygen variability by altering organic matter production, export, and oxygen consumption (Ito & Deutsch 2010, Deutsch et al. 2011).

The challenge of distinguishing the natural variability in oxygen from anthropogenic trends or forcing was recognized decades ago (Hasselmann 1993, Garcia et al. 2005). The concept of time of emergence is now used to examine how long it will take for anthropogenic forcing of deoxygenation to be distinguished from background (natural) variability (Henson et al. 2017). Such analyses and



**Figure 4**

The pace of oxygen signal emergence at 200–600 m, showing the median number of years between the start of climate change and the emergence of the anthropogenic signal (for oxygen loss or gain) under representative concentration pathway (RCP) 8.5 based on output from nine Intergovernmental Panel on Climate Change Earth system models. In black areas, the signal does not emerge by 2100. The start of climate change is the year when the time series of annual extrema in the conjoined historical and warming scenario runs exhibits an inflection point [located by calculating the cumulative sum of the gradient in  $Y_t(qY/qt)$  that exceeds zero (for a positive trend) or drops below zero (for a negative trend) for the remainder of the time series. Adapted from Henson et al. (2017) under the Creative Commons Attribution 4.0 International license (<https://creativecommons.org/licenses/by/4.0>).

time-of-emergence maps now exist for oxygen using several different projections and approaches (Andrews et al. 2013, Frölicher et al. 2016, Long et al. 2016, Henson et al. 2017) (**Figure 4**).

Andrews et al. (2013) performed an optimal fingerprinting analysis to examine oxygen changes between 1970 and 1992 (based on data from Helm et al. 2011), using two ESMs [the Max Planck Institute’s low-resolution ESM (MPI-ESM-LR) and the Met Office Hadley Centre’s Global Environment Model 2 ESM (HadGEM2-ES)] to evaluate whether external forcing influenced observed oxygen trends. The models underestimated oxygen response to external forcing, especially at low latitudes, suggesting a very conservative outcome. The signal emergence is most evident at high latitudes, particularly in the Pacific and Southern Oceans, but is not evident in the North Atlantic (Andrews et al. 2013). Using fields from the Community Earth System Model Large Ensemble experiment to identify the emergence of the oxygen signal, Long et al. (2016) found that a signal of oxygen loss beyond natural variability already exists in the southern Indian Ocean and parts of the eastern tropical Pacific and Atlantic basins, whereas globally forced deoxygenation should be detectable in 15–25 years in many other areas. Frölicher et al. (2016) used a suite of CMIP5 models run from 1950 to 2100 to project time of emergence for oxygen and found that 23% of the ocean area would experience an emerging  $O_2$  signal by the end of the century under representative concentration pathway (RCP) 8.5, but only 2% would emerge under RCP 2.6. This study projected the earliest emergence at midlatitudes in the North Pacific and Southern Ocean (Pacific) and in parts of the North Atlantic.

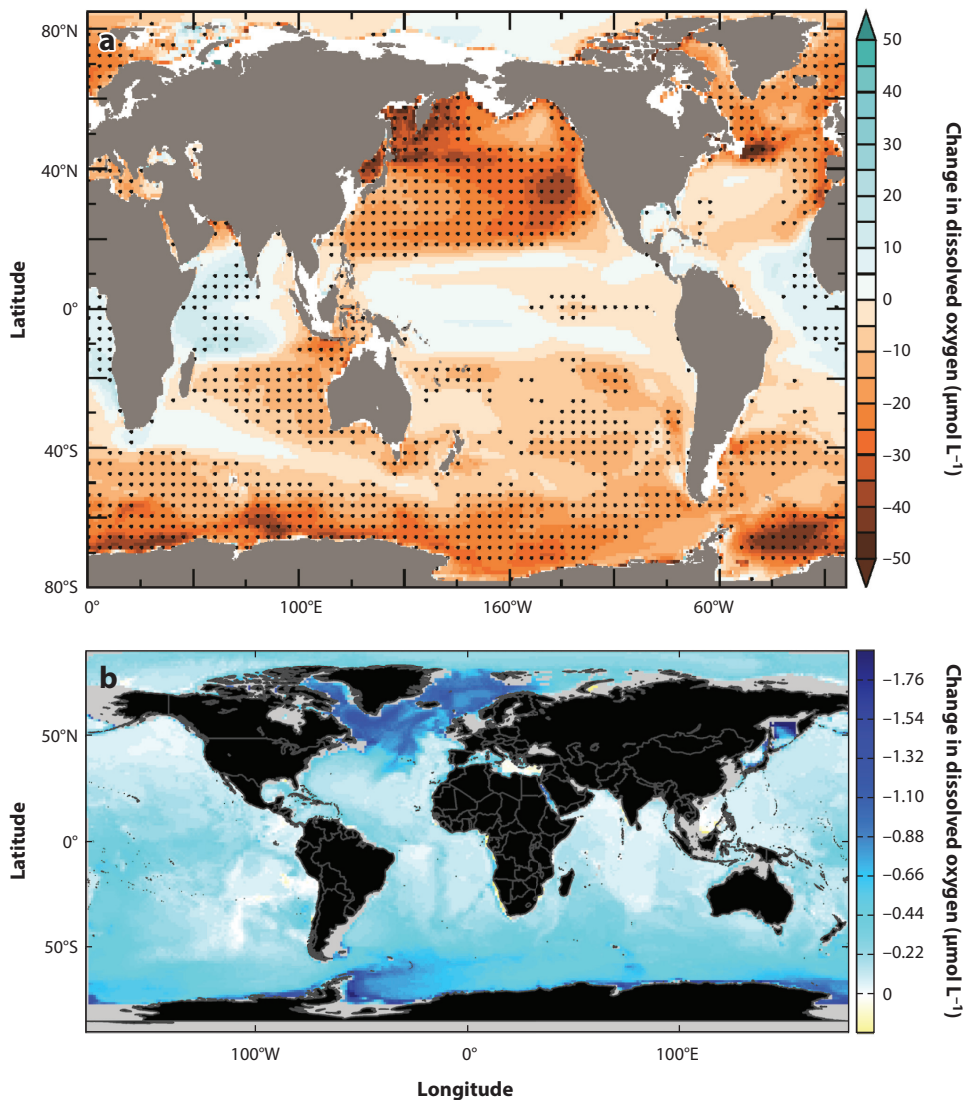
Signal emergence does not automatically mean that oxygen reaches a threshold dangerous for life in a region; however, animal tolerance thresholds span a broad range, from  $<2 \mu\text{mol kg}^{-1}$  (e.g., snails, gutless oligochaetes, and some fishes) to  $150 \mu\text{mol kg}^{-1}$  (billfish and tuna), so it is not inconceivable that small changes will matter for some taxa. All of the time-of-emergence analyses speak to a need to better understand the causes, magnitudes, and trends of oxygen variability to fully predict and interpret ocean deoxygenation. Social science studies suggest that climate variability can reduce support for mitigation policies and can delay willingness to act or adapt (Ricke & Caldeira 2014), so demonstrating emergence may be fundamental to enabling policy development.

