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 dissolved O_2 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 O_2 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 O_2 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 O_2 declines in the future suggests the need for an improved observing system for tracking ocean O_2 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 μmol 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 ~5 μmol kg^{-1}, nitrate becomes important in respiration, eventually replacing O_2 as
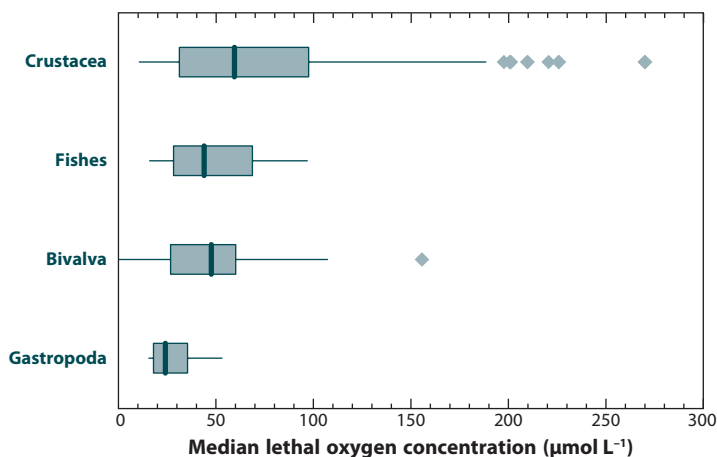

Figure 1

Median lethal oxygen concentration (LC_{50}, in μmol 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 * 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

[a]Including all waters with potential density less than $\sigma_\Theta < 27.2$ kg m^{-3}. These figures can be converted to percentage of total ocean volume by dividing by 1.44×10^{18} m^3.

the primary electron acceptor, a condition termed suboxic. When O_2 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 O_2 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). O_2 levels also control the oceanic production of nitrous oxide (N_2O), a powerful greenhouse gas, which is produced both under suboxic conditions as a by-product of denitrification and under oxic conditions during nitrification. Production of N_2O by both pathways will increase if O_2 levels drop (Codispoti et al. 2001, Jin & Gruber 2003, Nevison et al. 2003), thus potentially amplifying global warming (Gruber 2008). O_2 also influences the cycling of the marine phosphorous (P) cycle, with greater recyling of P from sediments occuring when O_2 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 middepths over wide expanses of the North Pacific and in smaller regions of the South Pacific and North Indian Ocean, as summarized in **Table 1**. Hypoxic conditions also occur in the eastern tropical Atlantic and Pacific Oceans. 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 O_2 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 O_2 consumption in subsurface waters and sediments. Additional O_2 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 O_2 declines in the open ocean because the O_2 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 the oceanic O_2 supply in warmer climates.

The threat of ocean deoxygenation raises many questions. Is O_2 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 O_2 is changing is important, not just because of the impact on marine organisms, but because measured changes in O_2, together with changes in nutrients, are a useful diagnostic of changing biogeochemistry (Matear et al. 2000, Keeling & Garcia 2002, Joos et al. 2003). Dissolved O_2 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 O_2 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.

O_2 is directly linked to carbon via photosynthesis and respiration, so the distribution of O_2 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 CO_2 from the atmosphere via ocean measurements. Understanding changes in oceanic O_2 is also important for the interpretation of measurements of atmospheric O_2, particularly the ability to use such measurements to determine the global land and ocean carbon sinks of CO_2 (Keeling 1988, Manning & Keeling 2006). Conversely, measurements of atmospheric O_2 can provide additional insights into changing ocean O_2 (Hamme & Keeling 2008).

