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Ocean Deoxygenation in a Warming World

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Key Words

global warming, ocean oxygen depletion, oxygen utilization, hypoxia, stratification, ventilation, carbon cycle, oxygen cycle, eutrophication

Abstract

Ocean warming and increased stratification of the upper ocean caused by global climate change will likely lead to declines in the dissolved O₂ in the ocean interior (ocean deoxygenation) with implications for ocean productivity, nutrient cycling, carbon cycling, and marine habitat. Ocean models predict declines of 1 to 7% in the global ocean O₂ inventory over the next century, with declines continuing for a thousand years or more into the future. An important consequence may be an expansion in the area and volume of so-called oxygen minimum zones, where O₂ levels are too low to support many macrofauna and profound changes in biogeochemical cycling occur. Significant deoxygenation has occurred over the past 50 years in the North Pacific and tropical oceans suggesting larger changes are looming. The potential for larger O₂ declines in the future suggests the need for an improved observing system for tracking ocean O₂ changes.

INTRODUCTION

A potentially serious consequence of global warming that has gained attention only recently is a decrease in the dissolved O_2 content of the world's oceans. The loss of dissolved O_2 , or "deoxygenation," is predicted, not just because O_2 is less soluble in warmer water but also because global warming may increase upper ocean stratification, thereby reducing the O_2 supply to the ocean interior (Sarmiento et al. 1998, Matear et al. 2000, Plattner et al. 2001, Bopp et al. 2002, Keeling & Garcia 2002).

Systematic deoxygenation of the ocean will have widespread consequences. O_2 plays a direct role in the biogeochemical cycling of carbon, nitrogen, and many other biogeochemically important elements (P, Fe, Mn, etc.). O_2 is also fundamental for all aerobic life, including organisms living in the dark ocean interior. If the oceans were to stagnate, many regions of the ocean interior would become devoid of O_2 in a matter of decades due to the continual consumption of O_2 by deep-dwelling organisms (Feely et al. 2004, Whitney et al. 2007).

The sensitivity of organisms, particularly macroorganisms, to low O_2 is highly nonlinear. Most organisms are not very sensitive to O_2 levels as long as the concentrations are high enough. But once O_2 drops below a certain threshold, the organism suffers from a variety of stresses, leading ultimately to death if the concentrations stay too low for too long. Such conditions are termed hypoxic. Thresholds for hypoxia vary greatly between marine taxa, with fish and crustaceans tending to be the most sensitive, as shown in **Figure 1** (Vaquer-Sunyer & Duarte 2008). A typical threshold for hypoxia is approximately $60 \mu\text{mol kg}^{-1}$ (Gray et al. 2002); zones with lower O_2 are effectively "dead zones" for many higher animals. As a complication, the thresholds for hypoxia typically depend, not just on O_2 levels, but also on levels of CO_2 and temperature. The consequences of deoxygenation in a warming world must therefore be considered in close concert with the effects of warming and acidification (Pörtner & Farrell 2008, Brewer & Peltzer 2009).

At very low O_2 concentrations, major changes in biogeochemical cycling occur. When O_2 drops below $\sim 5 \mu\text{mol kg}^{-1}$, nitrate becomes important in respiration, eventually replacing O_2 as

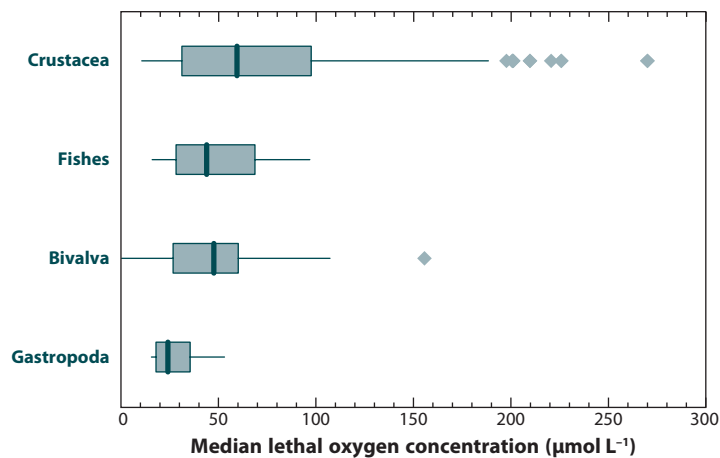


Figure 1

Median lethal oxygen concentration (LC_{50} , in $\mu\text{mol L}^{-1}$) among four different taxa. The box runs from the lower (Q_1 , 25%) to the upper (Q_3 , 75%) quartile and also includes the median (*thick vertical line*). The range of data points not considered outliers is defined as 1.5 times the difference between the quartiles ($Q_3 - Q_1$), also known as interquartile range (IQR). The whiskers show the location of the lowest and highest datum within this range, i.e., $1.5 * \text{IQR}$. Shaded diamonds are outliers as per this definition. Redrawn after Vaquer-Sunyer & Duarte (2008). Copyright (2008) National Academy of Sciences, U.S.A.

Table 1 Summary of oxygen minimum zone characteristics from Karstensen et al. (2008)

	Minimum O ₂ value (μmol kg ⁻¹)	Depth of minimum (m)	Total volume (10 ¹⁵ m ³) ^a		
			O ₂ < 4.5 μmol kg ⁻¹ (suboxic)	O ₂ < 45 μmol kg ⁻¹	O ₂ < 90 μmol kg ⁻¹
North Atlantic	~40	~420	0	0	0.9
South Atlantic	~20	~400	0	0.2	1.6
North Pacific	~0.1	250 to 400	0.44	11.3	21.3
South Pacific	~0.3	150 to 300	0.001	4.4	8.4
Indian Ocean	~0.3	100 to 650	0.02	2.7	6.1

^aIncluding all waters with potential density less than $\sigma_{\theta} < 27.2 \text{ kg m}^{-3}$. These figures can be converted to percentage of total ocean volume by dividing by $1.44 \times 10^{18} \text{ m}^3$.

the primary electron acceptor, a condition termed suboxic. When O₂ levels drop to zero, the water is termed anoxic. Once nitrate is exhausted, the biogeochemistry then tends to be dominated by sulfate-reducing microbes, which convert sulfate to sulfide.

The effect of low O₂ on nitrogen cycling has global implications. The extent of suboxia controls the loss of fixed nitrogen in the ocean via denitrification, and thus influences the supply of nitrate, a limiting nutrient for global ocean productivity (Codispoti et al. 2001, Gruber 2004). O₂ levels also control the oceanic production of (N₂O), a powerful greenhouse gas, which is produced both under suboxic conditions as a byproduct of denitrification and under oxic conditions during nitrification. Production of N₂O by both pathways will increase if O₂ levels drop (Codispoti et al. 2001, Jin & Gruber 2003, Nevison et al. 2003), thus potentially amplifying global warming (Gruber 2008). O₂ also influences the cycling of marine phosphorous cycle, with greater recycling of P from sediments occurring when O₂ levels are low in the overlying water (Wallmann 2003). Anoxia is rare in the water column of the modern ocean. Suboxic and hypoxic conditions occur, however, at mid depths over wide expanses of the North Pacific and in smaller regions of the South Pacific and North Indian Ocean. Hypoxic conditions also occur in the eastern tropical Atlantic and Pacific Oceans, as summarized in **Table 1**. A major concern is that these so-called oxygen minimum zones (OMZs) will expand in the future as the upper ocean warms and becomes more stratified. Recent studies suggest that the O₂ levels in the subpolar North Pacific and in tropical OMZs have indeed declined over the past 50 years (Ono et al. 2001, Whitney et al. 2007, Stramma et al. 2008).

Hypoxic, suboxic, and anoxic conditions frequently occur in coastal waters and estuaries, where high rates of photosynthetic production lead to high rates of O₂ consumption in subsurface waters and sediments. Additional O₂ loss from eutrophication by agricultural runoff or sewage inputs is a serious problem in many freshwater and coastal systems around the world (Diaz & Rosenberg 1995, Breitburg et al. 2009). This problem could be exacerbated in certain coastal systems by O₂ declines in the open ocean because the O₂ supply to these systems is often partly via seawater exchange with the open ocean. Anoxic conditions also occur in isolated enclosed basins, such as the Black Sea, the Baltic Sea, and the Cariaco Basin.

Although anoxia is rare in the modern ocean, ocean anoxic events (OAEs), characterized by sedimentary evidence of wide-spread anoxia, have occurred episodically throughout the geologic record (Wignall & Twitchett 1996, Jones & Jenkyns 2001, Cohen et al. 2007). The OAEs were often associated with evidence of warmer climate conditions, rises in sea level, and occasionally with mass extinctions. Although their cause remains uncertain, their occurrence underscores the potential vulnerability of oceanic O₂ supply in warmer climates.

The threat of ocean deoxygenation raises many questions. Is O₂ loss already starting to occur? How could such changes be monitored? What are the main controlling processes? How will these processes change in the future? What will be the consequences for organisms, for ecosystems, for fisheries, etc?

Understanding how oceanic O₂ is changing is important, not just because of the impact on marine organisms, but because measured changes in O₂, together with changes in nutrients, are a useful diagnostic of changing biogeochemistry (Matear et al. 2000, Keeling & Garcia 2002, Joos et al. 2003). Dissolved O₂ is the most commonly measured property of seawater that is sensitive to biological cycling, and is therefore the first place to look for changes in ocean biogeochemistry in a warming world. The measurement of O₂ in seawater began as modern science with the careful analyses of 77 water samples by Dittmar (1884) aboard the H.M.S. *Challenger* expedition from 1873–1876. The invention of an elegant and precise wet-chemical method by Winkler (1888) represented a major breakthrough in methodology. The Winkler method, with various improvements (e.g., Carpenter 1965), remains the standard method to this day.

O₂ is directly linked to carbon via photosynthesis and respiration, so the distribution of O₂ in the ocean is a diagnostic of the rate at which organic matter is produced, redistributed, and decomposed in the ocean. Understanding this natural biological pump and how it is changing with global warming is critical to tracking the uptake of excess CO₂ from the atmosphere via ocean measurements. Understanding changes in oceanic O₂ is also important for the interpretation of measurements of atmospheric O₂, particularly the ability to use such measurements to determine the global land and ocean carbon sinks of CO₂ (Keeling 1988, Manning & Keeling 2006). Conversely, measurements of atmospheric O₂ can provide additional insights into changing ocean O₂ (Hamme & Keeling 2008).

Dissolved O₂ measurements also can provide information on ocean circulation. The difference between the observed O₂ level and that expected at equilibrium with the atmosphere, a quantity known as the apparent oxygen utilization (AOU), reflects a water parcel's biogeochemical history, increasing with time as the parcel "ages" below the surface. Thus, changes in AOU can provide information on changing circulation not revealed in measurements of physical properties, such as temperature and salinity.

Here we review what is known and not known about the controls on O₂ distribution in the modern ocean, how it may change in the future, how it has changed over the past few decades, and how it impacts estimates of ocean carbon uptake. We also outline the challenges and opportunities for further research on these topics based on ocean and atmospheric measurements and modeling. To keep the scope of this review manageable, we do not address several important related questions, such as the impact of low O₂ on organisms, ecosystems, or chemical processes. Nor do we attempt to review changes in O₂ driven by eutrophication in freshwater and coastal systems. For readers interested in impacts of low O₂ or problems of eutrophication, we refer readers to several recent reviews: Levin 2003, Neretin 2006, Diaz & Rosenberg 2008, Breitburg et al. 2009, Vaquer-Sunyer & Duarte 2008.

OXYGEN DISTRIBUTION AND CONTROLS

The distribution of O₂ in the ocean interior is controlled by the interplay between air-sea exchange, circulation, and biology. In a given subsurface water parcel, there are three main governing factors: the initial O₂ that the parcel contained when it was last at the surface, the rate at which O₂ is consumed by the oxidation of organic matter (termed oxygen utilization rate, or OUR), and the time elapsed since the parcel was last at the surface, sometimes known as the ventilation age. These factors may vary in concert; e.g., changes in mixing can influence the transport of O₂ and nutrients

in ways that influence all three factors. The factors are nevertheless conceptually distinguishable and quantifiable.

Initial O_2 levels are largely determined by conditions at higher latitudes in winter, when most subsurface waters are formed. The most important control in surface waters is the O_2 solubility, which increases with lower temperatures. Despite the rapidity of air-sea gas exchange, equilibration with atmosphere O_2 is never perfect, however (Ito et al. 2004). Subpolar surface waters are typically undersaturated by 3 to 10% in winter, with undersaturations exceeding 20% in some regions near Antarctica (Gordon & Huber 1990, Garcia et al. 2006).

Oxygen utilization is driven mostly by bacterial oxidation of organic particles sinking from the sunlit layers near the surface. Higher utilization is found beneath regions of high surface productivity and export production. Under both productive and unproductive surface waters, the utilization rate falls off rapidly with depth, decreasing, e.g., by a factor of 10 to 50 between 100 and 1000 m (Jenkins 1987, Martin et al. 1987, Feely et al. 2004, Karstensen et al. 2008). Example profiles are shown in **Figure 2**. The sinking flux of organic matter, which depletes O_2 while adding carbon and nutrients to subsurface waters, is known as the biological pump.

The ventilation age is roughly determined by the time required for water on a given (potential) density surface to transit from a high-latitude region where water of that density “outcrops” at the surface. Ventilation ages typically increase with depth (or density) in the upper ocean and increase with distance from the outcrop regions, following the interior flow patterns. Waters with low

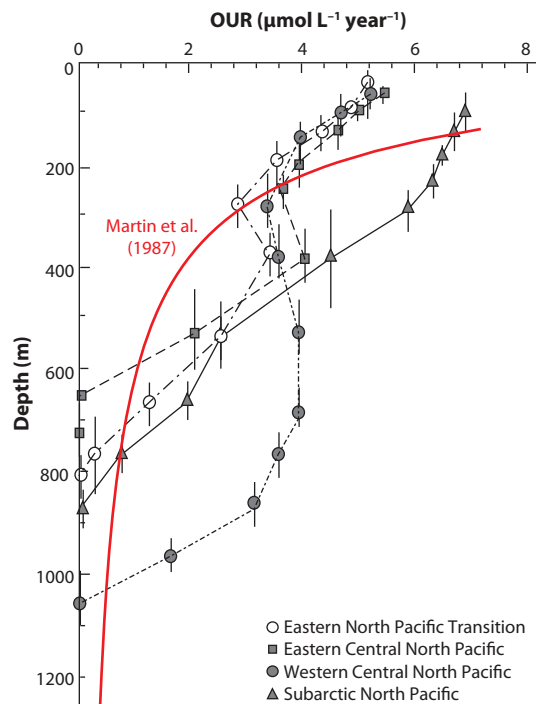


Figure 2

The oxygen utilization rate (OUR) in $\mu\text{mol L}^{-1} \text{ year}^{-1}$ (*thick red line*) versus depth from the model of Martin et al. (1987) and from a recent compilation of Pacific profiles for North Pacific oceans based on apparent oxygen utilization and CFC ages from Feely et al. (2004). Adapted from Sarmiento & Gruber (2006). Copyright (2006) Princeton University Press.

ventilation ages are said to be well ventilated, i.e., in rapid contact with the atmosphere. We use the term ventilation to refer to all processes supplying atmospheric gases to the ocean interior, including air-sea gas exchange, exchange between the surface mixed layer and the immediate subsurface layer (i.e., mixed layer detrainment), and circulation in the ocean interior. Others have used the term more narrowly, referring only to the combination of air-sea exchange and detrainment (e.g., Deutsch et al. 2006).