Technological advances in both sensors and platforms have improved detection of oxygen variability. The addition of full-ocean-depth oxygen sensing to observing programs involving floats (e.g., Argo), gliders, shipboard hydrography [the Global Ocean Ship-Based Hydrographic Investigations Program (GO-SHIP)], moorings (OceanSITES), and observatories (e.g., Ocean Networks Canada, the Ocean Observatories Initiative, and Hausgarten) will greatly enhance our grasp of oxygen variability over multiple spatial and temporal scales. Although there are nearly 4,000 Argo floats in the water, fewer than 300 measured oxygen as of July 2017 (Gruber et al. 2010, <http://www.jcommops.org/board?t=Argo>), providing minimal ocean coverage. Biogeochemical-Argo (BGC-Argo), with sensors for  $\text{O}_2$ , chlorophyll *a*, pH, and nitrate (Bittig et al. 2015), offers not only expanded  $\text{O}_2$  measurements, but also improved understanding of biogeochemical forcing of ocean deoxygenation. The BGC-Argo implementation plan suggests that 1,000 floats are needed to adequately reflect biogeochemical variability and trends (Biogeochem. Argo Plan. Group 2016). Other innovations are also under way; for example, animal-borne devices can use both fishes (Coffey & Holland 2015) and mammals (Bailleul et al. 2015) to expand the spatial and temporal resolution of dissolved oxygen measurements in situ.

## FUTURE OXYGEN PROJECTIONS

Most early climate models projected that future oxygen loss would accompany ocean warming (Sarmiento et al. 1998, Plattner et al. 2001, Bopp et al. 2002). Recent projections that incorporate more complexity generally project future oxygen losses in the upper (intermediate) mesopelagic layer (100–600 m) (Bopp et al. 2013, 2017; Cocco et al. 2013), especially at middle and high latitudes (**Figure 5a**). Using 7 ESMs under a business-as-usual scenario (SRES-A2, similar to RCP 8.5), Cocco et al. (2013), predicted declines in ocean oxygen content by 2–4% globally from 1870 to 2100, and Bopp et al. (2013) reported a similar global result ( $3.45\% \pm 0.44\%$  loss of oxygen) based on 10 ESMs under CMIP5 from the 1990s to the 2090s. Most projections to 2100 under RCP 8.5 predict relatively small changes in the total volume of hypoxic and suboxic waters (Bopp et al. 2013, 2017; Cocco et al. 2013), in contrast to the substantial oxygen declines (2%) observed to date (Stramma et al. 2010, Schmidtko et al. 2017). These studies project regional variation in amounts and trend direction, influenced by regional variation in temperature, circulation, production, and remineralization. Deoxygenation in the intermediate layer is predicted for the North Pacific (especially the northwest), the tropical and subtropical South Pacific, the Southern Ocean, the eastern part of the Indian Ocean, and the subpolar North Atlantic. Using 9 ESMs, Bopp et al. (2017) projected oxygen losses within 200–600-m water depths by 2090 to be approximately  $10 \mu\text{mol kg}^{-1}$  at middle and high latitudes but only  $0.8 \pm 2.7 \mu\text{mol kg}^{-1}$  in the tropics ( $20^\circ\text{N}$ – $20^\circ\text{S}$ ). Models do not agree about the direction of change in tropical waters. Some increases in oxygen are projected in the tropical Atlantic and the tropical Indian Ocean (**Figure 5a**), caused by decreasing primary productivity, export, and remineralization.





**Figure 5**

Projected changes in oxygen from the present to 2100 (*a*) at 200–600 m under representative concentration pathway (RCP) 8.5 and (*b*) at the seafloor. Panel *a* adapted from Bopp et al. (2013) under the Creative Commons Attribution 3.0 Unported license (<https://creativecommons.org/licenses/by/3.0>); panel *b* adapted from Sweetman et al. (2017) under the Creative Commons Attribution 4.0 International license (<https://creativecommons.org/licenses/by/4.0>).

Even for the high-mitigation scenario (RCP 2.6), 10 ESMs predict a  $1.81\% \pm 0.31\%$  loss of oxygen globally (from the 1990s) by 2100 (Bopp et al. 2013), with each model predicting an increase (1–9%) in the volume of waters with an oxygen concentration below  $80 \mu\text{mol kg}^{-1}$ . There was less agreement for volume changes in intermediate waters with much lower oxygen content.



Notably, empirical observations reviewed above suggest that this amount of oxygen loss is likely underestimating future changes in oxygen.

A pervasive problem with model projections is the inability of many ESMs to adequately reproduce existing oxygen conditions or yield a consistent direction of future oxygen change in the tropical thermocline, where OMZs are vast and expanding (Stramma et al. 2012; Andrews et al. 2013, 2017; Cocco et al. 2013; Moore et al. 2013; Cabre et al. 2015; Bopp et al. 2017; Oschlies et al. 2017). Recent hindcasting efforts to understand this problem suggest that model uncertainty in the sign and magnitude of oxygen change could derive from parameterization of  $p\text{CO}_2$  (ocean acidification)–sensitive C:N ratios in carbon fixation (which affect organic carbon export and remineralization), imposed atmospheric forcing (i.e., air-sea fluxes of heat, water, and momentum; Andrews et al. 2017), and wind-driven changes in low-latitude oceanic ventilation (Oschlies et al. 2017).

Models reflect the complexity of the drivers, with potential influences from land-derived nutrients (Duce et al. 2008, Ito et al. 2016), changes in the heat and salt balance causing convection along isopycnals and degree of upwelling (Gnanadesikan et al. 2013), climate modes such as the North Atlantic Oscillation and Pacific Decadal Oscillation, changes in the Atlantic meridional overturning circulation, and volcanic forcing (Frölicher et al. 2009). In addition, biological responses will involve effects of multiple interacting stressors (e.g., oxygen, temperature,  $\text{CO}_2$ , and carbonate saturation state) on export flux, oxygen demand, and tolerances. Most current models do not find a clear link between climate change and oxygen declines in the tropics; however, this conclusion is constrained by limited understanding of how biological and biogeochemical processes will evolve as ocean temperatures and  $\text{CO}_2$  rise (Oschlies et al. 2008, 2017; Steinacher et al. 2010).

Only recently have global-scale changes in oxygenation been projected at the seafloor (**Figure 5b**). Seafloor projections of oxygen in 2100 were generated using 31 ESMs (from 18 centers in nine countries) as part of CMIP5 for the Intergovernmental Panel on Climate Change's Fifth Assessment Report (Mora et al. 2013, Sweetman et al. 2017). Oxygen losses of up to 4% are projected at the seafloor. A reduction in bottom-water oxygenation of  $0.03\text{--}0.05\text{ mL L}^{-1}$  ( $1.3\text{--}2.2\text{ }\mu\text{mol kg}^{-1}$ ) could occur by 2100 at bathyal seafloor habitats in the North Pacific, North Atlantic, Arctic, and Southern Oceans (Sweetman et al. 2017), which represents a 0.7–3.7% oxygen loss. As indicated above, this magnitude of change, although small, can be significant in intermediate waters and on the bathyal seabed on upwelling margins and seamounts where existing oxygen levels are near biological thresholds (Sperling et al. 2016). Although a reduced Atlantic meridional overturning circulation may lead to declines in the oxygenation of deeper waters (Schmittner et al. 2007, Rahmstorf et al. 2015), less change [ $0.03\text{ mL L}^{-1}$  (0.05%)] is projected for abyssal regions (Sweetman et al. 2017). Longer-term projections under doubling and quadrupling of atmospheric  $\text{CO}_2$  on millennial rather than centennial timescales predict increased oxygenation (and overshoot from present levels) after 500 years owing to the influence of enhanced ventilation in the Weddell Sea on the Antarctic Bottom Water and to warming-reduced export production and shoaling of remineralization depths (Yamamoto et al. 2015). By contrast, Schaffer et al. (2009), using low-resolution ESMs under several emission scenarios, projected oxygen loss and OMZ expansion over the next 100,000 years, exacerbated by climate feedbacks and a reduced strength of the Atlantic meridional overturning circulation.