Dissolved O_2 measurements also can provide information on ocean circulation. The difference between the observed O_2 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 O_2 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 O_2 on organisms, ecosystems, or chemical processes. Nor do we attempt to review changes in O_2 driven by eutrophication in freshwater and coastal systems. For readers interested in impacts of low O_2 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 O_2 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 O_2 that the parcel contained when it was last at the surface, the rate at which O_2 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 O_2 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 to10% 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
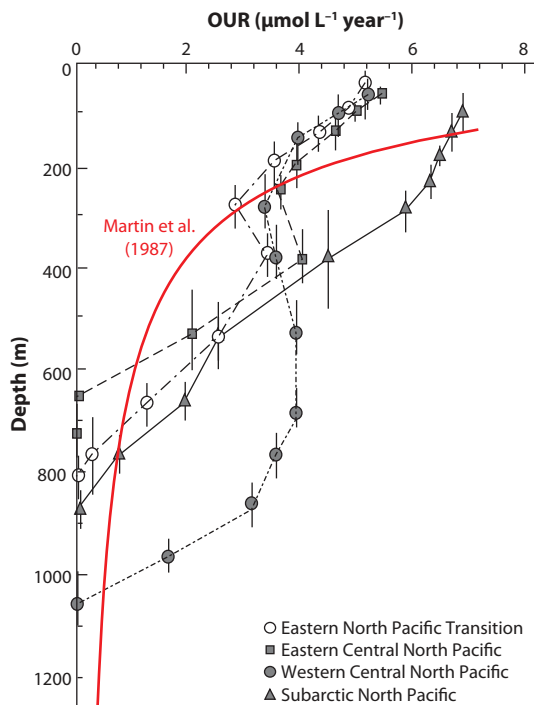

Figure 2

The oxygen utilization rate (OUR) in μmol L^{-1} year^{-1} (*thick red line*) versus depth from the model of Martin et al. (1987) and from a recent compilation of profiles from the North Pacific based on apparent oxygen utilization and chloroflurocarbon (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 O_2 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 O_2 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 O_2 minimum (Sverdrup 1938, Wyrtki 1962). Shallower waters tend to have higher O_2 because they are better ventilated, despite higher rates of utilization, while deeper waters tend to have higher O_2 because of lower utilization rates and higher initial O_2 levels, despite longer ventilation ages. The O_2 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 hot spots where O_2 levels are especially low.

The OMZs are typically located in regions without unusually high rates of O_2 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 O_2 depletion within the tropical gyres varies greatly from gyre to gyre, with the North Pacific tropical gyre hosting the worlds largest OMZ and the Atlantic gyres hosting much smaller OMZs. The control on the O_2 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. Krahmann, et al., unpublished paper). Karstensen et al. (2008) have shown that the difference in the degree of O_2 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 worlds 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 O_2 and high utilization probably both being relevant. The lowest O_2 levels in the
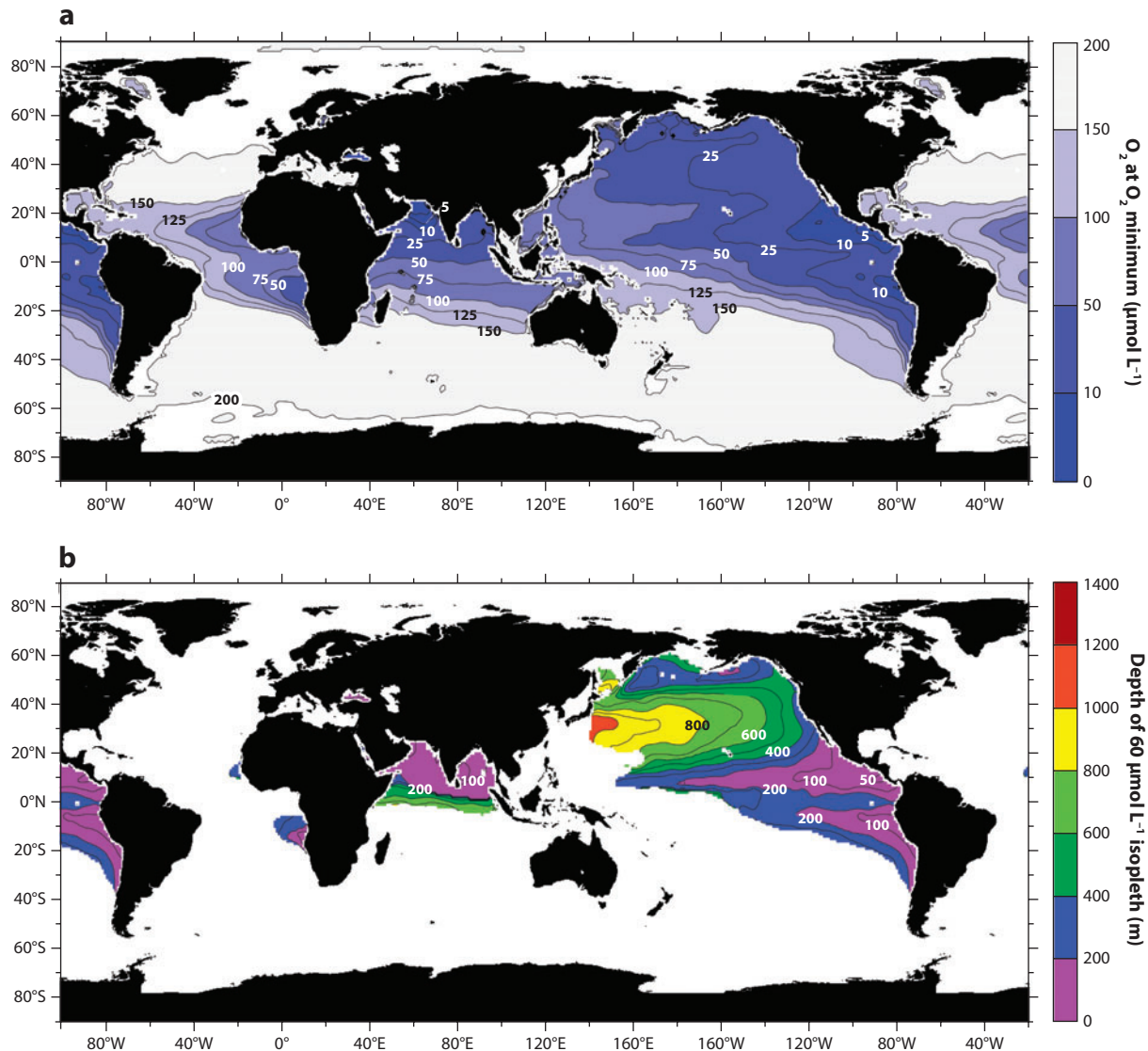
Figure 3