Ventilation ages can be estimated from the distribution of radiocarbon, tritium, or chlorofluorocarbons (CFCs) in the ocean. From a combination of the ventilation age and the O₂ distribution, the basin-averaged utilization rates can be estimated versus depth or density (Jenkins 1987, Broecker et al. 1991, Feely et al. 2004, Karstensen et al. 2008). Utilization rates can also be determined from the decrease in the sinking flux of organic carbon with depth (Martin et al. 1987). None of these approaches is entirely satisfactory, however. Accurate determination of local O₂ utilization rates is an important unsolved problem in observational oceanography.

As has long been understood, the combination of significant utilization and weak ventilation leads to a mid-depth O₂ minimum (Sverdrup 1938, Wyrki 1962). Shallower waters tend to have higher O₂ because they are better ventilated, despite higher rates of utilization, while deeper waters tend to have higher O₂ because of lower utilization rates and higher initial O₂ levels, despite longer ventilation ages. The O₂ minimum is typically at depths between 400 and 1200 m, near the base of the permanent thermocline, as shown in **Figure 3**. Within this layer, the OMZs are local hotspots where O₂ levels are especially low.

The OMZs are typically located in regions without unusually high rates of O₂ utilization but where the circulation is most sluggish and ventilation times are longest (Karstensen et al. 2008). In the Atlantic and Pacific, the most poorly ventilated waters are found in relatively stagnant cyclonic gyres that exist north and south of the Equator in the east in subsurface layers (see **Figure 4**). These wedge-shaped eastern tropical gyres, sometimes called shadow zones (Luyten et al. 1983), are distinct from the subtropical gyres to the north and south, where waters are much better ventilated, owing to efficient transport and mixing from outcrop regions.

The degree of O₂ depletion within the tropical gyres varies greatly from gyre to gyre, with the North Pacific tropical gyre hosting the world's largest OMZ and the Atlantic gyres hosting much smaller OMZs. The control on the O₂ supply to the tropical gyres is a matter of ongoing research, but a major pathway includes transport along eastward flowing subsurface equatorial jets (Brandt et al. 2008; P Brandt, V. Hormann, A. Körtzinger, M. Visbeck, G. Krahnemann, et al., unpublished paper). Karstensen et al. (2008) have shown that the difference in the degree of O₂ depletion can be explained mostly by differences in the overall ventilation of the basin in which the gyre is embedded. Thus the North Pacific hosts the world's largest OMZ because of the relatively poor ventilation at its high latitudes. In fact, much of the North Pacific, not just the tropical gyre, can be considered an OMZ. The thermocline in the Southern Hemisphere tends to be well ventilated, owing to the efficient outcropping and ventilation of thermocline waters associated with the Antarctic Circumpolar Current system (Sarmiento et al. 2004).

Watermass transport across the Equator can also be important to the OMZs. For example, the North Atlantic tropical gyre tends to be relatively well ventilated owing partially to the strong inflow of water from the South Hemisphere as part of the Atlantic overturning circulation (Karstensen et al. 2008). Weakening of the overturning could thus increase the extent of this OMZ.

The OMZ in the North Indian Ocean doesn't fit the pattern of an OMZ being hosted by an eastern tropical gyre. The Indian Ocean is unique in lacking a source of subpolar water from within the hemisphere. The origin of the Indian OMZ is a matter of discussion (Gruber 2004), with low initial O₂ and high utilization probably both being relevant. The lowest O₂ levels in the

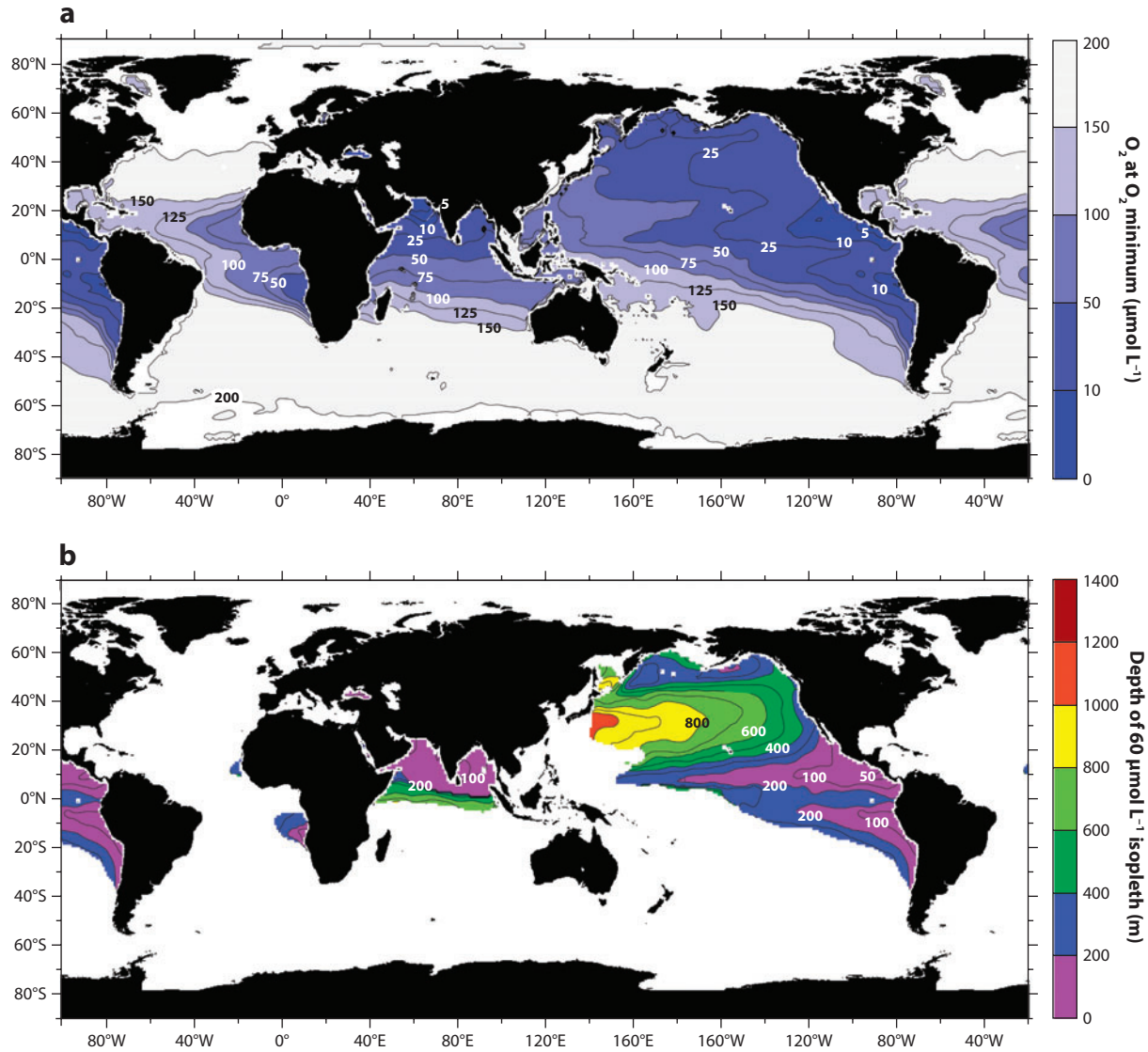


Figure 3

(a) Colors indicate O_2 concentrations at the depth of minimum O_2 . (b) Depth of the $60 \mu\text{mol L}^{-1}$ isopleth in meters. Based on data from World Ocean Database, 2001 (Conkright et al. 2002).

Indian Ocean are found in the Arabian Sea, which contains the largest volume of suboxic water outside the North Pacific.

An important measure of the impact of OMZs on marine organisms is the shallowest depth at which waters become hypoxic, i.e., the depth of hypoxia (DOH). As shown in **Figure 3**, the DOH (based on a $60 \mu\text{mol L}^{-1} \approx 60 \mu\text{mol kg}^{-1}$) shoals to less than 200 m in association with the OMZs in the Pacific, Indian, and South Atlantic. In the Indian Ocean, the DOH shoals to even shallower depths in the Bay of Bengal than in the Arabian Sea. The DOH shoals to less than 400 over most of the northern and eastern margin of the Pacific.

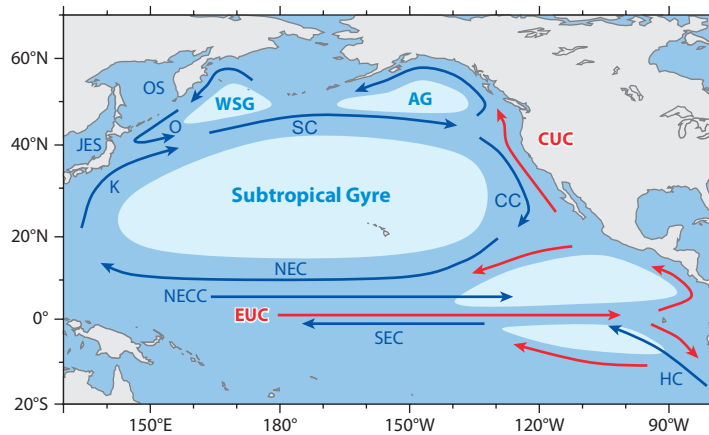


Figure 4

Currents (arrows) and gyres (shaded areas) of the Equatorial and North Pacific. Surface currents are indicated in blue and subsurface currents in red. The tropical gyres are the light blue patches in the eastern tropical Pacific. WSG = Western Subarctic Gyre, AG = Alaska Gyre, OS = Okhotsk Sea, JES = Japan/East Sea, O = Oyashio, K = Kuroshio, SC = Subarctic Current, CC = California Current, CUC = California Undercurrent, NEC = North Equatorial Current, NECC = North Equatorial Counter Current, EUC = Equatorial Undercurrent, SEC = South Equatorial Current, HC = Humboldt Current.

THE FUTURE OCEAN—WHAT MODELS TELL

The prediction that global warming will cause reductions in ocean O_2 is supported by multiple modeling studies, as summarized in **Table 2**. The available estimates are based on coarse-resolution-coupled ocean-atmosphere models, with simple embedded schemes to account for biological cycling. Part of the O_2 decline in all models results simply from the reduction in the solubility of O_2 in warmer water. But all models show a substantial additional O_2 loss resulting from the changes in ocean circulation and biology. The most important cause of these changes is the effect of global warming on upper ocean stratification, particularly at high latitudes, where reductions in surface density result from both warming and freshening due to an enhanced hydrological cycle (Sarmiento et al. 1998, Bopp et al. 2002).

By reducing the exchange between surface and subsurface waters, stratification has two competing effects on O_2 . First, the stratification reduces the supply of nutrients from subsurface to surface waters, thus reducing the production and export of organic carbon and reducing subsurface oxygen utilization rates. By itself, this effect would cause subsurface O_2 levels to increase. Second, the stratification reduces the exchange of surface and subsurface water, reducing the transport of O_2 into the ocean interior, and causing interior O_2 levels to decline. The models consistently predict that the effect on ventilation exceeds the effect on utilization, leading to an overall decrease in interior ocean O_2 .

The tendency for subsurface O_2 to decline under increased stratification appears to have a straightforward explanation linked to changes in surface inorganic nutrients (Keeling & Garcia 2002). Nutrient elements can be transported from the surface to the ocean interior either as a component of sinking organic matter or by downward mixing from surface waters in their inorganic forms. The first (organic) of these pathways leads to O_2 consumption in the ocean interior, while the second pathway (inorganic) does not. Most models predict that stratification leads to more complete nutrient utilization in surface waters, thus strengthening the organic pathway compared to the inorganic pathway, causing a net lowering of the O_2 content of subsurface waters. The

Table 2 Model predictions of average ocean O₂ decrease by year 2100

Study	Model	Forcing	O ₂ decrease (μmol kg ⁻¹) ^a	Solubility contribution (%)	O ₂ /Heat ratio nmol J ⁻¹
Sarmiento et al. (1998)	GFDL		7 ^b		
Matear et al. (2000)	CSIRO	IS92A	7	18	
Plattner et al. (2001, 2002)	Bern 2D	SRES A1	12	35	5.9 ^c
Bopp et al. (2002)	OPAICE-LMD5	SRES A2 CO ₂ only	4	25	6.1
OPAICE-LMD5	HAMOCC-3				6.6
Matear & Hirst (2003)	CSIRO		9	26	
Schmittner et al. (2008)	UVic	SRES A2	9		6.7 ^d
Oschlies et al. (2008)	UVic	SRES A2	9		6.7 ^d
	UVic-variable C/N	SRES A2	12		
Fröhlicher et al. (2009)	NCAR CSM1.4-CCCM	SRES A2	4	50	
		SRES B1	3		

^aConversions assume a total ocean mass of 1.48×10^{21} kg.

^bTime frame only through 2065.

^cO₂/Heat ratio for simulation through year 2000.

^dO₂/Heat ratio from Oschlies, pers. commun.

decrease in O₂ inventory caused by stratification is proportional to the decrease in the inventory of preformed nutrients, i.e., nutrients delivered to the interior in inorganic form by water mixing and transport.

A useful basis for comparing models is the predicted decline in global average dissolved O₂ over the next century, as summarized in **Table 1**. Declines by year 2100 vary from 2 to 12 μmol kg⁻¹ depending on the model (**Table 2**). Compared to the average ocean O₂ concentration of ~178 μmol kg⁻¹ (Sarmiento & Gruber 2006), this corresponds to reductions of between 1 and 7%. The range reflects not only differences in the biological and physical models, but also from different assumptions about future climate forcing and sensitivity.