Over much smaller spatial and temporal scales, high-resolution seasonal forecasting of regional oxygen conditions offers the potential to plan and manage fisheries in response to deoxygenation (Siedlecki et al. 2016). Regional Ocean Modeling System models with biogeochemistry added did a good job of predicting seasonal phasing and variability of bottom oxygenation in the northeastern

Pacific off Washington and Oregon (Siedlecki et al. 2016). In shallow waters (<60 m), sediment oxygen demand contributes significantly to hot spots of oxygen depletion (Siedlecki et al. 2015).

## WHY DOES DEOXYGENATION MATTER?

A detailed understanding of oxygen loss in the open ocean is valuable because oxygen availability affects a vast array of biological attributes at all organizational levels, from gene expression to ecosystems (D. Breitburg, L.A. Levin, A. Oschlies, M. Grégoire, F.P. Chavez, et al., manuscript in review). Several recent reviews have addressed the consequences of oxygen loss, and it is beyond the scope (and space) of this article to examine in detail the biological impacts of deoxygenation. For open ocean ecosystems, much of our knowledge of responses to oxygen loss derives from studies across modern natural oxygen gradients associated with OMZs. Such studies of benthic (Levin 2003; Levin et al. 2009; Sperling et al. 2013, 2016; Gallo & Levin 2016; Papiol et al. 2017) and pelagic (Ekau et al. 2010, Seibel 2011, Wishner et al. 2013) ecosystems demonstrate morphological and metabolic adaptations and shifts in body size, taxonomic composition, diversity, lifestyles, life stage, and trophic patterns. The effects of OMZ expansion on pelagic ecosystems (Gilly et al. 2013) and metabolism (Deutsch et al. 2015) have been summarized, but outside of the historical record (e.g., Moffitt et al. 2015a), relatively few time-series studies have documented the effects of deoxygenation on offshore, deepwater benthos (but see Sato et al. 2017). Hypoxia may alter physiological functions, including vision (McCormick & Levin 2017); inhibit reproduction; increase vulnerability to disease; alter behavior; and compress geographic or vertical distributions (D. Breitburg, L.A. Levin, A. Oschlies, M. Grégoire, F.P. Chavez, et al., manuscript in review). Microbial composition and activity are extremely sensitive to changes in oxygen (Wright et al. 2012); for example, in the eastern tropical North Pacific, 5% of microbial operational taxonomic units change with each  $1 \mu\text{mol kg}^{-1}$  change in dissolved oxygen (Beman & Carolan 2013). Thus, microbes, which can be monitored autonomously with instrumentation such as the Environmental Sample Processor, may be most amenable to long-term study. However, for changing open ocean ecosystems, many questions remain about deoxygenation effects on sources of primary production, species interactions, trophic webs, energy transfer, and the resulting ecosystem services (Cooley 2012).

One of the greatest challenges in tracking the consequences of ocean deoxygenation is the simultaneous change in other climate variables, such as temperature and  $\text{CO}_2$  (affecting pH and carbonate saturation states) (Gruber 2011, Bopp et al. 2013, Henson et al. 2017), as well as changes in derived influences, such as nutrient fluxes, primary and export production, mineral ballast, respiration rates, circulation patterns, and other direct human influences (e.g., fishing or pollution). Advances in predicting the course, distribution, and intensity of ocean deoxygenation will depend on improved understanding of the roles of physics, microbial processes, and faunal responses to deoxygenation with co-occurring stressors in space and time.

Given the well-documented declines in oxygen, the clear attribution to global warming in many regions of the ocean, and the existence of sharp biological thresholds, it is surprising that the recent planetary boundaries framework that advocates for linking human society and the sustainability of the Earth system (Steffen et al. 2015) does not recognize open ocean deoxygenation to be a major threat. Nevertheless, growing attention to ocean deoxygenation is exemplified by the newly formed Intergovernmental Oceanographic Commission Global Ocean Oxygen Network (GO<sub>2</sub>NE), which is devoted to raising awareness about ocean deoxygenation (IOC 2017), and multiple international collaborative projects focused on specific oxygen issues. The expansion of one component of the Argo float program to incorporate biogeochemical sensors (BGC-Argo), including oxygen sensors, will help to expand oxygen observations, advance mechanistic understanding, and improve prediction.

## SUMMARY POINTS

1. Global ocean deoxygenation is well documented, continues to occur, and is understood to be a major consequence of climate change arising from the effects of warming on solubility, stratification, and potentially respiration.
2. Oxygen loss in the open ocean is most intense in mode and intermediate waters (100–600 m), where it affects major components of the biological pump.
3. Although the world ocean has lost ~2% of its oxygen, regional oxygen losses are much greater in the North Pacific, tropical ocean, and Southern Ocean, with magnitudes high enough to have notable biological impacts.
4. Warming-induced ocean deoxygenation can be exacerbated by changes in circulation; upwelling; increased atmospheric, riverine, and groundwater nutrient inputs; hydrocarbon release; pollution; various biogeochemical feedbacks; and other forms of human disturbance.
5. The paleo-record and historical record provide an understanding of mechanisms and feedbacks underlying shifts in open ocean oxygenation that play out over centennial to millennial timescales.
6. Open ocean deoxygenation is superimposed on intense natural oxygen variability, but the emergence of the anthropogenic signal has already occurred in some regions and is expected in many other areas within the next 30 years.
7. Ocean deoxygenation is a complex product of physical, biogeochemical, and ecological drivers, some of which remain poorly understood. Accurate modeling and forecasting will require expertise from many disciplines to develop a sufficiently detailed, mechanistic understanding of processes controlling oxygen.

## FUTURE ISSUES

1. Processes responsible for deoxygenation trends in the tropics currently elude us. A better understanding is needed and may well require integrated research in atmospheric sciences, ocean physics, biogeochemistry, and multiple biological disciplines.
2. High-resolution studies of the circulation and biogeochemistry of oxygen minimum zones, particularly within suboxic zones, will help inform global oxygen trends and feedbacks.
3. More comprehensive global observation of oxygen in space and time, including transient events and mesoscale features, is required to evaluate deoxygenation status and the consequences of warming and other drivers. Enhanced oxygen networking among global observing programs would be beneficial.
4. An improved mechanistic knowledge of linkages and feedbacks is needed to predict the effects of deoxygenation on greenhouse gas fluxes and to assess those effects on future climate change.

5. Heightened awareness and understanding of deoxygenation among scientists, regulators, and policy makers will facilitate integrated solutions. To be effective, these must address deoxygenation in the context of multiple environmental stressors, including warming, ocean acidification, and changes in nutrient and food supply.
6. Ocean deoxygenation and its consequences should be integrated into regional and international programs that address societal needs, including, for example, UN Sustainable Development Goal partnerships, Intergovernmental Panel on Climate Change reporting, treaty development for Biodiversity Beyond National Jurisdiction, UN Food and Agriculture Organization regional fisheries management, International Seabed Authority management of the seafloor environment, and International Maritime Organization regulation of marine geoengineering.