(*a*) Colors indicate O_2 concentrations at the depth of minimum O_2. (*b*) Depth of the 60 μmol L^{-1} isoline 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 μmol L^{-1} ≈ 60 μmol 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 m over most of the northern and eastern margin of the Pacific.
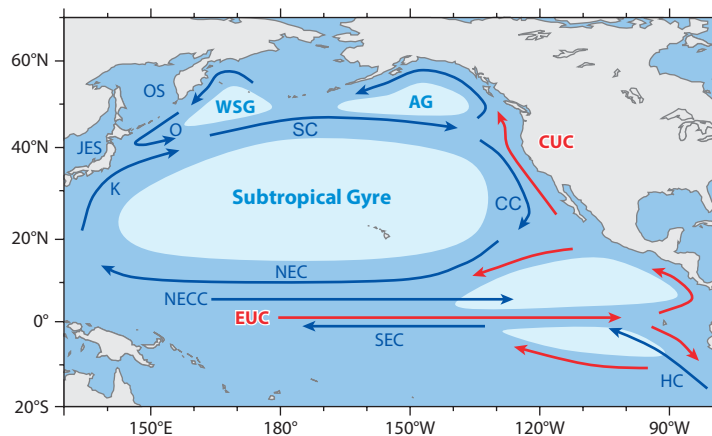
Figure 4

Currents (*arrows*) and gyres (*gray*) of the Equatorial and North Pacific. Surface currents are indicated in blue and subsurface currents in red. The tropical gyres are the light 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 O_2 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
	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		
Frölicher et al. (2009)	NCAR CSM1.4-CCCM	SRES A2	4	50	
		SRES B1	3		

[a]Conversions assume a total ocean mass of 1.48×10^{21} kg.

[b]Time frame only through 2065.

[c]O_2/heat ratio for simulation through year 2000.

[d]O_2/heat ratio from Oschlies, pers. commun.

decrease in O_2 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 O_2 over the next century, as summarized in **Table 2**. Declines by year 2100 vary from 2 to 12 μmol kg^{-1} depending on the model. Compared to the average ocean O_2 concentration of $\sim$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 climate sensitivity.