Keeling & Garcia (2002) suggested that natural warming (or cooling) of water masses in the ocean typically involves losses (or gains) of O₂ in a ratio of approximately 5 nmol J⁻¹, a ratio characteristic of the ocean's thermocline accounting for both thermal and biological impacts (e.g., Gruber et al. 2001). They also speculate that similar ratios may apply to future warming. Indeed, many models predict future O₂ changes characterized by a similar ratio of around 6 nmol of O₂ loss per Joule of ocean warming, regardless of differences in model details (see **Table 2**). This ratio is around four times larger than expected from solubility changes alone. However, recent results from the NCAR model (Fröhlicher et al. 2009) yield O₂ changes only twice as large as expected from solubility alone. Plattner et al. (2002) suggest the O₂/heat ratio will decrease substantially over the next century, as the oceans continue to warm.

The models also provide insight into the possible patterns of O₂ change in the ocean interior. In detail, there are large differences between models, but some features common to two or more models bear mentioning. In the deep North Atlantic, several models predict that O₂ will decline over the next century (e.g., by ~30 μmol kg⁻¹), associated with reductions in NADW formation (Plattner et al. 2001, Fröhlicher et al. 2009). Brennan et al. (2008) propose using this change as a means to improve detection of overturning changes. In the Southern Ocean, several models predict that O₂ will decrease at 200–400 m around 60°S, associated with reduced Antarctic convection (Matear et al. 2000, Plattner et al. 2001, Matear & Hirst 2003, Fröhlicher et al. 2009). In

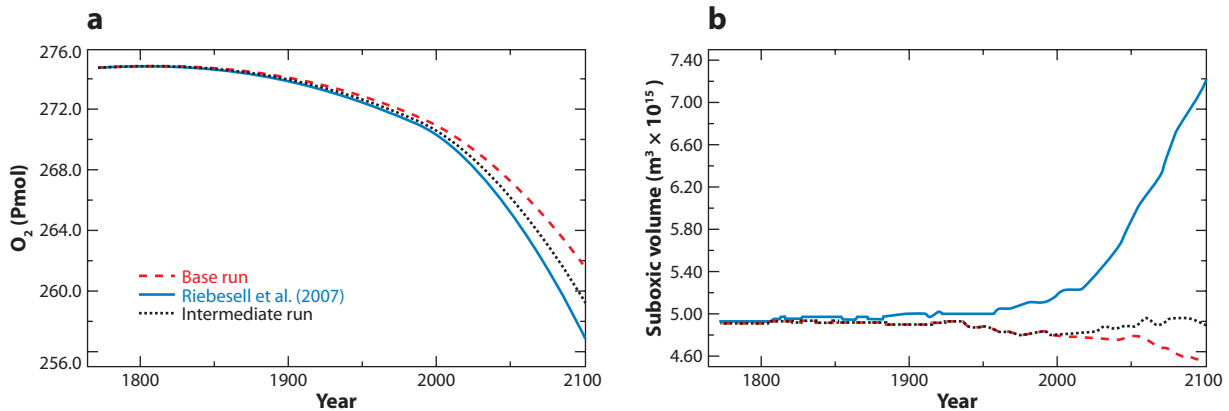


Figure 5

Changes in (a) the oceanic oxygen inventory and (b) volume of suboxic waters, here defined by $O_2 < 5 \mu\text{mol L}^{-1}$ as simulated by the UVic model. Red dashed lines refer to the base run with constant C/N ratios, which predicts declining suboxic volume with global warming. Solid blue lines refer to a run with C/N ratios increasing with $p\text{CO}_2$ roughly per Riebesell et al. (2007), which shows a marked increase in suboxic volume with global warming. Dotted black lines refer to an intermediate run with C/N ratios varying only poleward of 35° latitude. Adapted from Oschlies et al. (2008).

the North Pacific, a fairly consistent prediction is that O_2 will decline significantly (e.g., by up to $50 \mu\text{mol kg}^{-1}$) in the 200–400 m depth range, particularly in the subarctic waters, presumably associated with increasing stratification in the Pacific subarctic region (Plattner et al. 2001, Fröhlicher et al. 2009). In the tropical thermocline, most models predict relatively small changes, with some models predicting increases and others decreases in specific water masses. Some models predict a contraction in the extent of tropical OMZs despite overall ocean O_2 declines, as illustrated in **Figure 5**.

A few models have been run for much longer periods, extending hundreds or thousands of years into the future under business-as-usual scenarios. These show continuing deoxygenation for 1000 years or more into the future, even after atmospheric CO_2 stops rising. This longer timescale is dictated by the slow turnover of the deep waters. The declines in the total O_2 inventory are as large as 30%, with large increases in the extent of hypoxia and suboxia (Matear & Hirst 2003, Schmittner et al. 2008, Shaffer et al. 2009).

Given the known limitations of coarse-resolution ocean models in simulating today's O_2 distribution (e.g., Jin & Gruber 2003), the model predictions on all time and space scales are speculative. The depiction of the tropical OMZs is especially challenging because the models do not resolve the tropical jets relevant to O_2 supply. Coarse-resolution models typically suffer from excessive diapycnal mixing in the thermocline, which may lead to excessive upwelling and nutrient trapping in the subsurface. Gnanadesikan et al. (2007) show that a common feature of coarse resolution models is a tendency for the ventilation age in the tropical thermocline to decrease under global warming due to reduced upwelling of old deep waters at low latitudes. This process likely accounts for the O_2 increases seen in some of the models. Given that this mechanism is tied to high rates of diapycnal mixing, it seems likely to be a model artifact. Predicted changes in tropical OMZs also hinge on poorly constrained aspects of biogeochemistry, such as dependency of the maximum photosynthetic rate on water temperature (Matear & Hirst 2003), the dependency of particle sinking rates on acidification via mineral ballasting effects (Hofmann & Schellnhuber 2009), and the dependency of C/N ratios of marine organic carbon on $p\text{CO}_2$ (Oschlies et al. 2008). The sensitivity to C/N ratios is illustrated in simulations shown in **Figure 5**.

Major questions involve the impact of changes in wind forcing on circulation, aspects of which cannot yet be properly accounted for in coarse-resolution models (Böning et al. 2008). The westerlies have shifted polewards and strengthened over the past 40 years, partly as a result of rising CO₂ and partly as a result of stratospheric ozone loss (Gillett & Thompson 2003). Further wind shifts seem possible in the future (Toggweiler & Russell 2008). One school of thought argues that this will lead to a strengthening of the Atlantic deep overturning circulation, which is sensitive to the strength of the wind stress on the Antarctic Circumpolar Current (ACC) (Toggweiler & Russell 2008). So the prediction that global warming will weaken the Atlantic overturning and the implications of such weakening for ocean O₂ does not rest on a completely secure footing.

Models suggest that wind changes over the past few decades have caused increased upwelling of deep waters around Antarctica, reducing the net uptake of CO₂ in the Southern Ocean (Wetzel et al. 2005, Lovenduski et al. 2007, Le Quéré et al. 2008) while increasing the uptake of O₂ (Lovenduski et al. 2008). Wind changes may also account for increased thermocline ventilation in the South Indian and Pacific over the last 10 or 20 years via an acceleration in the circulation of Subantarctic mode water (Oke & England 2004, McDonagh et al. 2005, Murata et al. 2007), which is also a major source water to the eastern tropical Pacific (Toggweiler et al. 1991). If these effects dominated globally, we might expect the oceans as a whole, via the Antarctic response to wind changes, to become better ventilated in a warming world. So far, no model has predicted such a global response, but the uncertainties are large.

THE PAST OCEAN—CLUES FROM THE GEOLOGIC RECORD

The geologic record provides ample evidence of changes in ocean O₂ occurring throughout Earth's history, including episodic widespread anoxia. We restrict our attention here, however, to changes of the late Pleistocene, where we have the benefit that critical boundary conditions influencing ocean O₂ levels, such as the configuration of the continents and atmospheric O₂ levels, were similar to today.

Ice core records show that during the cold periods of the Pleistocene, atmospheric CO₂ levels were lower by some 80 ppm compared to the more recent Holocene (Petit et al. 1999). The details of how this occurred remain controversial, but most viable mechanisms require that deep waters stored a larger allotment of carbon of respiratory origin (Sigman & Boyle 2000), which would require increases in deep ocean oxygen utilization. However, as there is little evidence for deep anoxia, the effect of increased O₂ utilization must have been partly countered by increases in O₂ solubility in colder water or through more efficient ventilation of O₂ versus CO₂ in regions of convection or through leads in sea ice (Stephens & Keeling 2000, Toggweiler et al. 2003).

At shallower depths, O₂ concentrations appear to have been greater during colder times, both during full glacial conditions as well as in the briefer stadial events, as indicated by changes in nitrogen isotopes (Ganeshram et al. 2002), laminations (Kennett & Ingram 1995, van Geen et al. 2003), apatite formation (Ganeshram et al. 2002), and Cd and Mo abundances (Dean et al. 2006) in marine sediments. Changes occurred both in the eastern North Pacific and Arabian Sea (Schulz et al. 1998). Perhaps most intriguingly, there is evidence for expanded OMZs compared to today during certain previous warm intervals. The pattern is complex. During the warm Bølling-Allerød warm period from ~15 ka to 13 ka BP, which followed a very abrupt warming, O₂ levels decreased off the central California coast but increased in the low O₂ waters off Baja California to the south. During previous warm interstadial events, in contrast, lower O₂ conditions were recorded more prominently off Baja but not to the north (van Geen et al. 2003). The patterns suggest that controls on low O₂ conditions in tropical OMZ in the North Pacific are partly decoupled from conditions

farther north, with both regions being capable of having lower O₂ levels than today under warm conditions.

Whether insight from these changes can be applied to future warming is far from clear, because the changes occurred mostly in association with transitions to a colder not warmer world, driven mostly by factors other than changing CO₂. Also, the records may not capture behaviors associated with rapid transient warming, such as dense waters becoming completely isolated as remnants of a colder climate, as seen for example in the CSIRO model (Matear & Hirst 2003). Nevertheless, the Pleistocene records paint a general picture of ocean warming reducing the ventilation of thermocline waters, including expansion of OMZs. The records thus tend to heighten concerns regarding the fate of the OMZs in a warming world.

THE PRESENT OCEAN—RECENT TRENDS

The database of dissolved O₂ in the ocean now comprises millions of individual measurements of varying quality, collected for diverse purpose by a wide range of programs. Despite data limitations, it is feasible to detect significant changes over time in some regions. A rich literature documenting O₂ changes has emerged in the past decade, as summarized in **Table 3** and **Figure 6**. The studies cover different time frames and regions, making a global synthesis difficult. We thus restrict our attention to several of the more noteworthy findings.

Open North Pacific

The region with the best-resolved changes is the North Pacific, where several records with annual or better resolution are available, some for as long as 50 years. Time series from mid-depth waters in the Oyashio current region off Japan (Ono et al. 2001, Watanabe et al. 2003) and at Station P in the Alaskan gyre (Whitney et al. 2007) are shown in **Figure 7**. Both records show long-term declines of order 7 μmol kg⁻¹ decade⁻¹ superimposed on a bidecadal oscillation. At densities of approximately $\sigma_T = 26.8$, the changes in the east are strongly correlated with those in the west with a lag of ~7 years, consistent with the timescale expected for waters to transit from west to east via the Subarctic Current system (Whitney et al. 2007). Long-term declines of similar magnitude have been observed in the Western Subarctic Gyre and the Okhotsk Sea (Andreev & Kusakabe 2001) showing that the changes have occurred over a wide expanse of the subarctic North Pacific. (See **Figure 4** for geographic references.)

Repeat hydrographic sections of the North Pacific provide a complementary perspective. Sections along 47°N, 165°E, and 147°W confirm that O₂ declines occurred throughout the subpolar waters from the mid-1980s to late 1990s (Emerson et al. 2001; Watanabe et al. 2001; Mecking et al. 2006, 2008). The 147°W transect, shown in **Figure 8**, shows that the O₂ declines extend into the subtropical gyre in the eastern Pacific (Emerson et al. 2001; Mecking et al. 2006, 2008). The largest declines are concentrated on the $\sigma_T = 26.6$ isopycnal level, near the base of the subarctic mode waters (Watanabe et al. 2001, Emerson et al. 2004, Mecking et al. 2008).

Modeling studies (Deutsch et al. 2006) and estimates of changing water ages based on chlorofluorocarbons (Watanabe et al. 2001, Mecking et al. 2006) indicate that changes in ventilation (in the broad sense) rather than changes in oxygen utilization are the dominant cause of the North Pacific O₂ variations. In the subpolar gyre, a major factor may be reduced outcropping and subduction (i.e., “ventilation in the narrow sense”) (Emerson et al. 2004; Deutsch et al. 2006; Mecking et al. 2006, 2008). The relevant density layers outcrop in the northwest corner of the Pacific, in the Okhotsk Sea, the western subarctic gyre, and the Oyashio region, where winter cooling drives

convection, restoring the O₂ content of these subsurface layers locally. This region is therefore critical to the O₂ supply throughout the North Pacific.

The bi-decadal variability in North Pacific O₂ appears strongly correlated with the North Pacific Index (NPI), a measure of the strength of the Aleutian low-pressure system, as well as with the 18.6-year nodal tide (Andreev & Baturina 2006, Yasuda et al. 2006). The nodal tide is caused by the precession of the moon's orbital axis, which modulates the strength of the diurnal tide. Changes in ventilation in the Northwest Pacific driven by variations in the diurnal tide is an appealing explanation for the bi-decadal O₂ variability (Andreev & Baturina 2006). The idea is that tidal mixing in the straits between the sea of Okhotsk and the open Pacific helps to break down the surface halocline, thus weakening surface stratification and promoting convection and ventilation (Yasuda et al. 2006). North Pacific ventilation rates are doubtlessly also influenced by atmospheric forcing. However, the correlation between O₂ and the NPI is hard to interpret in this context because the nodal tide may also influence the atmospheric pressure field via changes in sea-surface temperature and storm-track activity (Yasuda et al. 2006).

The longer-term declines in O₂ may be driven by reductions in ventilation tied to long-term freshening of subpolar Pacific surface waters (Freeland et al. 1997, Ono et al. 2001, Andreev & Watanabe 2002) and atmospheric warming in northeastern Asia (Nakanowatari et al. 2007). These longer trends may have contributions from both global warming as well as natural Pacific climate variability on 50-year timescales (Minobe 1999, Andreev & Kusakabe 2001).

O₂ concentrations on the $\sigma_T = 26.6$ isopycnal layer may be especially sensitive to variations in climate. Climatological data indicate that this is the densest layer to outcrop in the open North Pacific in winter (Emerson et al. 2004). The outcrop area is therefore highly sensitive to small changes in surface salinity, temperature, and mixing. Emerson et al. (2004) suggest that the $\sigma_T = 26.6$ layer may have ceased to ventilate following the climate regime shift of 1977.