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## LITERATURE CITED

- Altieri AH, Gedan KB. 2015. Climate change and dead zones. *Glob. Change Biol.* 21:1395–406
- Andrews OD, Bindoff NL, Halloran PR, Ilyina T, Le Quéré C. 2013. Detecting an external influence on recent changes in oceanic oxygen using an optimal fingerprinting method. *Biogeosciences* 10:1799–813
- Andrews OD, Buitenhuis E, Le Quéré C, Suntharalingam P. 2017. Biogeochemical modeling of dissolved oxygen in a changing ocean. *Philos. Trans. R. Soc. A* 375:20160328
- Arévalo-Martínez DL, Kock A, Löscher CR, Schmitz RA, Bange HW. 2015. Massive nitrous oxide emissions from the tropical South Pacific Ocean. *Nat. Geosci.* 8:530–35
- Bailleul F, Vacquie-Garcia J, Guinet C. 2015. Dissolved oxygen sensor in animal borne instruments: an innovation for monitoring the health of oceans and investigating the functioning of marine ecosystems. *PLOS ONE*:10:e0132681
- Bakun A. 1990. Global climate change and the intensification of coastal upwelling. *Science* 247:198–201
- Belmadani A, Echevin V, Codron F, Takahashi K, Junquas C. 2014. What dynamics drive future wind scenarios for coastal upwelling off Peru and Chile? *Clim. Dyn.* 43:1893–914
- Beman JM, Carolan MT. 2013. Deoxygenation alters bacterial diversity and community composition in the ocean’s largest oxygen minimum zone. *Nat. Commun.* 4:2705
- Bianchi D, Dunne JP, Sarmiento JL, Galbraith ED. 2012. Data-based estimates of suboxia, denitrification, and N<sub>2</sub>O production in the ocean and their sensitivities to dissolved O<sub>2</sub>. *Glob. Biogeochem. Cycles*: 26:GB2009

- Bianchi D, Galbraith ED, Carozza DA, Mislan AS, Stock CA. 2013. Intensification of open-ocean oxygen depletion by vertically migrating animals. *Nat. Geosci.* 6:545–48
- Biogeochem.-Argo Plan. Group. 2016. *The Scientific Rationale, Design and Implementation Plan for a Biogeochemical-Argo Float Array*. Ed. K Johnson, H Claustre. Issy-les-Moulineaux, Fr.: IFREMER
- Bittig H, Kortzinger A, Johnson K, Claustre H, Emerson S, et al. 2015. *SCOR WG 142: quality control procedures for oxygen and other biogeochemical sensors on floats and gliders. Recommendation for oxygen measurements from Argo floats, implementation of in-air-measurement routine to assure highest long-term accuracy*. Rep., Sci. Comm. Ocean. Res., Int. Counc. Sci., Paris. <https://doi.org/10.13155/45917>
- Boetius A, Wenzhöfer F. 2013. Seafloor oxygen consumption fuelled by methane from cold seeps. *Nat. Geosci.* 6:725–34
- Bograd SJ, Bul MP, Di Lorenzo E, Castro CG, Schroeder ID, et al. 2015. Changes in source waters to the Southern California Bight. *Deep-Sea Res. II* 112:42–52
- Bograd SJ, Castro CG, Di Lorenzo 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
- Bopp L, Le Quéré C, Heimann M, Manning AC, Monfray P. 2002. Climate-induced oceanic oxygen fluxes: implications for the contemporary carbon budget. *Glob. Biogeochem. Cycles* 16:6–13
- Bopp L, Resplandy L, Orr JC, Doney SC, Dunne JP, et al. 2013. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences* 10:6225–45
- Bopp L, Resplandy L, Untersee A, Le Mezo P, Kageyama M. 2017. Ocean (de)oxygenation from the Last Glacial Maximum to the twenty-first century: insights from Earth System models. *Philos. Trans. R. Soc. A* 375:20160323
- Bowyer F, Wood RA, Poulton SW. 2017. Controls on the evolution of Ediacaran metazoan ecosystems: a redox perspective. *Geobiology* 2017:1–36
- Brandt P, Hormann V, Kortzinger A, Visbeck M, Krahmann G, Stramma L. 2012. Changes in the ventilation of the oxygen minimum zone of the tropical North Atlantic. *J. Phys. Oceanogr.* 40:1784–801
- Brenneke GA, Herrmann AD, Algeo TJ, Anbar AD. 2011. Rapid expansion of oceanic anoxia immediately before the end Permian mass extinction. *PNAS* 108:17631–34
- Brewer PG, Peltzer ET. 2016. Ocean chemistry, ocean warming, and emerging hypoxia. *J. Geophys. Res. Oceans* 121:3659–67
- Brewer PG, Peltzer ET. 2017. Depth perception: the need to report ocean biogeochemical rates as functions of temperature, not depth. *Philos. Trans. R. Soc. A* 375:20160319
- Bristow LA, Dalsgaard T, Tiano L, Mills DB, Bertagnolli AD, et al. 2016. Ammonium and nitrite oxidation at nanomolar oxygen concentrations in oxygen minimum zone waters. *PNAS* 113:10601–6
- Cabre A, Marinov I, Bernardello R, Bianchi D. 2015. Oxygen minimum zones in the tropical Pacific across CMIP5 models: mean state differences and climate change trends. *Biogeosciences* 12:5429–54
- Capotondi AM, Alexander A, Bond NA, Curchitser EN, Scott JD. 2012. Enhanced upper ocean stratification with climate change in the CMIP3 models. *J. Geophys. Res. Oceans* 117:C04031
- Caswell B, Coe A. 2013. Primary productivity controls on opportunistic bivalves during Early Jurassic oceanic deoxygenation. *Geology* 41:1163–66
- Cocco VF, Joos M, Steinacher TL, Frölicher TL, Bopp L, et al. 2013. Oxygen and indicators of stress for marine life in multi-model global warming projections. *Biogeosciences* 10:1849–68
- Codispoti LA, Brandes JA, Christensen JP, Devol AH, Naqvi SWA, et al. 2001. The oceanic fixed nitrogen and nitrous oxide budgets: moving targets as we enter the Anthropocene? *Sci. Mar.* 65:85–105
- Coffey DM, Holland KN. 2015. First autonomous recording of in situ dissolved oxygen from free-ranging fish. *Anim. Biotelem.* 3:47
- Cooley SR. 2012. How human communities could ‘feel’ changing ocean biogeochemistry. *Curr. Opin. Environ. Sustain.* 4:258–63
- Crawford WR, Peña MA. 2013. Declining oxygen on the British Columbia continental shelf. *Atmos.-Ocean* 51:88–103
- Dale AW, Graco M, Wallmann K. 2017. Strong and dynamic benthic-pelagic coupling and feedbacks in a coastal upwelling system (Peruvian Shelf). *Front. Mar. Sci.* 4:29