Keeling & Garcia (2002) suggested that natural warming (or cooling) of water masses in the ocean typically involves losses (or gains) of O_2 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 O_2 changes characterized by a similar ratio of around 6 nmol of O_2 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 (Frölicher et al. 2009) yield O_2 changes only twice as large as expected from solubility alone. Plattner et al. (2002) suggest the O_2/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 O_2 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 O_2 will decline over the next century (e.g., by $\sim$30 μmol kg^{-1}), associated with reductions in NADW formation (Plattner et al. 2001, Frölicher 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 O_2 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, Frölicher et al. 2009). In
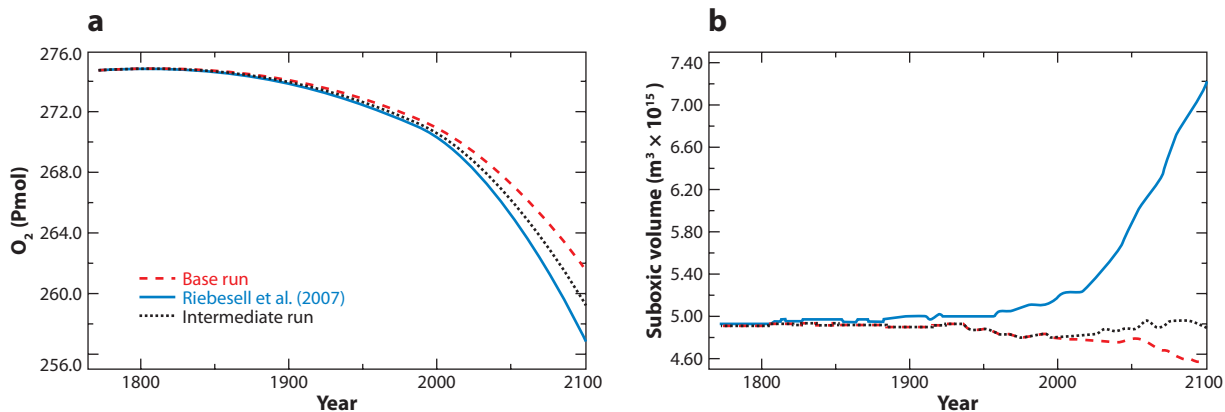
Figure 5

Changes in (*a*) the oceanic oxygen inventory and (*b*) volume of suboxic waters, here defined by $O_2 < 5$ μmol 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 pCO$_2$ 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 μmol 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, Frölicher 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 course 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 pCO$_2$ (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 poleward and strengthened over the past 40 years, partly as a result of rising CO_2 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 O_2 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 CO_2 in the Southern Ocean (Wetzel et al. 2005, Lovenduski et al. 2007, Le Quéré et al. 2007) while increasing the uptake of O_2 (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 O_2 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 O_2 levels, such as the configuration of the continents and atmospheric O_2 levels, were similar to today.

Ice core records show that during the cold periods of the Pleistocene, atmospheric CO_2 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 O_2 utilization must have been partly countered by increases in O_2 solubility in colder water or through more efficient ventilation of O_2 versus CO_2 in regions of convection or through leads in sea ice (Stephens & Keeling 2000, Toggweiler et al. 2003).

At shallower depths, O_2 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, O_2 levels decreased off the central California coast but increased in the low O_2 waters off Baja California to the south. During previous warm interstadial events, in contrast, lower O_2 conditions were recorded more prominently off Baja but not to the north (van Geen et al. 2003). The patterns suggest that controls on low O_2 conditions in tropical OMZ in the North Pacific are partly decoupled from conditions

farther north, with both regions being capable of having lower O_2 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 CO_2. 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 O_2 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 O_2 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 $\sigma_\Theta = 26.8$, 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 O_2 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 O_2 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 $\sigma_\Theta = 26.6$ 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 O_2 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 O_2 content of these subsurface layers locally. This region is therefore critical to the O_2 supply throughout the North Pacific.

The bidecadal variability in North Pacific O_2 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 bidecadal O_2 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 O_2 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 O_2 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).

O_2 concentrations on the $\sigma_\Theta = 26.6$ 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 $\sigma_\Theta = 26.6$ layer may have ceased to ventilate following the climate regime shift of 1977.

Even if the recent O_2 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 O_2 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 μmol kg^{-1} surface) has shoaled from 400 to 300 m at station P from the 1950s to the present. Considering that O_2 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 O_2 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 bidecadal 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 O_2 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°N), a wide region of the inner