Even if the recent O₂ variability in the North Pacific has been partly naturally driven, the implications for the future appear ominous. The declines over the past 50 years demonstrate that O₂ levels in the thermocline of the North Pacific are highly sensitive to climate changes. Whitney et al. (2007) have shown that the depth of hypoxia (taken as the 60 $\mu\text{mol kg}^{-1}$ surface) has shoaled from 400 to 300 m at station P from the 1950s to the present. Considering that O₂ levels within the North Pacific have probably not fully responded to climate changes that have occurred to date, and considering that large increases in precipitation and surface temperature are predicted for the coming century (Meehl et al. 2007), continuing O₂ decreases seem inevitable. The zone of hypoxia in the North Pacific is already the most extensive and the shallowest of any of the major oceans, so even relatively small declines may extend hypoxic conditions into critical habit of many species.

North Pacific Margin

Evidence of long-term deoxygenation has emerged from locations around the margins of the North Pacific. In the Japan/East Sea, between Korea and Japan, records from the 1960s to the 1990s show a long-term decline superimposed on bi-decadal variability (Gamo 1999, Watanabe et al. 2003). The changes are strikingly similar to those reported by Ono et al. (2001) in the Oyashio Region of the open Pacific despite the Japan/East Sea having isolated deepwater circulation (Watanabe et al. 2003). Watanabe et al. (2003) suggest that the similarity may arise because the formation of deepwater in the Japan/East Sea, which occurs via winter cooling in the north of the Sea, is also sensitive to climate variability tied to the NPI.

Significant O₂ declines have been reported at several locations along the western shelf of North America. In the upwelling system of the central Oregon coast ($\sim 44^\circ\text{N}$), a wide region of the inner



Table 3 Studies documenting ocean dissolved O₂ changes

Reference	Location	Latitude (degrees)	Longitude (degrees)	Depth (m)	Dates	Quantity	Ref. coord.	O ₂ change (μmol kg ⁻¹)
North Atlantic								
Garcia et al. (1998)	Subtropical North Atlantic	24.5N section	21–71W	700–1700	1981–1992	O ₂	Depth	-7
Johnson & Gruber (2007)	Eastern North Atlantic	30–66N	20W section	500–1000	1988–2003	AOU	Depth	-8
Stramma et al. (2008)	Labrador Sea	56–59N	50–54W	100–1000	1960–present	O ₂	Depth	No trend
North Pacific								
Emerson et al. (2001)	Eastern North Pacific	27–47N	152W section	120–700	1981–1997	AOU	Density	-8 to -32
Ono et al. (2001)	Oyashio domain	39–42N	143–145E	500–800	1969–1997	AOU	Density	-20 to -30
Andreev & Kusakabe (2001)	Western Subarctic Gyre	48–60N	160–170E	200–420	1950–2000	AOU	Density	-21
Andreev & Kusakabe (2001)	Okhotsk Sea–Kuroil Basin	47N	150E	200–420	1950–2000	AOU	Density	-38
Watanabe et al. (2001)	Western North Pacific	20–45N	165E section	300–700	1987–2000	AOU	Density	-10 to -70
Watanabe et al. (2001)	Subpolar North Pacific	47N section	148E–215E	120–250	1985–1999	AOU	Density	-10 to -80
Andreev & Watanabe (2002)	Western Subarctic Gyre	48–60N	160–170E	220–380	1952–2000	AOU	Density	-15
Andreev & Watanabe (2002)	Alaskan Gyre	49–59N	141–150W	220–380	1952–2000	AOU	Density	-15
Keller et al. (2002)	Entire North Pacific			300–500	1970s–1990s	AOU	Density	No trend
Mecking et al. (2006)	Eastern North Pacific	24N section	118–153W	150–550	1991–2000	AOU	Density	-24 to +16
Mecking et al. (2006)	Eastern North Pacific	21–45N	152W section	100–500	1991–1997	AOU	Density	+8 to -16
Osafune & Yasuda (2006)	Oyashio domain	40–43N	143–146E	$\sigma_T = 26.8$	1935–1998	AOU	Density	-58
Whimney et al. (2007)	Station PAPA	50N	145W	100–400	1956–2006	O ₂	Density	-20 to -35
Nakanowatari et al. (2007)	Okhotsk Sea	44–54N	144–154E	$\sigma_T = 26.8$ to 27.4	1960–2002	AOU	Density	-11 to -29
Nakanowatari et al. (2007)	Oyashio domain	39–44N	142–149E	$\sigma_T = 26.8$ to 27.4	1960–2002	AOU	Density	-5 to -16
Nakanowatari et al. (2007)	Subarctic Current	41–49N	51–72E	$\sigma_T = 26.8$ to 27.4	1960–2002	AOU	Density	-6 to -14
Mecking et al. (2008)	Eastern North Pacific	27–55N	152W section	150–550	1984–2006	AOU	Density	-10 to -25
Mecking et al. (2008)	Subtropical/tropical gyre boundary	25–27N	152W section	150–550	1984–2006	AOU	Density	0 to +20
Mecking et al. (2008)	Subtropical North Pacific	30N section	140–180W	250–750	1994–2004	AOU	Density	0 to -20

Tropical Waters										
Peng et al. (1998)	Tropical Indian	20S–5N	80E	300–1000	1978–1995	O ₂	Density	+3 to –11		
Stramma et al. (2008)	Tropical North Atlantic	10N–14N	20–30W	300–700	1960–2006	O ₂	Depth	–16 ± 6		
Stramma et al. (2008)	Equatorial Atlantic	3S–3N	18–28W	300–700	1960–2006	O ₂	Depth	–9 ± 5		
Stramma et al. (2008)	Tropical South Atlantic	8S–14S	4–12E	300–700	1960–2006	O ₂	Depth	–8 ± 6		
Stramma et al. (2008)	Eastern equatorial Pacific	5S–5N	105–115W	300–700	1960–2006	O ₂	Depth	–6 ± 15		
Stramma et al. (2008)	Central equatorial Pacific	5S–5N	165–175W	300–700	1960–2006	O ₂	Depth	–8 ± 9		
Stramma et al. (2008)	Tropical Indian	5S–Eq.	90–98E	300–700	1960–2006	O ₂	Depth	–4 ± 10		
South Pacific										
Shaffer et al. (2000)	Eastern South Pacific	28S	72 to 82W	800–1200	1967–1995	O ₂	Density	–8 to –12		
Murata et al. (2007)	South Pacific	32S section	152E to 171W	$\sigma_T = 26.9$	1992–2003	AOU	Density	+2 to +9		
South Indian Ocean										
Bindoff & McDougall (2000)	Subtropical South Indian	32S section	30–115E	300–800	1962–1987	O ₂	Depth	–8		
McDonagh et al. (2005)	Subtropical South Indian	32S section	30–115E	400–1300	1987–2002	O ₂	Theta	+8		
Southern Ocean										
Matear et al. (2000)	Southern Ocean	50–60S	110–170E	400	1968–1995	O ₂	Density	–10		
Aoki et al. (2005)	Southern Ocean	30–66S	30–55E	400	1960–1980 to 1980–1996	O ₂	Density	0 to –20		
Aoki et al. (2005)	Southern Ocean	38–63S	100–120E	400	1960–1980 to 1980–1996	O ₂	Density	0 to –40		
Aoki et al. (2005)	Southern Ocean	40–66S	140–160E	400	1960–1980 to 1980–1996	O ₂	Density	+20 to –65		
Jacobs (2006)	Southern Ocean									
Coastal Waters										
Gamo (1999)	Eastern Japan Sea Basin	42N	138E	2000–3500	1965–1998	O ₂	Depth	–21		
Watanabe et al. (2003)	Eastern Japan Sea Basin	40–43N	136–139E	2000–3500	1961–2001	O ₂	Depth	–20		
Watanabe et al. (2003)	Yamato Basin, Japan Sea	37–39N	134–136E	>2000	1961–2001	O ₂	Depth	–13		
Gilbert et al. (2005)	St. Lawrence estuary	49N	68W	295–355	1932–2003	O ₂	Depth	–65		
Whitney et al. (2007)	Station P4	49N	127W	150	1987–2006	O ₂	Density	–23		
Monteiro et al. (2008)	Benguela shelf	23S	14E	100	1994–2003	O ₂	Depth	No trend		
Chan et al. (2008)	Oregon Coast	42–46N		<100	1950–2006	O ₂	Depth	≈40		
Bograd et al. (2008)	Southern California Current System	30–35N	118–124W	200–300	1984–2006	O ₂	Depth	–11 to –33		



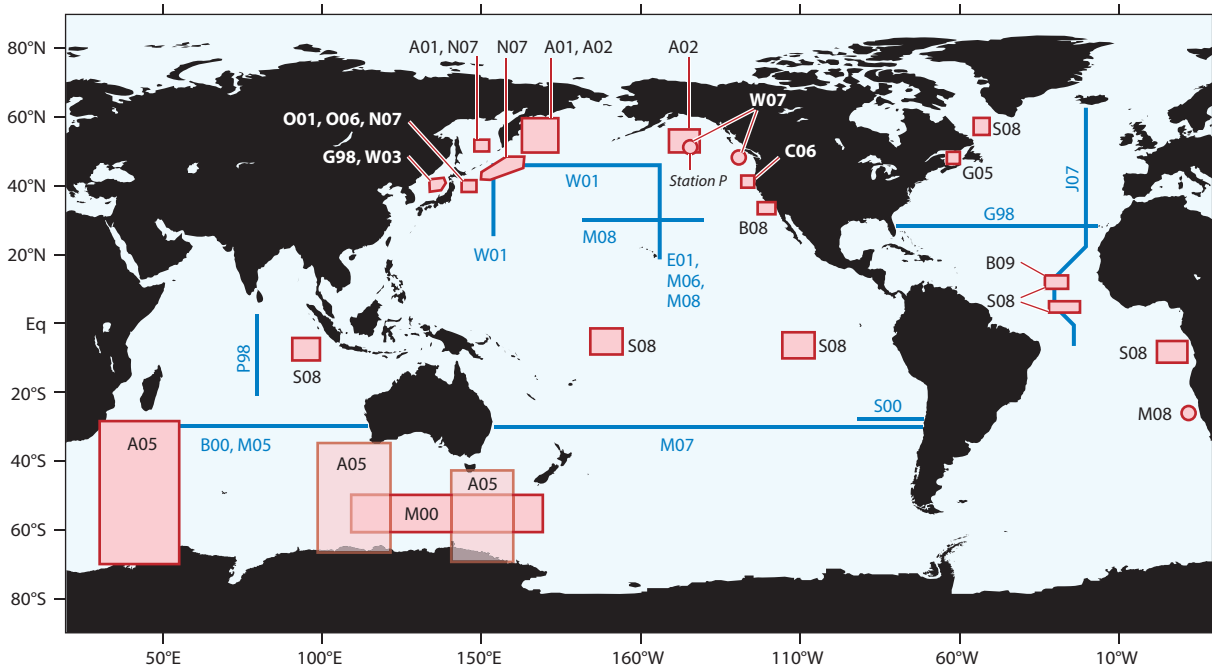


Figure 6

Location of studies examining changes in dissolved O_2 . Labeling uses the first letter of first author's last name and a two-digit year; e.g., W07 refers to Whitney et al. (2007). See **Table 3** for further details. Open ocean and coastal studies not driven by eutrophication are indicated. See Diaz & Rosenberg (2008) for a comprehensive map of coastal studies.

shelf (<70m) was exposed to severe hypoxia in 2002, resulting in massive fish and crab die-offs (Grantham et al. 2004). Surveys off central Oregon in 2006 revealed the widespread occurrence, not just of hypoxia, but also anoxia. Such occurrences of anoxia and widespread hypoxia appear unprecedented in the five previous decades (Chan et al. 2008). At station P4 (49°N), located in 1300 m of water off British Columbia, an O_2 decline of $12 \mu\text{mol kg}^{-1} \text{decade}^{-1}$ from 1987 to 2006 was found on $\sigma_T = 26.7$, nearly twice the trend seen at Station P in the Alaskan Gyre (Whitney et al. 2007). Declines of similar magnitude were noted from 1984 to 2004 over an array of stations off the coast of Southern California near 33°N (Bograd et al. 2008), as shown in **Figure 9**. The declines were associated with a shoaling of the depth of hypoxia by up to 100 m, particularly in the near-shore regions.

The O_2 declines on the North American shelf appear to have resulted from a combination of factors acting in concert. O_2 has declined in the primary source waters feeding the coastal upwelling, including the southward flowing California Current and the deeper, northward flowing California Undercurrent (Whitney et al. 2007, Bograd et al. 2008, Chan et al. 2008) (see **Figure 4**). The changes on the shelf may therefore have a connection with O_2 declines observed as far away as the subarctic and equatorial Pacific. Local factors are probably also involved. As suggested by Bakun & Weeks (2004), increased longshore wind strength tied to global warming may be increasing upwelling and O_2 demand on the shelf by fueling enhanced export production. In the coastal waters of Southern California, surface warming may have increased stratification, reducing ventilation of subsurface waters on the shelf (Bograd et al. 2008). It is worrisome that all of these factors may be amplified in the future by continued global warming.