- De Leo FC, Gauthier M, Nephin J, Mihaly S, Juniper SK. 2016. Bottom trawling and oxygen minimum zone influences on continental slope benthic community structure off Vancouver Island (NE Pacific). *Deep-Sea Res. II* 137:404–19
- Deutsch C, Berelson W, Thunell R, Weber T, Tems C, et al. 2014. Centennial changes in North Pacific anoxia linked to tropical trade winds. *Science* 345:665–68
- Deutsch C, Brix H, Ito T, Frenzel H, Thompson L. 2011. Climate-forced variability of ocean hypoxia. *Science* 333:336–39
- Deutsch C, Emerson S, Thompson L. 2006. Physical-biological interactions in North Pacific oxygen variability. *J. Geophys. Res. Oceans* 111:C09S90
- Deutsch C, Ferrel A, Seibel B, Pörtner H-O, Huey RB. 2015. Climate change tightens a metabolic constraint on marine habitats. *Science* 348:1132–35
- Diaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321:926–29
- Dickson AJ, Cohen AS, Coe AL. 2012. Seawater oxygenation during the Paleocene-Eocene Thermal Maximum. *Geology* 40:639–42
- Diffenbaugh NS, Snyder MA, Sloan LC. 2004. Could CO<sub>2</sub>-induced land-cover feedbacks alter near-shore upwelling regimes? *PNAS* 101:27–32
- D’Souza NA, Subramaniam A, Juhl AR, Hafez M, Chekalyuk A, et al. 2016. Elevated surface chlorophyll associated with natural oil seeps in the Gulf of Mexico. *Nat. Geosci.* 9:215–18
- Du M, Kessler JD. 2012. Assessment of the spatial and temporal variability of bulk hydrocarbon respiration following the Deepwater Horizon oil spill. *Environ. Sci. Technol.* 46:10499–507
- 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
- Duteil O, Böning CW, Oschlies A. 2014. Variability in subtropical-tropical cells drives oxygen levels in the tropical Pacific Ocean. *Geophys. Res. Lett.* 41:8926–34
- Dutkiewicz S, Scott JR, Follows MJ. 2013. Winners and losers: ecological and biogeochemical changes in a warming ocean. *Glob. Biogeochem. Cycles* 27:463–77
- Ekau W, Auel H, Pörtner HO, Gilbert D. 2010. Impacts of hypoxia on the structure and processes in the pelagic community (zooplankton, macro-invertebrates and fish). *Biogeosciences* 7:1669–99
- Emerson S, Watanabe YW, Ono T, Mecking S. 2004. Temporal trends in apparent oxygen utilization in the upper pycnocline of the North Pacific: 1980–2000. *J. Oceanogr.* 60:139–47
- Frölicher TL, Joos F, Plattner G-K, Steinacher M, Doney SC. 2009. Natural variability and anthropogenic trends in oceanic oxygen in a coupled carbon cycle-climate model ensemble. *Glob. Biogeochem. Cycles* 23:GB1003
- Frölicher TL, Rodgers KB, Stock CA, Cheung WL. 2016. Sources of uncertainties in 21st century projections of potential ocean ecosystem stressors. *Glob. Biogeochem. Cycles* 30:1224–43
- Gallo ND, Levin LA. 2016. Fish ecology and evolution in the world’s oxygen minimum zones and implications of ocean deoxygenation. In *Advances in Marine Biology*, Vol. 74, ed. BE Curry, pp. 117–98. London: Academic
- Gallo ND, Victor DG, Levin LA. 2017. Ocean commitments under the Paris Agreement. *Nat. Clim. Change*. In press
- García HE, Boyer TP, Levitus S, Locarnini RA, Antonov J. 2005. On the variability of dissolved oxygen and apparent oxygen utilization content for the upper world ocean: 1955 to 1998. *Geophys. Res. Lett.* 32:L09604
- García-Reyes M, Sydeman WJ, Schoeman DS, Rykaczewski RR, Black BA, et al. 2015. Under pressure: climate change, upwelling and eastern boundary upwelling ecosystems. *Front. Mar. Sci.* 2:109
- Garreaud RD, Falvey M. 2009. The coastal winds off western subtropical South America in future climate scenarios. *Int. J. Climatol.* 29:543–54
- Gilbert D, Rabalais NN, Diaz RJ, Zhang J. 2010. Evidence for greater oxygen decline rates in the coastal ocean than in the open ocean. *Biogeosciences* 7:2283–96
- Gilbert D, Sundby B, Gobeil C, Mucci A, Tremblay GH. 2005. A seventy-two year record of diminishing deep-water oxygen in the St. Lawrence estuary: the northwest Atlantic connection. *Limnol. Oceanogr.* 50:1654–66



- Gilly WF, Beman JM, Litvin SY, Robison BH. 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annu. Rev. Mar. Sci.* 5:393–420
- Glecker PJ, Durack PJ, Stouffer RJ, Johnson GC, Forest CE. 2016. Industrial-era global ocean heat uptake doubles in recent decades. *Nat. Clim. Change* 6:394–98
- Gnanadesikan AD, Bianchi D, Pradal MA. 2013. Critical role for mesoscale eddy diffusion in supplying oxygen to hypoxic ocean waters. *Geophys. Res. Lett.* 40:5194–98
- Goericke R, Bograd S, Grundle DS. 2015. Denitrification and flushing of the Santa Barbara Basin bottom waters. *Deep-Sea Res. II* 112:53–60
- Gooday AJ, Jorissen F, Levin LA, Middelburg JJ, Naqvi W, et al. 2009. Historical records of coastal eutrophication and hypoxia. *Biogeosciences* 6:1707–45
- Gruber N. 2008. The marine nitrogen cycle: overview and challenges. In *Nitrogen in the Marine Environment*, ed. DG Capone, DA Bronk, MR Mulholland, EJ Carpenter, pp. 1–50. San Diego, CA: Academic. 2nd ed.
- Gruber N. 2011. Warming up, turning sour, losing breath: ocean biogeochemistry under global change. *Philos. Trans. R. Soc. A* 369:1980–86
- Gruber N, Doney SC, Emerson SR, Gilbert D, Kobayashi T, et al. 2010. Adding oxygen to ARGO: developing a global in situ observatory for ocean deoxygenation and biogeochemistry. In *Proceedings of OceanObs'09: Sustained Ocean Observations and Information for Society, Venice, Italy, 21–25 September 2009*, Vol. 2: *Community White Papers*, ed. J Hall, DE Harrison, D Stammer, chap. 39. ESA Publ. WPP-306. Paris: Eur. Space Agency. <http://www.oceanobs09.net/proceedings/cwp/cwp39/>
- Hall POJ, Almroth Rosell E, Bonaglia S, Dale AW, Hylén A, et al. 2017. Influence of natural oxygenation of Baltic Proper deep water on benthic recycling and removal of phosphorus, nitrogen, silicon and carbon. *Front. Mar. Sci.* 4:27
- Hansman RL, Thurber AR, Levin LA, Aluwihare LI. 2017. Methane fates in the benthos and water column at cold seep sites along the continental margin of Central and North America. *Deep-Sea Res. I* 120:122–31
- Harrison CS, Hales B, Siedlecki S, Samelson RM. 2016. Potential and timescales for oxygen depletion in coastal upwelling systems: a box-model analysis. *J. Geophys. Res. Oceans* 121:3202–27
- Hasselmann K. 1993. Optimal fingerprints for the detection of time-dependent climate change. *J. Clim.* 6:1957–71
- Helm KP, Bindoff NL, Church JA. 2011. Observed decreases in oxygen content of the global ocean. *Geophys. Res. Lett.* 38:L23602
- Henson SA, Beaulieu C, Ilyina T, John JG, Long M, et al. 2017. Rapid emergence of climate change in environmental drivers of marine ecosystems. *Nat. Commun.* 8:14682
- Hofmann M, Schellnhuber HJ. 2009. Oceanic acidification affects marine carbon pump and triggers extended marine oxygen holes. *PNAS* 106:3017–22
- Holding JM, Duarte CM, Arrieta M, Vaquer-Sunyer R, Coello-Camba A, et al. 2013. Experimentally determined temperature thresholds for Arctic plankton community metabolism. *Biogeosciences* 10:357–70
- IOC (Intergov. Oceanogr. Comm.). 2017. *Deoxygenation – open ocean and coastal waters*. <http://www.unesco.org/new/en/natural-sciences/ioc-oceans/sections-and-programmes/ocean-sciences/global-ocean-oxygen-network>
- IPCC (Intergov. Panel Clim. Change). 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Ed. TF Stocker, D Qin, G-K Plattner, M Tignor, SK Allen, et al. Cambridge, UK: Cambridge Univ. Press
- Ito T, Deutsch C. 2010. A conceptual model for the temporal spectrum of oceanic oxygen variability. *Geophys. Res. Lett.* 37:L03601
- Ito T, Nenes A, Johnson MS, Meskhidze N, Deutsch C. 2016. Acceleration of oxygen decline in the tropical Pacific over the past decades by aerosol pollutants. *Nat. Geosci.* 9:443–47
- Karstensen J, Fiedler B, Schute F, Brandt P, Kortzinger A, et al. 2015. Open ocean dead zones in the tropical North Atlantic Ocean. *Biogeosciences* 12:2597–605
- Keeling RF, Garcia HE. 2002. The change in oceanic O<sub>2</sub> inventory associated with recent global warming. *PNAS* 99:7848–53
- Keeling RF, Kortzinger A, Gruber N. 2010. Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* 2:199–229