Table 3 Studies documenting ocean dissolved O_2 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–Kuril 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	$\sigma_{\Theta} = 26.8$	1935–1998	AOU	Density	–58
Whitney 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	$\sigma_{\Theta} = 26.8$ to 27.4	1960–2002	AOU	Density	–11 to –29
Nakanowatari et al. (2007)	Oyashio domain	39–44N	142–149E	$\sigma_{\Theta} = 26.8$ to 27.4	1960–2002	AOU	Density	–5 to –16
Nakanowatari et al. (2007)	Subarctic Current	41–49N	51–72E	$\sigma_{\Theta} = 26.8$ 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	$\sigma_\Theta = 26.9$	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
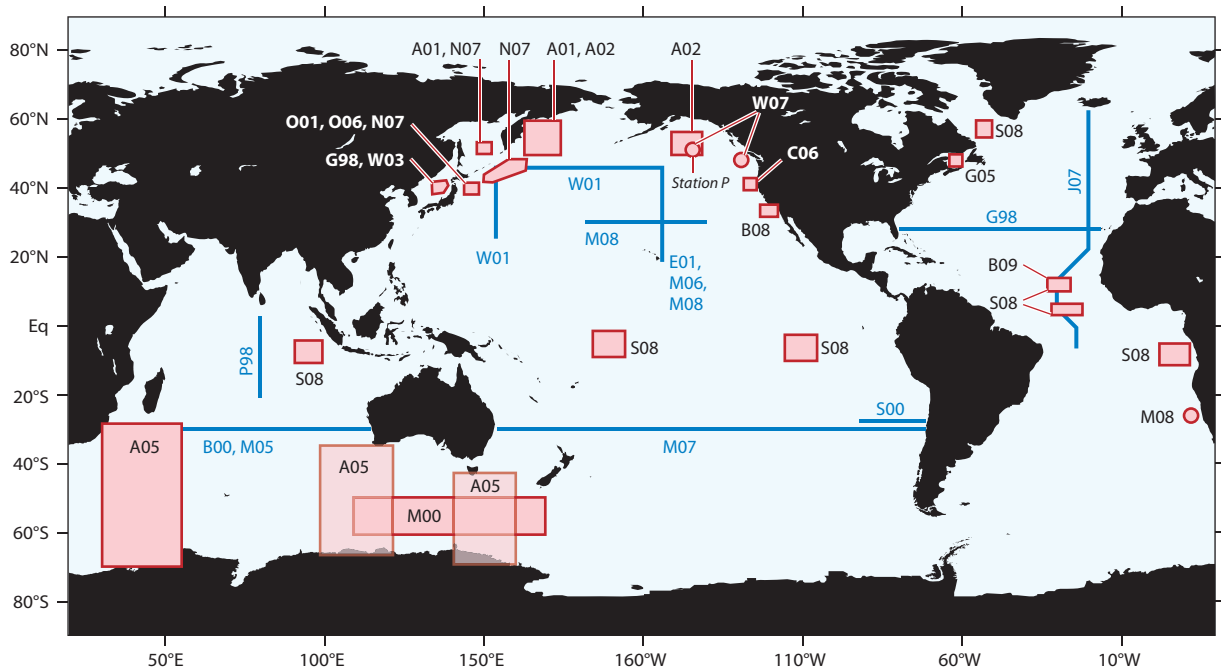
Figure 6

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 of not just 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 μmol kg^{-1} decade^{-1} from 1987 to 2006 was found on $\sigma_\Theta = 26.7$, 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 flow-ing 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.
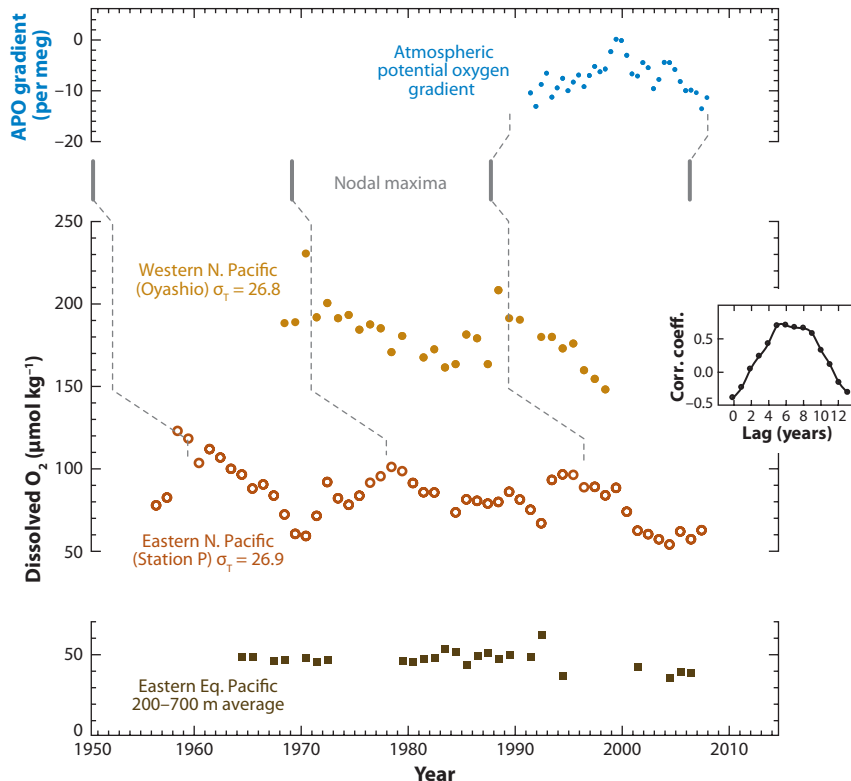
Figure 7