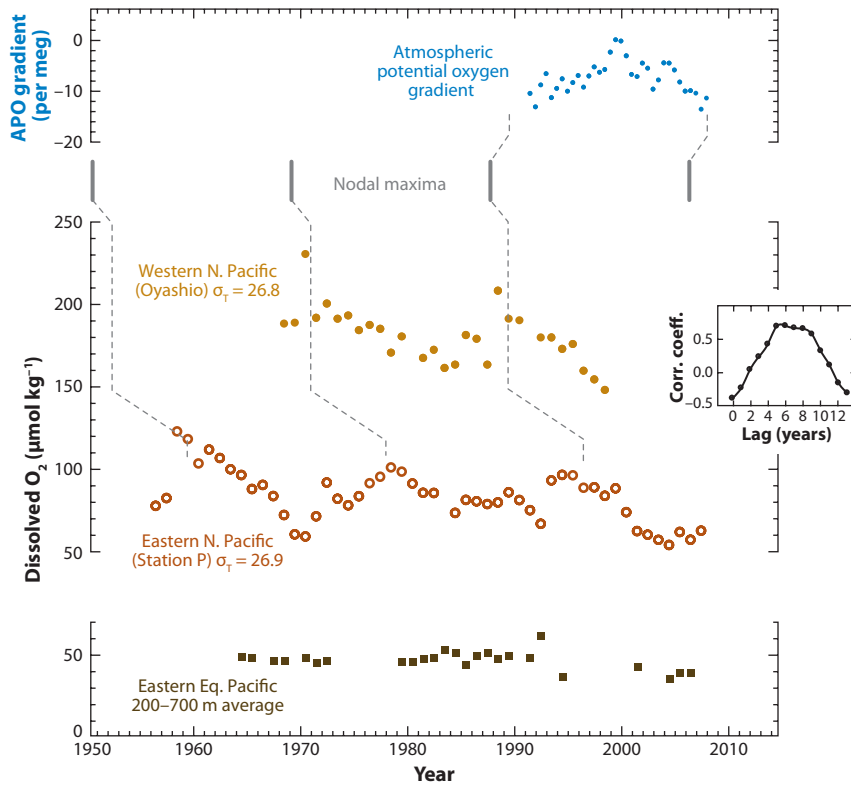


Figure 7

Dissolved O_2 in the western North Pacific in the Oyashio Current region ($\sim 39^\circ\text{--}42^\circ\text{N}$, $143^\circ\text{--}145^\circ\text{E}$) (Ono et al. 2001, Watanabe et al. 2003), in eastern North Pacific at Station P (50°N , 145°W) (Whitney et al. 2007), and in the eastern equatorial Pacific ($3^\circ\text{S--}3^\circ\text{N}$, $105^\circ\text{--}115^\circ\text{W}$) (Stramma, pers. commun.). The points at Station P are calendar year averages (based on daily data provided by Whitney (pers. commun.)). Inset: Lagged correlation between eastern and western O_2 time series. Top Panel (blue): Interhemispheric gradient in atmospheric potential oxygen (APO) (north minus south) from the Scripps O_2 program. Northern value from average of Alert Station (82°N , 63°W) and La Jolla (33°N , 117°W). Southern value from Cape Grim (41°S , 145°E). APO points are annual averages shown at 6-month intervals. Time of maxima nodal tide (based on K1 amplitude) also shown, with dotted lines to show phase relationships.

Tropical Oceans

Stramma et al. (2008) constructed 50-year time series of O_2 in selected regions of OMZs in the tropical Atlantic, Pacific, and Indian oceans using both historical and recent observations. In the Atlantic and Pacific, downward trends in O_2 of 0.9 to $3.4 \mu\text{mol kg}^{-1} \text{decade}^{-1}$ were found in the 300 to 700 m layer, accompanied by a vertical expansion of the zone of hypoxia, including a shoaling of the depth of the $60 \mu\text{mol kg}^{-1}$ horizon from 245 to 170 m in the eastern Pacific region. In the tropical Indian Ocean, the trends found by Stramma were not significant. Stramma et al. speculate that a combination of thermal, biological, and dynamical factors may be involved in the tropical changes. Brandt et al. (P. Brandt, V. Hormann, A. Körtzinger, M. Visbeck, G. Krahnemann, et al., unpublished paper) found a significant weakening in the eastward, north-equatorial jet at 9°N in the Atlantic between the periods 1972–1985 and 1999–2008 that was associated with reduced oxygen supply to the eastern tropical North Atlantic. A possible explanation may be changes in the

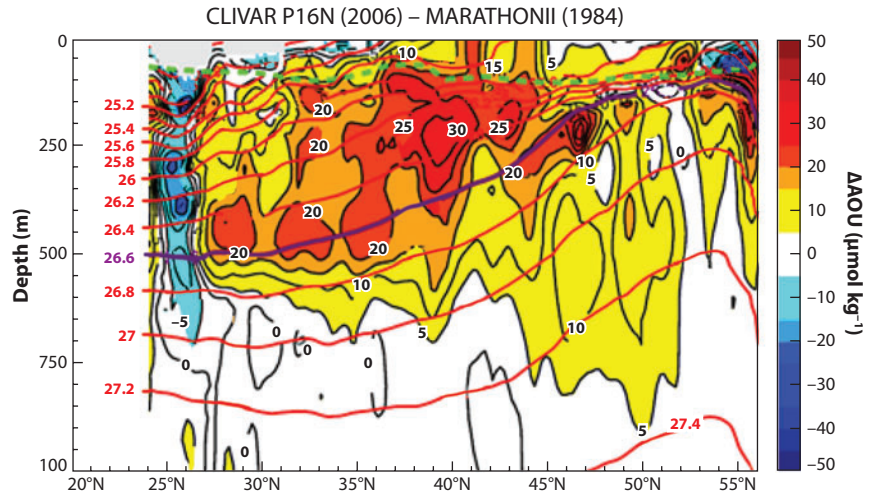


Figure 8

Changes in apparent oxygen utilization (AOU) in the North Pacific along 147°W from 1984 to 2006. Differences were computed on density surfaces and then projected onto depth. Isopycnals are shown as red or purple contours. Winter mixed-layer depth shown as green dashed line. Note that largest declines are seen along the $\sigma_T = 26.6$ isopycnal surface. Adapted from Mecking et al. (2008).

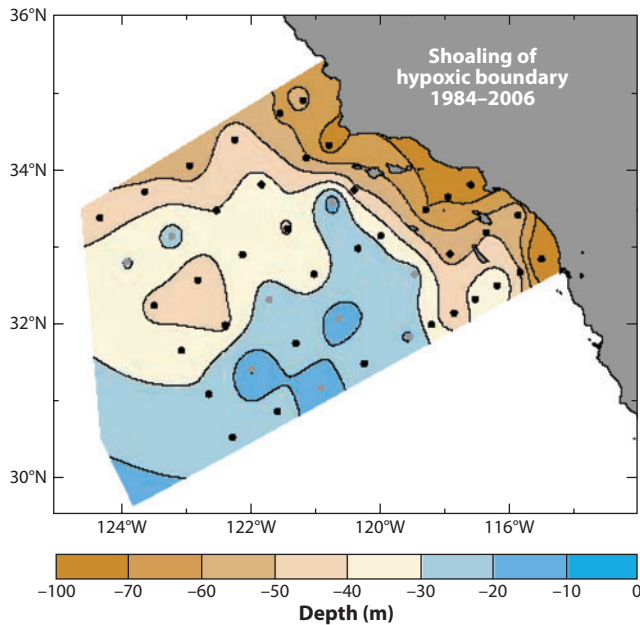


Figure 9

Change in depth in meters of the hypoxic boundary ($60 \mu\text{mol kg}^{-1}$ threshold) from 1984 to 2006 based on linear trends in O_2 versus time at hydrographic stations (black dots). Adapted from Bograd et al. (2008).



wind forcing associated with the Atlantic Multidecadal Oscillation (AMO) (Foltz & McPhaden 2008).

More work is also needed to resolve changes in the horizontal extent of the tropical OMZs. Deutsch et al. (2006) suggested that the tropical/subtropical gyre boundary in the North Pacific shifted equatorwards from the 1980s to the 1990s, associated with a wind-driven strengthening of the subtropical gyre circulation. This shift was the apparent cause of increased O₂ found in the North Pacific near 26°N between 150 to 700 m depth from 1984 to 2006 by Mecking et al. (2008) (**Figure 8**). Systematic shifts in the subtropical/tropical gyre boundary could have a large impact on the area and volume of the ocean impacted by low-O₂ waters. The impact of long-term global warming on this boundary is unclear.

Other Studies

Outside the North Pacific and the tropics, the evidence for systematic long-term O₂ changes is weaker. In the thermocline of the South Indian Ocean, O₂ decreased from 1962 to 1987 (Bindoff & McDougall 2000) but then increased 1987 to 2002, paralleling a similar reversal in salinity and temperature associated with decadal variations in ventilation and gyre circulation (McDonagh et al. 2005). A similar recent O₂ increase has been seen in the South Pacific (Murata et al. 2007). In the North Atlantic, an O₂ decrease from 1988 to 2003 near the base of subpolar mode waters has been attributed to changes in the displacements of subpolar and subtropical water masses and possibly also to changes in the intensity of convection associated with the North Atlantic Oscillation (NAO) (Johnson & Gruber 2007). In the Antarctic, a significant decline has been noted from approximately 1970 to 1990 in the waters beneath the base of the winter mixed layer in the Polar Front Zone, possibly tied to increased stratification (Matear et al. 2000, Aoki et al. 2005, Jacobs 2006) or increased wind-driven upwelling (Lovenduski et al. 2008) and similar to predictions of models under global warming (Matear et al. 2000, Plattner et al. 2001, Matear & Hirst 2003, Fröhlicher et al. 2009).

A consistent finding is that the main driver of recent O₂ changes has been physical circulation rather than changes in export production. Natural decadal variability is more clearly evident in most cases than long-term trends. A high level of natural O₂ variability tied to physical causes is consistent with model studies (McKinley et al. 2003, Deutsch et al. 2006, Friedrich et al. 2006, Verdy et al. 2007, Lovenduski et al. 2008, Fröhlicher et al. 2009). The most sensitive layers appear to be those near the base of the subpolar mode waters, which are ventilated over very small areas at rates very sensitive to small changes in surface conditions. This is true in the North Pacific as well as elsewhere. A greater tendency to find declines rather than increases in O₂ can be noted in **Table 3**. It remains difficult, however, to draw firm conclusions about global trends.

ATMOSPHERIC O₂ MEASUREMENTS

A direct link exists between changes in ocean and atmospheric O₂ inventories. At the global or basin scale, the net air-to-sea flux of O₂ in mol yr⁻¹, F_{O₂}, is related to the change in ocean O₂ inventory, I, according to

$$dI/dt = F_{O_2} + \alpha dC_{org}/dt \quad (1)$$

where C_{org} is the oceanic inventory of organic carbon, including both particulate and dissolved forms, and α is the O₂/C oxidative ratio for destruction or production of marine organic matter, e.g., (Körtzinger et al. 2001), and where small terms related to river and sediment transports have been neglected (Keeling & Garcia 2002). The term dC_{org}/dt accounts for the column- and

area-integrated net production of O_2 by marine photosynthesis and respiration, thus measuring the extent to which the ocean is net heterotrophic or autotrophic. This term is typically small, although not necessarily negligible, because the main effect of the marine biological pump is to redistribute inorganic materials within the ocean, rather than to cause accumulation or destruction of organic carbon. The change in O_2 inventory must therefore be approximately equal to the net air-to-sea O_2 flux ($dI/dt \approx F_{O_2}$). Locally, a balance similar to Equation (1) also holds, if transport of O_2 and C_{org} within the ocean is also taken into account.

Precise measurements atmospheric the O_2 concentration (reported as O_2/N_2 ratio) started in 1989 at La Jolla, California, followed by a measurements at a growing number of background air stations to the present day (Keeling & Shertz 1992, Battle et al. 2006, Tohjima et al. 2008). Such measurements show that atmospheric O_2 is decreasing at a rate largely explained by the O_2 loss due to fossil-fuel burning but also influenced by long-term exchanges with the land biosphere and oceans. In relative terms, the annual decrease is very small, amounting to approximately 20 molecules of O_2 for each million O_2 molecules in the air. Superimposed on this decrease are seasonal cycles, gradients, and interannual variability, which contain a rich spectrum of information on ocean and land exchanges, including information relating to exchanges of O_2 with the oceans (Keeling et al. 1996, Battle et al. 2006).

The exchanges of O_2 and CO_2 with the land biosphere are strongly correlated with a molar O_2/C exchange ratio of approximately 1.1, dictated by the stoichiometry of photosynthesis and respiration (Severinghaus 1995). In contrast, the exchanges of O_2 and CO_2 across the air-sea interface are not strongly correlated, owing to the complex interplay of biological and thermal processes and complexities of the inorganic chemistry of the CO_2 system in seawater.

By combining O_2 and CO_2 data, one can compute the tracer “atmospheric potential oxygen” (APO), defined according to $APO = O_2 + 1.1CO_2$ (Stephens et al. 1998). By design, APO is insensitive to exchanges with the land biosphere, which by virtue of the nearly fixed stoichiometry, tends to produce compensating changes in O_2 and CO_2 . APO can be influenced by air-sea exchanges of CO_2 , O_2 , and N_2 , as well as by O_2 and CO_2 exchanges caused by fossil-fuel burning, which has a characteristic O_2/C ratio of approximately 1.4 in the global mean, but which varies by fuel type. APO extracts the new information provided by O_2 data beyond that provided by CO_2 data.

Trends in the APO concentration at two stations, one in each hemisphere, are shown in **Figure 10**, showing a long-term downward trend as well as seasonal cycles. The downward

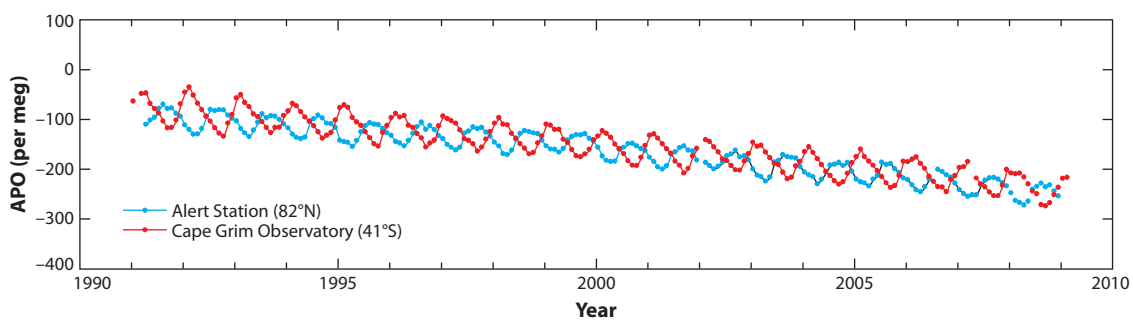


Figure 10

Trends in atmospheric potential oxygen (APO) based on monthly averages of measurements from the Scripps O_2 program. The seasonal cycles largely reflect exchanges of O_2 with the oceans. The APO concentration (δAPO) is expressed following Manning & Keeling (2006): $\delta APO = \delta(O_2/N_2) + 1.1/(0.2095) X_{CO_2}$ where $\delta(O_2/N_2) = (O_2/N_2)/(O_2/N_2)_{reference} - 1$ and X_{CO_2} is the CO_2 mole fraction in dry air. δAPO is multiplied by 10^6 and expressed in “per meg” units. The factor 1.1 is the assumed O_2/C exchange ratio with land biota and 0.2095 is the nominal O_2 mole fraction in dry air, needed for unit conversion between $\delta(O_2/N_2)$ and mole-fraction units.

trend results mostly from fossil-fuel burning and ocean uptake of CO₂, with small contributions from long-term air-sea exchanges of O₂ and N₂ (Manning & Keeling 2006). The seasonal cycles in APO are predominantly caused by air-sea exchange of O₂, making this a tracer of seasonal variations in upper-ocean biological production and ventilation. The APO cycles, now recorded at more than 20 stations around the world, provide a means to detect changes in processes influencing ocean O₂ supply.