- Kim TW, Lee K, Najjar RG, Jeong HD, Jeong HJ. 2011. Increasing N abundance in the northwestern Pacific Ocean due to atmospheric nitrogen deposition. *Science* 334:505–9
- Knoll AH, Carroll SB. 1999. Early animal evolution: emerging views from comparative biology and geology. *Science* 284:2129–37
- Kvenvolden K, Rogers B. 2005. Gaia's breath: global methane exhalations. *Mar. Petrol. Geol.* 22:579–90
- Le Quéré CO, Aumont OA, Monfray P, Orr J. 2003. Propagation of climatic events on ocean stratification, marine biology, and CO<sub>2</sub>: case studies over the 1979–1999 period. *J. Geophys. Res. Oceans* 108:3375
- Levin LA. 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanogr. Mar. Biol.* 41:1–45
- Levin LA, Breitburg D. 2015. Connecting coasts and seas to address ocean deoxygenation. *Nat. Clim. Change* 5:401–3
- Levin LA, Ekau W, Gooday A, Jorissen F, Middelburg J, et al. 2009. Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences* 6:2063–98
- Levin LA, Liu KK, Emeis KC, Breitburg DL, Cloern J, et al. 2015. Comparative biogeochemistry-ecosystem-human interactions on dynamic continental margins. *J. Mar. Syst.* 141:3–17
- Levin LA, Mengerink K, Gjerde KM, Rowden AA, Van Dover CL, et al. 2016. Defining “serious harm” to the marine environment in the context of deep-seabed mining. *Mar. Policy* 74:245–59
- Levin LA, Orphan VJ, Rouse GW, Ussler W, Rathburn AE, et al. 2012. A hydrothermal seep on the Costa Rica margin: middle ground in a continuum of reducing ecosystems. *Proc. R. Soc. B* 279:2580–88
- Levin LA, Whitcraft C, Mendoza GF, Gonzalez J, Cowie G. 2009. Oxygen and organic matter thresholds for benthic faunal activity on the Pakistan Margin oxygen minimum zone (700–1100 m). *Deep-Sea Res. II* 56:449–71
- Long MC, Deutsch C, Ito T. 2016. Finding forced trends in oceanic oxygen. *Glob. Biogeochem. Cycles* 30:381–97
- Löscher CR, Fischer MA, Neulinger SC, Fiedler B, Philippi M, et al. 2015. Hidden biosphere in an oxygen-deficient Atlantic open-ocean eddy: future implications of ocean deoxygenation on primary production in the eastern tropical North Atlantic. *Biogeosciences* 12:7467–82
- Lyons TW, Reinhard CT, Planavsky NJ. 2014. The rise of oxygen in Earth's early ocean and atmosphere. *Nature* 506:307–15
- Matear RJ, Hirst AC, McNeil BI. 2000. Changes in dissolved oxygen in the Southern Ocean with climate change. *Geochem. Geophys. Geosyst.* 1:1050
- 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
- McCormick LR, Levin LA. 2017. Physiological and ecological implications of ocean deoxygenation for vision in marine organisms. *Philos. Trans. R. Soc. A* 375:20160322
- McDonagh EL, Bryden HL, King BA, Sanders RJ, Cunningham SA, Marsh R. 2005. Decadal changes in the south Indian Ocean thermocline. *J. Clim.* 18:1575–90
- McInerney FA, Wing SL. 2011. The Paleocene-Eocene Thermal Maximum: a perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annu. Rev. Earth Planet. Sci.* 39:489–516
- Mecking S, Langdon C, Feely RA, Sabine CL, Deutsch CA, Min DH. 2008. Climate variability in the North Pacific thermocline diagnosed from oxygen measurements: an update based on the U.S. CLIVAR/CO<sub>2</sub> Repeat Hydrography cruises. *Glob. Biogeochem. Cycles* 22:GB3015
- Meinvielle M, Johnson GC. 2013. Decadal water-property trends in the California Undercurrent, with implications for ocean acidification. *J. Geophys. Res. Oceans* 118:6687–703
- Moffitt SE, Hill TM, Roopnarine PD, Kennett JP. 2015a. Response of seafloor ecosystems to abrupt global climate change. *PNAS* 112:4684–89
- Moffitt SE, Moffitt RA, Sauthoff W, Davis CV, Hewett K, Hill TM. 2015b. Paleooceanographic insights on recent oxygen minimum zone expansion: lessons for modern oceanography. *PLOS ONE* 10:e0115246
- Montes E, Muller-Karger FE, Cianca A, Lomas MW, Lorenzoni L, Habtes S. 2016. Decadal variability in the oxygen inventory of North Atlantic subtropical underwater captured by sustained, long-term oceanographic time series observations. *Glob. Biogeochem. Cycles* 30:460–78
- Montes I, Dewitte B, Gutknecht E, Paulmier A, Dadou I, et al. 2014. High-resolution modeling of the Eastern Tropical Pacific oxygen minimum zone: sensitivity to the tropical oceanic circulation. *J. Geophys. Res. Oceans* 119:5515–32