As seen in **Figure 10**, the seasonal cycles in APO are out of phase between the hemispheres such that the interhemispheric gradient in APO undergoes a large seasonal cycle. On an annually averaged basis, however, the gradient is not zero. This annual-mean gradient provides a constraint on the meridional fluxes of O₂ with the ocean, including fluxes related to deep ventilation (Stephens et al. 1998). As shown in **Figure 7**, the gradient increased from 1991 to 1999 by approximately 10 per meg and then fell from 1999 to 2008 by approximately 10 per meg, returning to near the initial value. The ~17-year oscillation has an intriguing resemblance to the changes seen in dissolved O₂ in the North Pacific. Indeed, the sense of the changes is also consistent with the timing of ventilation increases related to tidal mixing; i.e., APO is relatively low in the Northern Hemisphere during years following nodal maxima, etc., as expected due to enhanced ocean ventilation at this time. The changes likely reflect exchanges not just with the North Pacific, but also with the North Atlantic and the Southern Ocean so the data may defy a simple interpretation, although variations in ventilation are the implicated cause (Hamme & Keeling 2008). Using atmospheric transport models, the APO variations can be analyzed using “inversion calculations” to obtain constraints on large-scale fluxes of O₂ (Rödenbeck et al. 2008). A primary application of atmospheric O₂ (or APO) measurements is the partitioning of the total global CO₂ sink into land and oceanic components. The application, however, is sensitive to uncertainties in the long-term fluxes of O₂ between the atmosphere and oceans. The issue can be understood in relation to the downward trend in APO: To resolve the contribution from ocean CO₂ uptake requires accounting for the other terms, including air-sea exchange of O₂. Interestingly, if the air-sea O₂ term is assumed to be zero, the oceanic sink that is obtained is smaller by approximately $0.5 \pm 0.5 \text{ Pg C yr}^{-1}$ than estimated independently from ocean tracer data (Sabine et al. 2004, Manning & Keeling 2006, Gruber et al. 2009). Optimal agreement is obtained between the atmospheric and ocean tracer methods if the oceans are losing $\sim 40 \text{ Tmol O}_2 \text{ yr}^{-1}$, which is comparable to the ocean O₂ loss calculated from recent ocean warming of $6 \times 10^{21} \text{ J yr}^{-1}$ (Domingues et al. 2008) assuming a scaling of $6 \text{ nmol O}_2 \text{ J}^{-1}$. The comparison therefore supports the hypothesis that warming is triggering ocean deoxygenation, although the uncertainties are large.

Equation (1) shows that if it were possible to directly determine the changes in the ocean inventory of O₂ and C_{org}, the global net air-sea O₂ flux would be determined, thus improving the basis for estimating land (and ocean) CO₂ sinks from atmospheric O₂ data. A key need is thus to develop in situ methods for tracking changes in the O₂ inventory. Most of the organic matter in the ocean is thousands of years old and probably inert, but this organic pool should also be tracked because the pool is large.

RESEARCH CHALLENGES

The threat of future ocean deoxygenation is important, both because of the direct environmental consequences of the O₂ changes as well as because of the implications for carbon cycle studies. Here we discuss briefly some of the important related research opportunities and challenges.

Towards an Ocean O₂ Observing System

An ambitious international program is now underway to track changes in ocean biogeochemistry and carbon cycling from repeated ship-based hydrographic measurements under the Climate Variability and Predictability (CLIVAR) Repeat Hydrography Program. The program involves reoccupying, roughly once or twice per decade, many of the hydrographic sections sampled in the 1990s under the World Ocean Circulation Experiment (WOCE). The program provides a means to measure the decadal changes in a wide suite of critical biogeochemical tracers, such as carbon species, nutrients, trace elements, etc., that are not easily measured by other means. However, despite the ambitious sampling of the CLIVAR program, it may take 20 or 30 years, continuing in this mode, to reliably establish the magnitude and severity of long-term O₂ trends that impact ecosystems and complicate carbon budgeting. Prior studies of O₂ variability illustrate well the difficulty of resolving long-term trends against a background of natural variability from infrequently repeated surveys. Ocean time series stations, such as at Station P, can more easily resolve long-term trends, but are inherently limited to a regional perspective.

With the recent advent of reliable and stable seawater O₂ sensors, such as the “optode” (Tengberg et al. 2006) and with the existence of the broad-scale global Argo array of profiling floats (Gould et al. 2004), a major leap is now possible in the observation of oceanic O₂ distributions and variability (Körtzinger et al. 2004, 2005; Gruber et al. 2007; Johnson et al. 2009). The Argo array provides high-quality measurements of temperature and salinity of the upper 2000 m of the ocean with nearly global coverage. If only 10% of the current array of more than 3000 floats were equipped with O₂ sensors, more than 10,000 profiles with 750,000 high-quality oxygen measurements in the upper 2000 m could be made in a single year. This would exceed the pace of measurements by the CLIVAR repeat hydrography program by almost a factor of 4 and also provide a three-dimensional synoptic and time-dependent picture of the global oceanic oxygen distribution, and hence overcome the limitations of the spatial and temporal aggregation of sparse shipboard measurements.

The goal of detecting long-term changes in oceanic O₂ places serious demands on the accuracy and long-term stability of the sensors. The target precision must allow detecting trends at the level of a few $\mu\text{mol kg}^{-1} \text{decade}^{-1}$, requiring high long-term stability and accuracy. To date, several Argo floats with O₂ sensors have been deployed. The applications thus far have mostly been limited to seasonal studies in the upper ocean, which place less stringent demands on stability and accuracy, but nevertheless compellingly demonstrate the value of such measurements (Körtzinger et al. 2004, Martz et al. 2008, Riser & Johnson 2008).

The most important issues for oxygen sensor technology are accuracy and long-term drift. Major improvements have been made in this regard. However, both competing technologies, i.e., Clark-type electrochemical versus optode-based sensing principles, still exhibit shortcomings in either accuracy or drift (Gruber et al. 2007). Further work on the improvement and characterization of these sensors is ongoing. In particular, the optode principle, only recently introduced in the field of oceanography, has room for significant improvement and hence high potential. On the other hand, it remains unclear whether the required long-term accuracy of a few $\mu\text{mol kg}^{-1} \text{decade}^{-1}$ can be achieved by a sensor and float-based autonomous observatory. More work is needed to push this technology to its limits including innovative ways of in-situ calibration, e.g., against air (Körtzinger et al. 2005).

The most promising approach would consist of a combination of the Repeat Hydrography Program and synoptic three-dimensional ARGO-based oxygen observatory, with the former providing more easily assessable long-term accuracy and the latter resolving scales of natural variability, knowledge of which is important in deconvoluting observations.



Determining Ocean CO₂ Uptake

A central goal of the CLIVAR Repeat Hydrography Program is to quantify the global CO₂ sink in order to establish the sensitivity of this sink to changing climate and biogeochemistry. In concept, the approach is very simple, relying on direct measurements of the increase in the dissolved inorganic content (DIC) of the water. The approach is one of several being pursued, including the atmospheric O₂ method, described above. But even as the CLIVAR program is proceeding, it remains unclear how best to use the DIC and complementary tracer data to quantify uptake.

The emphasis to date has been on tracking the uptake of “anthropogenic CO₂,” i.e., the uptake driven by rising atmospheric CO₂ but excluding contributions from internal ocean processes, such as changes in the biological pump. Concurrent measurements of dissolved O₂ are typically used to correct for the change in DIC driven by variations in respiratory carbon, thus making it possible to detect changes driven by the atmospheric CO₂ input despite internal variability (Peng et al. 1998). But this raises questions when systematic changes in O₂ also occur: To what extent does the resulting estimate of CO₂ uptake include contributions from changing circulation and biology? Are corrections needed for changes in ocean O₂ inventory (Keeling & Garcia 2002)? The challenge posed by systematic changes in O₂ was confronted recently in studies in the South and North Pacific (Murata et al. 2007, Sabine et al. 2008), but these questions remain largely unresolved (see, e.g., Levine et al. 2008). In any case, the relevant goal for assessing the sensitivity of the ocean CO₂ sink to climate changes is to determine the total CO₂ sink from the combination of all processes, including changes in circulation and the biological pump. These are most likely missed to some extent by existing techniques and a suitable method remains to be developed.

The possibility of augmenting the CLIVAR repeat hydrography program with additional measurements of O₂ from profiling floats suggests a possible way forward. The first step is to combine measurements of DIC and O₂ from repeat hydrographic measurements to form a quasi-conservative tracer with low internal variability. Although many tracer variants are possible, a suitable choice for illustration purposes is the “ocean potential oxygen” (OPO) tracer, which we define as

$$\text{OPO} = \text{O}_2 + \alpha(\text{DIC} - 1/2 \text{ALKn}) \quad (2)$$

where ALKn is the nitrate-corrected total alkalinity and α is the O₂/C ratio for formation/destruction of marine organic matter. OPO is conserved with respect to marine photosynthesis/respiration, which produces compensating effects on O₂ and DIC. OPO is also conserved with respect to carbonate precipitation/dissolution, which produces compensating effects on DIC and ALKn. OPO is influenced mainly by air-sea exchanges of O₂ and CO₂ across the air-sea interface. OPO is a close analogue of APO, being conservative with respect to marine rather than terrestrial photosynthesis/respiration but responding to air-sea fluxes of both O₂ and CO₂. (Note that OPO is essentially the same as the tracer C* introduced by Gruber et al. 1996.)

The second step is to integrate the changes in OPO, determined via repeat hydrography, over the basin to determine the change in the OPO inventory. From the definition of OPO, this inventory change can be seen to contain three terms, corresponding to the changes in the inventories of DIC, O₂, and alkalinity (ALKn). The sum of ALKn and DIC terms can easily be shown to be a measure of the total CO₂ uptake from the atmosphere, whether “anthropogenic” or otherwise. The O₂ term is a measure of the net air-sea O₂ exchange per Equation (1). The change in OPO inventory thus provides a measure of the combined air-sea exchanges of O₂ and CO₂ over the basin.

The final step is to use float-based O₂ measurements in the upper ocean, with high spatial and temporal coverage, combined with the ship-based measurements of O₂, to provide an independent measure of the change in O₂ inventory. Correcting the change in OPO inventory allows the net CO₂ uptake to be calculated. Although this last step must await the development of an expanded

ocean O₂ observing system, it is not clear that an alternative method is available that is free of restrictive assumptions for tracking the total long-term accumulation of CO₂ in the ocean in the face of a changing climate. The need for such an ambitious O₂ observing system is thus made even more compelling. Developing such an observing system may be the key to determining the total oceanic CO₂ uptake, whether using atmospheric O₂ measurements or ocean DIC measurements.

Other Challenges

Improving our ability to predict changes in ocean O₂ in a warming world, particularly the fate of OMZs, will require not only an improved ocean observing system, but also advances in understanding relevant processes and developing improved modeling capability.

A critical need is to improve understanding of the water transports influencing OMZs and develop a coupled physical/biological ocean general circulation model (OGCM) of sufficient resolution to realistically depict these transports. Existing models and observations emphasize the importance of physical transport mechanisms as the most important driver of internal O₂ variability. Yet existing global models don't represent well the undercurrents and jets that influence both open ocean and coastal OMZs, resulting in substantial biases in their ocean interior oxygen distribution. Existing models tend to underestimate interannual O₂ variability (Deutsch et al. 2006; Rödenbeck et al. 2008; P. Brandt, V. Hormann, A. Körtzinger, M. Visbeck, G. Krahnmann, et al., unpublished paper), suggesting that they may also underestimate the response to global warming. Critical research questions include: What are the critical paths of O₂ supply to OMZ? How stable are these in a warming world? How important are wind shifts versus changes in surface buoyancy forcing in regulating supply? How important are shifts in surface production and export? Developing models that can simulate observed variability is a critical first step.

Another need is to understand potential feedbacks between ocean O₂ supply and nutrients. Sediments bathed in low-oxygen waters preferentially release soluble iron (II) and labile particulate iron to the water, which can result in an enhanced supply of iron available to upwelling into surface waters, possibly fueling a positive feedback loop entailing increased export production and greater O₂ depletions at depth (Lohan & Bruland 2008). Low O₂ also decreases the burial efficiency of P in sediments, potentially driving a similar feedback loop (Ingall & Jahnke 1994), although the long residence time of P in the ocean of ~50,000 years (Lenton & Watson 2000) makes this less of a concern. An expansion of suboxic conditions would increase the loss of fixed nitrogen due to denitrification or anaerobic ammonia oxidation both in sediments and in the water column (Codispoti et al. 2001, Dalsgaard et al. 2005), potentially driving a feedback loop in the opposite direction. Reductions in ocean nitrate from deoxygenation might be countered, however, by feedbacks involving nitrogen fixation (Deutsch et al. 2007). The strength of these potential feedbacks remains unclear.

Ocean deoxygenation may be influenced by links with warming and acidification due to rising CO₂. Warming directly influences organism and ecosystem metabolic rates, with relevance both for export production and decomposition rates of sinking organic matter, which could influence the distribution of subsurface oxygen utilization. Respiration is likely more sensitive to temperature than photosynthesis, because respiration is a biochemical process whereas photosynthesis is photochemical. Because global rates of ocean photosynthesis and respiration are strongly coupled to one another (as a result of the short residence time of most organic matter in the oceans), the differential temperature response of photosynthesis and respiration may not be of direct importance, however, to the problem of deoxygenation. What is critical is the impact of these processes on the distribution of O₂ between the ocean and atmosphere. One clearly important variable is the depth scale of decomposition of organic matter, which is likely sensitive to both temperature

(Matsumoto et al. 2007) and O₂ (Van Mooy et al. 2002). Rising CO₂ may influence export production and decomposition by increases in the C/N ratios of sinking organic matter (Riebesell et al. 2007) or changes in mineral ballasting (Hofmann & Schellnhuber 2009). The structure of ecosystems may be impacted by warming, acidification, deoxygenation, nutrient supply, or circulation changes. All these linkages are potentially relevant to the pattern and rates of O₂ utilization. All remain poorly understood (Riebesell et al. 2009).

SUMMARY

The realization that future global warming might significantly impact ocean O₂ distributions is very recent, dating back only a decade (Sarmiento et al. 1998). The science of ocean deoxygenation is thus in early stages, and progress to date has mostly involved clarifying what is possible or conceivable within large uncertainties.

Nevertheless, there is a convergence of evidence suggesting that significant changes are looming. The strongest evidence is that O₂ changes already seem to be occurring, most notably in the North Pacific and tropical O₂ minimum zones. Changes in the North Pacific are tied to increased stratification in the subarctic region. O₂ declines are consistent with the predicted response to global warming in global ocean models, and the patterns of observed O₂ change can be reproduced with higher-resolution models driven by observed forcings. The relative rapidity of O₂ decreases in the subarctic Pacific and in coastal upwelling regions off the west coast of North America raises the specter of imminent impacts on marine habitat and fisheries. The cause of the O₂ declines in the tropics is unclear. Existing global models do not have the resolution or accurate parameterizations to adequately describe the controls on O₂ in these areas. But the fact that the tropical OMZs were occasionally expanded compared to today in previous warm periods of the Pleistocene suggests that the declines may also be tied to recent global warming.

Developing the observing system, modeling tools, and understanding of relevant processes to predict future O₂ levels will be challenging, because it will require advances across a broad range of oceanographic disciplines. Making advances in the understanding of how and why O₂ is changing will also improve our ability to document the uptake of CO₂ by the ocean, with links to concerns about ocean acidification and nutrient cycling. Dealing with the threat of future ocean deoxygenation will require a unified research agenda across the full range of oceanographic disciplines, including physical, biological, and chemical.

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LITERATURE CITED

- Andreev A, Watanabe S. 2002. Temporal changes in dissolved oxygen of the intermediate water in the subarctic North Pacific. *Geophys. Res. Lett.* 29, L12607, doi:10.1029/2008GL034185
- Andreev AG, Baturina VI. 2006. Impacts of tides and atmospheric forcing variability on dissolved oxygen in the subarctic North Pacific. *J. Geophys. Res.-Oceans* 111, C07S10, doi:10.1029/2005JC003103
- Andreev AG, Kusakabe M. 2001. Interdecadal variability in dissolved oxygen in the intermediate water layer of the Western Subarctic Gyre and Kuril Basin (Okhotsk Sea). *Geophys. Res. Lett.* 28:2453–56
- Aoki S, Bindoff NL, Church JA. 2005. Interdecadal water mass changes in the Southern Ocean between 30 degrees E and 160 degrees E. *Geophys. Res. Lett.* 32, L07607, doi:10.1029/2004GL022220
- Bakun A, Weeks SJ. 2004. Greenhouse gas buildup, sardines, submarine eruptions and the possibility of abrupt degradation of intense marine upwelling ecosystems. *Ecol. Lett.* 7:1015–23
- Battle M, Mikaloff Fletcher SE, Bender ML, Keeling RF, Manning AC, et al. 2006. Atmospheric potential oxygen: New observations and their implications for some atmospheric and oceanic models. *Glob. Biogeochem. Cycles* 20, GB1010, doi:10.1029/2005GB002534
- Bindoff NL, McDougall TJ. 2000. Decadal changes along an Indian ocean section at 32 degrees S and their interpretation. *J. Phys. Oceanogr.* 30:1207–22
- 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, doi:10.1029/2008GL034185
- Böning CW, Dispert A, Visbeck M, Rintoul SR, Schwarzkopf FU. 2008. The response of the Antarctic Circumpolar Current to recent climate change. *Nat. Geosci.* 1:864–69
- Bopp L, Le Quéré C, Heimann M, Manning AC, Monfray P. 2002. Climate-induced oxygen fluxes: implications for the contemporary carbon budget. *Glob. Biogeochem. Cycles* 16, 1022 doi:10.1029/2001GB001445
- Brandt P, Hormann V, Bourles B, Fischer J, Schott FA, et al. 2008. Oxygen tongues and zonal currents in the equatorial Atlantic. *J. Geophys. Res.-Oceans* 113, C04012, doi:10.1029/2007JC004435
- Breitburg DL, Hondorp DW, Davias LA, Diaz RJ. 2009. Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. *Annu. Rev. Mar. Sci.* 1:329–49
- Brennan CE, Matear RJ, Keller K. 2008. Measuring oxygen concentrations to improve the detection capabilities of an ocean circulation observation array. *J. Geophys. Res.-Oceans* 113, C02019, doi:10.1029/2007JC004113
- Brewer PG, Peltzer ET. 2009. Limits to marine life. *Science* 324:347–8
- Broecker WS, Blanton S, Smethie WM, Ostlund G. 1991. Radiocarbon decay and oxygen utilization in the deep Atlantic Ocean. *Glob. Biogeochem. Cycles* 5:87–117
- Carpenter JH. 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. *Limnol. Oceanogr.* 10:141–43
- Chan F, Barth JA, Lubchenco J, Kirincich A, Weeks H, et al. 2008. Emergence of anoxia in the California current large marine ecosystem. *Science* 319:920
- 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. Marina* 65:85–105
- Cohen AS, Coe AL, Kemp DB. 2007. The late Palaeocene-Early Eocene and Toarcian (Early Jurassic) carbon isotope excursions: a comparison of their time scales, associated environmental changes, causes and consequences. *J. Geol. Soc.* 164:1093–108
- Conkright ME, Antonov JI, Baranova O, Boyer TP, Garcia HE, et al. 2002. *NOAA Atlas NESDIS 42, WORLD OCEAN DATABASE 2001*. Volume 1: *Introduction*. Washington, DC: U.S. Gov. Printing Office. 160 pp.
- Dalsgaard T, Thamdrup B, Canfield DE. 2005. Anaerobic ammonium oxidation (anammox) in the marine environment. *Res. Microbiol.* 156:457–64
- Dean WE, Zheng Y, Ortiz JD, van Geen A. 2006. Sediment Cd and Mo accumulation in the oxygen-minimum zone off western Baja California linked to global climate over the past 52 kyr. *Paleoceanography* 21, PA4209, doi:10.1029/2005PA001239
- Deutsch C, Emerson S, Thompson L. 2006. Physical-biological interactions in North Pacific oxygen variability. *J. Geophys. Res.-Oceans* 111, C09S90, doi:10.1029/2005JC003179

- Deutsch C, Sarmiento JL, Sigman DM, Gruber N, Dunne JP. 2007. Spatial coupling of nitrogen inputs and losses in the ocean. *Nature* 445:163–67
- Diaz RJ, Rosenberg R. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. In *Oceanography and Marine Biology—An Annual Review*, vol 33, pp. 245–303. London: UCL Press
- Diaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321:926–29
- Dittmar W. 1884. Report on researches into the composition of ocean water collected by HMS Challenger during the years 1873–1876. In *Report on the Scientific Results of the Voyage of HMS Challenger: Physics and Chemistry*, ed. J Murray, vol. 1, pt. 1, pp. 251. London: HM Stationery Office
- Domingues CM, Church JA, White NJ, Gleckler PJ, Wijffels SE, et al. 2008. Improved estimates of upper-ocean warming and multi-decadal sea-level rise. *Nature* 453:1090–93
- Emerson S, Mecking S, Abell J. 2001. The biological pump in the subtropical North Pacific Ocean: Nutrient sources, Redfield ratios, and recent changes. *Glob. Biogeochem. Cycles* 15:535–54
- 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
- Feely RA, Sabine CL, Schlitzer R, Bullister JL, Mecking S, Greeley D. 2004. Oxygen utilization and organic carbon remineralization in the upper water column of the Pacific Ocean. *J. Oceanogr*: 60:45–52
- Foltz GR, McPhaden MJ. 2008. Trends in Saharan dust and tropical Atlantic climate during 1980–2006. *Geophys. Res. Lett.* 35, L20706, doi:10.1029/2008GL035042
- Freeland H, Denman K, Wong CS, Whitney F, Jacques R. 1997. Evidence of change in the winter mixed layer in the Northeast Pacific Ocean. *Deep-Sea Res. I* 44:2117–29
- Friedrich T, Oeschies A, Eden C. 2006. Role of wind stress and heat fluxes in interannual-to-decadal variability of air-sea CO₂ and O₂ fluxes in the North Atlantic. *Geophys. Res. Lett.* 33, L21S04, doi:10.1029/2006GL026538
- Fröhlicher TL, Joos F, Plattner GK, 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, doi:10.1029/2008GB003316
- Gamo T. 1999. Global warming may have slowed down the deep conveyor belt of a marginal sea of the northwestern Pacific: Japan Sea. *Geophys. Res. Lett.* 26:3137–40
- Ganeshram RS, Pedersen TF, Calvert SE, Francois R. 2002. Reduced nitrogen fixation in the glacial ocean inferred from changes in marine nitrogen and phosphorus inventories. *Nature* 415:156–59
- Garcia H, Cruzado A, Gordon L, Escanez J. 1998. Decadal-scale chemical variability in the subtropical North Atlantic deduced from nutrient and oxygen data. *J. Geophys. Res.-Oceans* 103:2817–30
- Garcia HE, Locarnini RA, Boyer TP, Antonov JI. 2006. *World Ocean Atlas 2005*. Volume 3: *Dissolved Oxygen, Apparent Oxygen Utilization, and Oxygen Saturation*, NOAA Atlas NESDIS 63. Washington, DC: U.S. Govt. Printing Office. 342 pp.
- 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
- Gillett NP, Thompson DWJ. 2003. Simulation of recent Southern Hemisphere climate change. *Science* 302:273–75
- Gnanadesikan A, Russell JL, Zeng F. 2007. How does ocean ventilation change under global warming? *Ocean Sci.* 3:43–53
- Gordon AL, Huber BA. 1990. Southern-Ocean Winter Mixed Layer. *J. Geophys. Res.-Oceans* 95:11655–72
- Gould J, Roemmich D, Wijffels S, Freeland H, Ignaszewsky M, et al. 2004. Argo profiling floats bring new era of in situ ocean observations. *Eos Trans. AGU* 85:179–84
- Grantham BA, Chan F, Nielsen KJ, Fox DS, Barth JA, et al. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* 429:749–54
- Gray JS, Wu RSS, Or YY. 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. *Mar. Ecol.-Prog. Ser.* 238:249–79
- Gruber N, Gloor M, Fan SM, Sarmiento SL. 2001. Air-sea flux of oxygen estimated from bulk data: Implications for the marine and atmospheric oxygen cycle. *Glob. Biogeochem. Cycles* 15:783–803

- Gruber N, Gloor M, Mikaloff-Fletcher SE, Doney SC, Dutkiewicz S, et al. 2009. Oceanic sources, sinks, and transport of atmospheric CO₂. *Glob. Biogeochem. Cycles* 23, GB1005, doi:10.1029/2008GB003349
- Gruber N. 2004. The dynamics of the marine nitrogen cycle and its influence on atmospheric CO₂. In *The ocean carbon cycle and climate*, ed. M Follows, T Oguz, pp. 97–148. Dordrecht: Kluwer Academic
- Gruber N. 2008. The marine nitrogen cycle: Overview of distributions and processes. In *Nitrogen in the marine environment*, ed. DG Capone, DA Bronk, MR Mulholland, EJ Carpenter, pp. 1–50. Amsterdam: Elsevier. 2nd ed.
- Gruber N, Doney SC, Emerson SR, Gilbert D, Kobayashi T, et al. 2007. The ARGO-Oxygen Program: A White Paper to Promote the Addition of Oxygen Sensors to the International ARGO Float Program. Paris: UNESCO. pp. 1–60. http://ioc3.unesco.org/ioccp/Docs/o2_argo_whitepaper_15feb07_r.pdf
- Gruber N, Sarmiento JL, Stocker TF. 1996. An improved method for detecting anthropogenic CO₂ in the oceans. *Glob. Biogeochem. Cycles* 10:809–37
- Hamme RC, Keeling RF. 2008. Ocean ventilation as a driver of interannual variability in atmospheric potential oxygen. *Tellus Ser. B-Chem. Phys. Meteorol.* 60:706–17
- Hofmann M, Schellnhuber HJ. 2009. Oceanic acidification affects marine carbon pump and triggers extended marine oxygen holes. *Proc. Natl. Acad. Sci. USA* 106:3017–22
- Ingall E, Jahnke R. 1994. Evidence for enhanced phosphorus regeneration from marine-sediments overlain by oxygen depleted waters. *Geochim. Cosmochim. Acta* 58:2571–75
- Ito T, Follows MJ, Boyle EA. 2004. Is AOU a good measure of respiration in the oceans? *Geophys. Res. Lett.* 31, L17305, doi:10.1029/2004GL020900
- Jacobs S. 2006. Observations of change in the Southern Ocean. *Philos. Trans. R. Soc. A. Math. Phys. Eng. Sci.* 364:1657–81
- Jenkins WJ. 1987. ³H and ³He in the Beta-Triangle—observations of gyre ventilation and oxygen utilization rates. *J. Phys. Oceanogr.* 17:763–83
- Jin X, Gruber N. 2003. Offsetting the radiative benefit of ocean iron fertilization by enhancing N₂O emissions. *Geophys. Res. Lett.* 30, 2249, doi:10.1029/2003GL018458
- Johnson GC, Gruber N. 2007. Decadal water mass variations along 20 degrees W in the Northeastern Atlantic Ocean. *Prog. Oceanogr.* 73:277–95
- Johnson KS, Berelson WM, Boss ES, Chase Z, Claustre H, Emerson SR, et al. 2009. Observing biogeochemical cycles at global scales with profiling floats and gliders: prospects for a global array. *Oceanogr.* 22:217–25
- Jones CE, Jenkyns HC. 2001. Seawater strontium isotopes, oceanic anoxic events, and seafloor hydrothermal activity in the Jurassic and Cretaceous. *Am. J. Sci.* 301:112–49
- Joos F, Plattner G-K, Stocker TF, Körtzinger A, Wallace DWR. 2003. Trends in marine dissolved oxygen: implications for ocean circulation changes and carbon budget. *Eos, Trans. Am. Geophys. Union* 84:197
- Karstensen J, Stramma L, Visbeck M. 2008. Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. *Prog. Oceanogr.* 77:331–50
- Keeling RF. 1988. *Development of an interferometric oxygen analyzer for precise measurement of the atmospheric O₂ mole fraction*. Cambridge: Harvard University. 178 pp.
- Keeling RF, Garcia H. 2002. The change in oceanic O₂ inventory associated with recent global warming. *Proc. Natl. Acad. Sci.* 99(12):7848–53
- Keeling RF, Piper SC, Heimann M. 1996. Global and hemispheric CO₂ sinks deduced from changes in atmospheric O₂ concentration. *Nature* 381:218–21
- Keeling RF, Shertz SR. 1992. Seasonal and interannual variations in atmospheric oxygen and implications for the global carbon-cycle. *Nature* 358:723–27
- Keller K, Slater RD, Bender M, Key RM. 2002. Possible biological or physical explanations for decadal scale trends in North Pacific nutrient concentrations and oxygen utilization. *Deep-Sea Res. Part II* 49:345–62
- Kennett JP, Ingram BL. 1995. A 20,000 year record of ocean circulation and climate-change from the Santa-Barbara Basin. *Nature* 377:510–14
- Körtzinger A, Hedges JI, Quay PD. 2001. Redfield ratios revisited: Removing the biasing effect of anthropogenic CO₂. *Limnol. Oceanogr.* 46:964–70
- Körtzinger A, Schimanski J, Send U. 2005. High quality oxygen measurements from profiling floats: A promising new technique. *J. Atmos. Oceanic Technol.* 22:302–08