- Moore JK, Lindsay K, Doney S, Long MC, Misumi K, et al. 2013. Marine ecosystem dynamics and biogeochemical cycling in the Community Earth System Model [CESM1(BGC)]: comparison of the 1990s with the 2090s under the RCP4.5 and RCP8.5 scenarios. *J. Clim.* 26:9291–312
- Mora C, Wei C-L, Rollo A, Amaro T, Baco AR, et al. 2013. Biotic and human vulnerability to projected changes in ocean biogeochemistry over the 21st century. *PLOS Biol.* 11:e1001682
- Myhre SE, Kroeker KJ, Hill TM, Roopnarine P, Kennett JP. 2017. Community benthic paleoecology from high-resolution climate records: Mollusca and foraminifera in post-glacial environments of the California margin. *Quat. Sci. Rev.* 155:179–97
- Nakanowatari T, Ohshima KI, Wakatsuchi M. 2007. Warming and oxygen decrease of intermediate water in the northwestern North Pacific, originating from the Sea of Okhotsk, 1955–2004. *Geophys. Res. Lett.* 34:L04602
- Naqvi SWA, Bange HW, Farias L, Monteiro PMA, Scranton MI, Zhang J. 2010. Marine hypoxia/anoxia as a source of CH<sub>4</sub> and N<sub>2</sub>O. *Biogeosciences* 7:2159–90
- Naqvi SWA, Naik H, Jayakumar DA, Shailaja MS, Narvekar PV. 2006. Seasonal oxygen deficiency over the western continental shelf of India. In *Past and Present Water Column Anoxia*, ed. LN Neretin, pp. 195–224. Dordrecht, Neth.: Springer
- Netburn AN, Koslow JA. 2015. Dissolved oxygen as a constraint on daytime deep scattering layer depth in the southern California current ecosystem. *Deep-Sea Res. I* 104:149–58
- O'Connor FM, Boucher O, Gedney N, Jones CD, Folberth GA, et al. 2010. Possible role of wetlands, permafrost, and methane hydrates in the methane cycle under future climate change: a review. *Rev. Geophys.* 48:RG4005
- Ono T, Midorikawa T, Watanabe YW, Tadokoro K, Saino T. 2001. Temporal increases of phosphate and apparent oxygen utilization in the subsurface waters of western subarctic Pacific from 1968 to 1998. *Geophys. Res. Lett.* 28:3285–88
- Oschlies A, Duteil O, Getzlaff J, Koeve W, Landolfi A, Schmidtko S. 2017. Patterns of deoxygenation: sensitivity to natural and anthropogenic drivers. *Philos. Trans. R. Soc. A* 375:20160325
- Oschlies A, Schulz KG, Riebesell U, Schmittner A. 2008. Simulated 21st century's increase in oceanic suboxia by CO<sub>2</sub>-enhanced biotic carbon export. *Glob. Biogeochem. Cycles* 22:GB4008
- Ostrander CM, Owens JD, Nielsen SG. 2017. Constraining the rate of oceanic deoxygenation leading up to a Cretaceous Oceanic Anoxic Event (OAE-2: ~94 Ma). *Sci. Adv.* 3:e1701020
- Papiol V, Hendrickx ME, Serrano D. 2017. Effects of latitudinal changes in the oxygen minimum zone of the northeast Pacific on the distribution of bathyal benthic decapod crustaceans. *Deep-Sea Res. II* 137:113–30
- Paulmier AD, Ruiz-Pino D, Garçon V. 2008. The oxygen minimum zone (OMZ) off Chile as intense source of CO<sub>2</sub> and N<sub>2</sub>O. *Cont. Shelf Res.* 28:2746–56
- Phrampus BJ, Hornbach MJ. 2012. Recent changes to the Gulf Stream causing widespread gas hydrate destabilization. *Nature* 490:527–30
- Pierce SD, Barth JA, Shearman RK, Erofeev A. 2012. Declining oxygen in the Northeast Pacific. *J. Phys. Oceanogr.* 42:495–501
- Plattner GK, Joos F, Stocker TF, Marchal O. 2001. Feedback mechanisms and sensitivities of ocean carbon under global warming. *Tellus B* 53:564–92
- Praetorius SK, Mix AC, Walczak MH, Wolhowe MD, Addison JA, et al. 2015. North Pacific deglacial hypoxic events linked to abrupt ocean warming. *Nature* 527:362–66
- Prather MJ, Ehhalt D, Dentener F, Derwent R, Dlugokencky E, et al. 2001. Atmospheric chemistry and greenhouse gases. In *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, ed. JT Houghton, Y Ding, DJ Griggs, M Noguer, PJ van der Linden, et al., pp. 239–87. Cambridge, UK: Cambridge Univ. Press.
- Rabalais NN, Cai WJ, Carstensen J, Conley DJ, Fry B, et al. 2014. Eutrophication-driven deoxygenation in the coastal ocean. *Oceanography* 27(1):172–83
- Rahmstorf S, Box JE, Feulner G, Mann ME, Robinson A, et al. 2015. Exceptional twentieth-century slowdown in Atlantic Ocean overturning circulation. *Nat. Clim. Change* 5:475–80
- Ren A. 2016. *Declining dissolved oxygen in the central California Current region*. MS Thesis, Univ. Maine, Orono. <http://digitalcommons.library.umaine.edu/etd/2539>

- Ricke KL, Caldeira K. 2014. Natural climate variability and future climate policy. *Nat. Clim. Change* 4:333–38
- Ruppel CD, Kessler JD. 2017. The interaction of climate change and methane hydrates. *Rev. Geophys.* 55:126–68
- Rykaczewski RR, Dunne JP. 2010. Enhanced nutrient supply to the California Current Ecosystem with global warming and increased stratification in an earth system model. *Geophys. Res. Lett.* 37:L21606
- Rykaczewski RR, Dunne JP, Sydeman WJ, García-Reyes M, Black BA, Bograd SJ. 2015. Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. *Geophys. Res. Lett.* 42:6424–31
- Santos GC, Kerr R, Azevedo JLL, Mendes CRB, da Cunha LC. 2016. Influence of Antarctic Intermediate Water on the deoxygenation of the Atlantic Ocean. *Dyn. Atmos. Oceans* 76:72–82
- Sarmiento JL, Hughes TMC, Stouffer RJ, Manabe S. 1998. Simulated response of the ocean carbon cycle to anthropogenic climate warming. *Nature* 393:245–49
- Sasano D, Takatani N, Kosugi N, Nakano T, Midorikawa M, Ishii M. 2015. Multidecadal trends of oxygen and their controlling factors in the western North Pacific. *Glob. Biogeochem. Cycles* 2:935–56
- Sato KN, Levin LA, Schiff K. 2017. Habitat compression and expansion of sea urchins in response to changing climate conditions on the California continental shelf and slope (1994–2013). *Deep-Sea Res. II* 137:377–89
- Schaffer G, Olsen SM, Pedersen JOP. 2009. Long-term ocean oxygen depletion in response to carbon dioxide emissions from fossil fuels. *Nat. Geosci.* 2:105–9
- Schmidtko S, Johnson GC. 2012. Multidecadal warming and shoaling of Antarctic Intermediate Water. *J. Clim.* 25:207–21
- Schmidtko S, Stramma L, Visbeck M. 2017. Decline in global oceanic oxygen content during the past five decades. *Nature* 542:335–39
- Schmittner A, Galbraith ED, Hostetler SW, Pederson TF, Zhang R. 2007. Large fluctuations of dissolved oxygen in the Indian and Pacific Oceans during Dansgaard-Oeschger oscillations caused by variations of North Atlantic Deep Water subduction. *Paleoceanography* 22:PA3207
- Scholz F, McManus J, Mix AC, Hensen C, Schneider RR, et al. 2014. The impact of ocean deoxygenation on iron release from continental margin sediments. *Nat. Geosci.* 7:433–37
- Seibel BA. 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *J. Exp. Biol.* 214:326–36
- Seibel BA, Schneider J, Kaartvedt S, Wishner KF, Daly KL. 2016. Hypoxia tolerance and metabolic suppression in oxygen minimum zone euphausiids: implications for ocean deoxygenation and biogeochemical cycles. *Integr. Comp. Biol.* 56:510–23
- Sekerci Y, Petrovskii S. 2016. Mathematical modeling of plankton–oxygen dynamics under the climate change. *Bull. Math. Biol.* 77:2325–53
- Siedlecki SA, Banas NS, Davis KA, Giddings S, Hickey B, et al. 2015. Seasonal and interannual oxygen variability on the Washington and Oregon continental shelves. *J. Geophys. Res. Oceans* 120:608–33
- Siedlecki SA, Kaplan IC, Hermann AJ, Nguyen TT, Bond NA, et al. 2016. Experiments with seasonal forecasts of ocean conditions for the northern region of the California Current upwelling system. *Sci. Rep.* 6: 27203
- Sluijs AL, van Roij L, Harrington GL, Schouten S, Sessa JA, et al. 2014. Warming, euxinia and sea level rise during the Paleocene-Eocene Thermal Maximum on the Gulf Coastal Plain: implications for ocean oxygenation and nutrient cycling. *Clim. Past* 10:1421–39
- Sperling EA, Frieder CA, Levin LA. 2016. Biodiversity response to natural gradients of multiple stressors on continental margins. *Proc. R. Soc. B* 283:20160637
- Sperling EA, Frieder CA, Raman A, Girguis PR, Levin LA, Knoll AH. 2013. Oxygen, ecology and the Cambrian radiation of animals. *PNAS* 110:13446–51
- Steffen W, Richardson K, Rockström J, Cornell SE, Fetzer I, et al. 2015. Planetary boundaries: guiding human development on a changing planet. *Science* 347:1259855
- Steinacher M, Joos F, Frölicher TL, Bopp L, Cadule P, et al. 2010. Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences* 7:979–1005