- Körtzinger A, Schimanski J, Send U, Wallace D. 2004. The ocean takes a deep breath. *Science* 306:1337–37
- Le Quéré C, Rödenbeck C, Buitenhuis ET, Conway TJ, Langenfelds R, et al. 2008. Saturation of the Southern Ocean CO₂ sink due to recent climate change. *Science* 319
- Lenton TM, Watson AJ. 2000. Redfield revisited 1. Regulation of nitrate, phosphate, and oxygen in the ocean. *Glob. Biogeochem. Cycles* 14:225–48
- Levin LA. 2003. Oxygen minimum zone benthos: Adaptation and community response to hypoxia. In *Oceanography and Marine Biology*, vol. 41, pp. 1–45. London: Taylor & Francis
- Levine NM, Doney SC, Wanninkhof R, Lindsay K, Fung IY. 2008. Impact of ocean carbon system variability on the detection of temporal increases in anthropogenic CO₂. *J. Geophys. Res.-Oceans* 113, C03019, doi:10.1029/2007JC004153
- Lohan MC, Bruland KW. 2008. Elevated Fe(II) and dissolved Fe in hypoxic shelf waters off Oregon and Washington: An enhanced source of iron to coastal upwelling regimes. *Environ. Sci. Technol.* 42:6462–68
- Lovenduski NS, Gruber N, Doney SC. 2008. Toward a mechanistic understanding of the decadal trends in the Southern Ocean carbon sink. *Glob. Biogeochem. Cycles* 22, GB3016, doi:10.1029/2007GB003139
- Lovenduski NS, Gruber N, Doney SC, Lima ID. 2007. Enhanced CO₂ outgassing in the Southern Ocean from a positive phase of the Southern Annular Mode. *Glob. Biogeochem. Cycles* 21, GB2026, doi:10.1029/2006GB002900
- Luyten JR, Pedlosky J, Stommel H. 1983. The Ventilated Thermocline. *J. Phys. Oceanogr.* 13:292–309
- Manning AC, Keeling RF. 2006. Global oceanic and land biotic carbon sinks from the Scripps atmospheric oxygen flask sampling network. *Tellus* 58B:95–116
- Martin JH, Knauer GA, Karl DM, Broenkow WW. 1987. Vertex-carbon cycling in the northeast Pacific. *Deep-Sea Res. I* 34:267–85
- Martz TR, Johnson KS, Riser SC. 2008. Ocean metabolism observed with oxygen sensors on profiling floats in the South Pacific. *Limnol. Oceanogr.* 53:2094–111
- Matear RJ, Hirst AC. 2003. Long-term changes in dissolved oxygen concentrations in the ocean caused by protracted global warming. *Glob. Biogeochem. Cycles* 17, 1125, doi:10.1029/2002GB001997
- Matear RJ, Hirst AC, McNeil BI. 2000. Changes in dissolved oxygen in the Southern Ocean with climate change. *Geochem. Geophys. Geosystems* 1, 2000GC000086
- 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
- McKinley GA, Follows M, Marshal J. 2003. Interannual variability of air-sea O₂ fluxes and the determination of CO₂ sinks using atmospheric O₂/N₂. *Geophys. Res. Lett.* 30:1101, doi:10.1029/2002GL016044
- 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 US CLIVAR/CO₂ Repeat Hydrography cruises. *Glob. Biogeochem. Cycles* 22, GB3015, doi:10.1029/2007GB003101
- Mecking S, Warner MJ, Bullister JL. 2006. Temporal changes in pCFC-12 ages and AOU along two hydrographic sections in the eastern subtropical North Pacific. *Deep-Sea Res. I* 53:169–87
- Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, et al. 2007. Global climate projections. In *Climate Change 2007, The Physical Science Basis, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, ch. 10, pp. 747–845. Cambridge: Cambridge Univ. Press
- Minobe S. 1999. Resonance in bidecadal and pentadecadal climate oscillations over the North Pacific: Role in climatic regime shifts. *Geophys. Res. Lett.* 26:855–58
- Monteiro PMS, Van Der Plas AK, Melice JL, Florenchie P. 2008. Interannual hypoxia variability in a coastal upwelling system: Ocean-shelf exchange, climate and ecosystem-state implications. *Deep-Sea Res. I* 55:435–50
- Murata A, Kumamoto Y, Watanabe S, Fukasawa M. 2007. Decadal increases of anthropogenic CO₂ in the South Pacific subtropical ocean along 32 degrees S. *J. Geophys. Res.-Oceans* 112, C05033, doi:10.1029/2005JC003405
- 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, doi:10.1029/2006GL028243

- Nevison C, Butler JH, Elkins JW. 2003. Global distribution of N₂O and the Delta N₂O-AOU yield in the subsurface ocean. *Glob. Biogeochem. Cycles* 17, 1119, doi:10.1029/2003GB002068
- Neretin LN, ed. 2006. *Past and Present Water Column Anoxia*, vols. 64. Dordrecht, Netherlands: Springer. 541 pp.
- Oke PR, England MH. 2004. Oceanic response to changes in the latitude of the Southern Hemisphere subpolar westerly winds. *J. Clim.* 17:1040–54
- 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
- Osafune S, Yasuda I. 2006. Bidecadal variability in the intermediate waters of the northwestern subarctic Pacific and the Okhotsk Sea in relation to 18.6-year period nodal tidal cycle. *J. Geophys. Res.-Oceans* 111, C05007, doi:10.1029/2005JC003277
- Oschlies A, Schulz KG, Riebesell U, Schmittner A. 2008. Simulated 21st century's increase in oceanic suboxia by CO₂-enhanced biotic carbon export. *Glob. Biogeochem. Cycles* 22, GB4008, doi:10.1029/2007GB003147
- Peng TH, Wanninkhof R, Bullister JL, Feely RA, Takahashi T. 1998. Quantification of decadal anthropogenic CO₂ uptake in the ocean based on dissolved inorganic carbon measurements. *Nature* 396:560–63
- Petit J, Jouzel J, Raynaud D, Barkov N, Barnola J, et al. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399:429–36
- Plattner GK, Joos F, Stocker TF. 2002. Revision of the global carbon budget due to changing air-sea oxygen fluxes. *Glob. Biogeochem. Cycles* 16, 1096, doi:10.1029/2001GB001746
- Plattner GK, Joos F, Stocker TF, Marchal O. 2001. Feedback mechanisms and sensitivities of ocean carbon uptake under global warming. *Tellus Ser. B-Chem. Phys. Meteorol.* 53:564–92
- Pörtner HO, Farrell AP. 2008. ECOLOGY Physiology and Climate Change. *Science* 322:690–92
- Riebesell U, Schulz KG, Bellerby RGJ, Botros M, Fritsche P, et al. 2007. Enhanced biological carbon consumption in a high CO₂ ocean. *Nature* 450:545–48
- Riebesell U, Körtzinger A, Oschlies A. 2009. Sensitivities of marine carbon fluxes to ocean change. *Proc. Natl. Acad. Sci. USA*. In press
- Riser SC, Johnson KS. 2008. Net production of oxygen in the subtropical ocean. *Nature* 451:323–25
- Rödenbeck C, Le Quéré C, Heimann M, Keeling RF. 2008. Interannual variability in oceanic biogeochemical processes inferred by inversion of atmospheric O₂/N₂ and CO₂ data. *Tellus Ser. B-Chem. Phys. Meteorol.* 60:685–705
- Sabine CL, Feely RA, Gruber N, Key RM, Lee K, et al. 2004. The oceanic sink for anthropogenic CO₂. *Science* 305:367–71
- Sabine CL, Feely RA, Millero FJ, Dickson AG, Langdon C, et al. 2008. Decadal changes in Pacific carbon. *J. Geophys. Res.-Oceans* 113, C07021, doi:10.1029/2007JC004577
- Sarmiento JL, Gruber N. 2006. *Ocean Biogeochemical Dynamics*. Princeton: Princeton Univ. Press. 503 pp.
- Sarmiento JL, Gruber N, Brzezinski MA, Dunne JP. 2004. High-latitude controls of thermocline nutrients and low latitude biological productivity. *Nature* 427:56–60
- Sarmiento JL, Hughes TMC, Stouffer RJ, Manabe S. 1998. Simulated response of the ocean carbon cycle to anthropogenic climate warming. *Nature* 393:245–49
- Schmittner A, Oschlies A, Matthews HD, Galbraith ED. 2008. Future changes in climate, ocean circulation, ecosystems, and biogeochemical cycling simulated for a business-as-usual CO₂ emission scenario until year 4000 AD. *Glob. Biogeochem. Cycles* 22, GB1013, doi:10.1029/2007GB002953
- Schulz H, von Rad U, Erlenkeuser H. 1998. Correlation between Arabian Sea and Greenland climate oscillations of the past 110,000 years. *Nature* 393:54–57
- Severinghaus JP. 1995. *Studies of the terrestrial O₂ and carbon cycles in sand dune gases and in Biosphere 2*. PhD thesis, Columbia Univ., New York
- Shaffer G, Leth O, Ulloa O, Bendtsen J, Daneri G, et al. 2000. Warming and circulation change in the eastern South Pacific Ocean. *Geophys. Res. Lett.* 27:1247–50
- Shaffer G, Olsen SM, Pedersen JOP. 2009. Long-term ocean oxygen depletion in response to carbon dioxide emissions from fossil fuels. *Nat. Geosci.* 2:105–109
- Sigman DM, Boyle EA. 2000. Glacial/interglacial variations in atmospheric carbon dioxide. *Nature* 407:859–69

- Stephens BB, Keeling RF. 2000. The influence of Antarctic sea ice on glacial-interglacial CO₂ variations. *Nature* 404:171–74
- Stephens BB, Keeling RF, Heimann M, Six KD, Murnane R, Caldeira K. 1998. Testing global ocean carbon cycle models using measurements of atmospheric O₂ and CO₂ concentration. *Glob. Biogeochem. Cycles* 12:213–30
- Stramma L, Johnson GC, Sprintall J, Mohrholz V. 2008. Expanding oxygen-minimum zones in the tropical oceans. *Science* 320:655–58
- Sverdrup HU. 1938. On the explanation of oxygen minima and maxima in the oceans. *J. Conseil Int. pour l'Exploration de Mer* 13:163–72
- Tengberg A, Hovdenes J, Andersson HJ, Brocandel O, Diaz R, et al. 2006. Evaluation of a lifetime-based optode to measure oxygen in aquatic systems. *Limnol. Oceanogr. Methods* 4:7–17
- Toggweiler JR, Dixon K, Broecker WS. 1991. The Peru upwelling and the ventilation of the South-Pacific thermocline. *J. Geophys. Res.-Oceans* 96:20467–97
- Toggweiler JR, Murnane R, Carson S, Gnanadesikan A, Sarmiento JL. 2003. Representation of the carbon cycle in boxmodels and GCMs: 2. Organic pump. *Glob. Biogeochem. Cycles* 17, 1027, doi:10.1029/2001GB001841
- Toggweiler JR, Russell J. 2008. Ocean circulation in a warming climate. *Nature* 451:286–88
- Tohjima Y, Mukai H, Nojiri Y, Yamagishi H, Machida T. 2008. Atmospheric O₂/N₂ measurements at two Japanese sites: estimation of global oceanic and land biotic carbon sinks and analysis of the variations in atmospheric potential oxygen (APO). *Tellus Ser. B-Chem. Phys. Meteorol.* 60:213–25
- van Geen A, Zheng Y, Bernhard JM, Cannariato KG, Carriquiry J, et al. 2003. On the preservation of laminated sediments along the western margin of North America. *Paleoceanography* 18, 1098, doi:10.1029/2003PA000911
- Van Mooy BAS, Keil RG, Devol AH. 2002. Impact of suboxia on sinking particulate organic carbon: Enhanced carbon flux and preferential degradation of amino acids via denitrification. *Geochim. Cosmochim. Acta* 66:457–65
- Vaquier-Sunyer R, Duarte CM. 2008. Thresholds of hypoxia for marine biodiversity. *Proc. Natl. Acad. Sci. USA* 105:15452–57
- Verdy A, Dutkiewicz S, Follows MJ, Marshall J, Czaja A. 2007. Carbon dioxide and oxygen fluxes in the Southern Ocean: Mechanisms of interannual variability. *Glob. Biogeochem. Cycles* 21, GB2020, doi:10.1029/2006GB002916
- Wallmann K. 2003. Feedbacks between oceanic redox states and marine productivity: A model perspective focused on benthic phosphorus cycling. *Glob. Biogeochem. Cycles* 17, Art No. 1084, doi:10.1029/2002GB001968
- Watanabe YW, Ono T, Shimamoto A, Sugimoto T, Wakita M, Watanabe S. 2001. Probability of a reduction in the formation rate of the subsurface water in the North Pacific during the 1980s and 1990s. *Geophys. Res. Lett.* 28:3289–92
- Watanabe YW, Wakita M, Maeda N, Ono T, Gamo T. 2003. Synchronous bidecadal periodic changes of oxygen, phosphate and temperature between the Japan Sea deep water and the North Pacific intermediate water. *Geophys. Res. Lett.* 30, 2273, doi:10.1029/2003GL018338
- Wetzel P, Winguth A, Maier-Reimer E. 2005. Sea-to-air CO₂ flux from 1948 to 2003: A model study. *Glob. Biogeochem. Cycles* 19, GB2005, doi:10.1029/2004GB002339
- 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
- Wignall PB, Twitchett RJ. 1996. Oceanic anoxia and the end Permian mass extinction. *Science* 272:1155–58
- Winkler LW. 1888. The determination of dissolved oxygen in water. *Ber. Dtsch. Chem. Ges.* 21:2843–57
- Wyrtki K. 1962. The oxygen minima in relation to ocean circulation. *Deep-Sea Res.* 9:11–23
- Yasuda I, Osafune S, Tatebe H. 2006. Possible explanation linking 18.6-year period nodal tidal cycle with bi-decadal variations of ocean and climate in the North Pacific. *Geophys. Res. Lett.* 33, L08606, doi:10.1029/2005GL025237