- Stendardo I, Gruber N. 2012. Oxygen trends over five decades in the North Atlantic. *J. Geophys. Res. Oceans* 117:C11004
- Stevens SW, Johnson RJ, Bates NR, Parsons RJ. 2016. *Physical and biogeochemical factors affecting deep oxygen minimum zone variability at the Bermuda Atlantic Time Series Site*. Presented at Ocean Sci. Meet., New Orleans, LA, Feb. 21–26
- Stramma L, Johnson GC, Sprintall J, Mohrholz V. 2008. Expanding oxygen minimum zones in the tropical oceans. *Science* 320:655–58
- Stramma L, Oschlies A, Schmidtko S. 2012. Mismatch between observed and modeled trends in dissolved upper-ocean oxygen over the last 50 yr. *Biogeosciences* 9:4045–57
- 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* 57:1–9
- Stramma L, Visbeck M, Brandt P, Tanhua T, Wallace D. 2009. Deoxygenation in the oxygen minimum zone of the eastern tropical North Atlantic. *Geophys. Res. Lett.* 36:L20607
- Sweetman AK, Chelsky A, Pitt KA, Andrade H, van Oevelen D, Renaud PE. 2016. Jellyfish decomposition at the seafloor rapidly alters biogeochemical cycling and carbon flow through benthic food-webs. *Limnol. Oceanogr.* 61:1449–61
- Sweetman AK, Thurber AR, Smith CR, Levin LA, Mora C, et al. 2017. Major impacts of climate change on deep-sea benthic ecosystems. *Elementa Sci. Anthr.* 5:4
- Sydeman WJ, García-Reyes M, Schoeman DS, Rykaczewski RR, Thompson SA, et al. 2014. Climate change and wind intensification in coastal upwelling ecosystems. *Science* 345:77–80
- Tagliabue A, Bopp L, Gehlen M. 2011. The response of marine carbon and nutrient cycles to ocean acidification: large uncertainties related to phytoplankton physiological assumptions. *Glob. Biogeochem. Cycles* 25:GB3017
- Takatani Y, Sasano D, Nakano T, Midorikawa T, Ishii M. 2012. Decrease of dissolved oxygen after the mid-1980s in the western North Pacific subtropical gyre along the 137°E repeat section. *Glob. Biogeochem. Cycles* 26:GB2013
- Talley L, Feely R, Sloyan B, Wanninkhof R, Baringer M, et al. 2016. Changes in ocean heat, carbon content, and ventilation: a review of the first decade of GO-SHIP global repeat hydrography. *Annu. Rev. Mar. Sci.* 8:185–215
- Thomas MK, Kremer CT, Klausmeier CA, Litchman E. 2012. A global pattern of thermal adaptation in marine phytoplankton. *Science* 338:1085–88
- Valentine DL. 2011. Emerging topics in marine methane biogeochemistry. *Annu. Rev. Mar. Sci.* 3:147–71
- Valentine DL, Fisher GB, Pizararo O, Kaiser CL, Yoerger D, et al. 2016. Autonomous marine robotic technology reveals an expansive benthic bacterial community relevant to regional nitrogen biogeochemistry. *Environ. Sci. Technol.* 50:11057–65
- Vaquer-Sunyer R, Duarte CM. 2008. Thresholds of hypoxia for marine biodiversity. *PNAS* 105:15452–57
- Vaquer-Sunyer R, Duarte CM. 2011. Temperature effects on oxygen thresholds for hypoxia in marine benthic organisms. *Glob. Change Biol.* 17:1788–97
- Vaquer-Sunyer R, Duarte CM, Regaudie-de-Gioux A, Holding J, García-Corral LS, et al. 2013. Seasonal patterns in Arctic planktonic metabolism (Fram Strait-Svalbard region). *Biogeosciences* 10:1451–69
- Wallmann K, Pinero E, Burwicz E, Haeckel M, Hensen C, et al. 2012. The global inventory of methane hydrate in marine sediments: a theoretical approach. *Energies* 5:2449–98
- Wang D, Gouhier T, Menge B, Ganguly A. 2015. Intensification and spatial homogenization of coastal upwelling under climate change. *Nature* 518:390–94
- Watson AJ. 2016. Oceans on the edge of anoxia. *Science* 354:1529–30
- Whitney FA, Bograd SJ, Ono T. 2013. Nutrient enrichment of the subarctic Pacific Ocean pycnocline. *Geophys. Res. Lett.* 40:2200–5
- 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

- Wishner KF, Outram DM, Seibel BA, Daly KL, Williams RL. 2013. Zooplankton in the eastern tropical North Pacific: boundary effects of oxygen minimum zone expansion. *Deep-Sea Res. I* 79:122–40
- Wright JJ, Konwar KM, Hallam SJ. 2012. Microbial ecology of expanding oxygen minimum zones. *Nat. Rev. Microbiol.* 10:381–94
- Yamamoto A, Abe-Ouchi A, Shigemitsu M, Oka A, Takahashi K, et al. 2015. Global deep ocean oxygenation by enhanced ventilation in the Southern Ocean under long-term global warming. *Glob. Biogeochem. Cycles* 29:1801–15