Dissolved O_2 in the western North Pacific in the Oyashio Current region (~39°–42°N, 143°–145°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°S–3°N, 105°–115°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 $\mu mol\,kg^{-1}\,decade^{-1}$ 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 $\mu mol\,kg^{-1}$ 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. Krahmann, 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
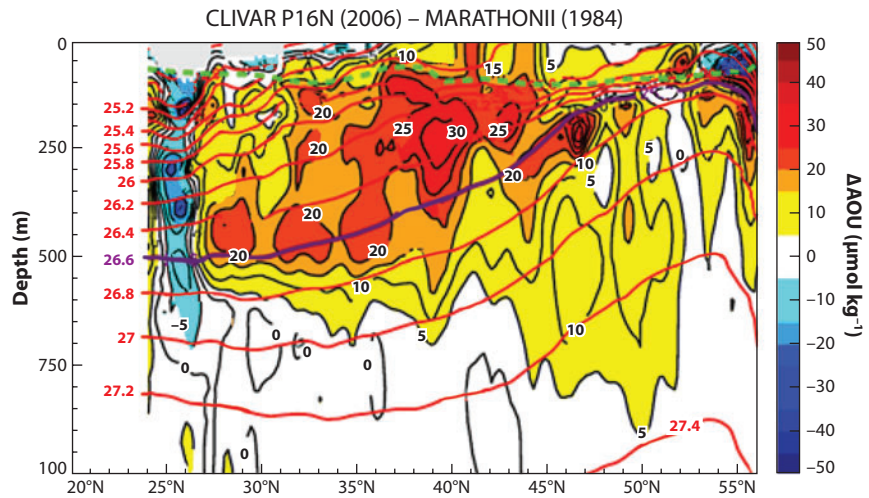
Figure 8

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 $\sigma_\Theta = 26.6$ isopycnal surface. Adapted from Mecking et al. (2008).
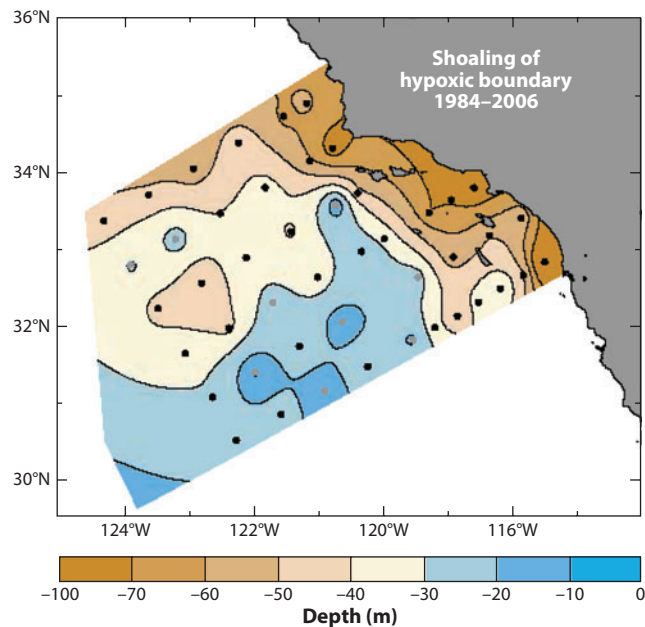

Figure 9

Change in depth in meters of the hypoxic boundary (60 μmol 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 equatorward 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 O_2 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-O_2 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 O_2 changes is weaker. In the thermocline of the South Indian Ocean, O_2 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 O_2 increase has been seen in the South Pacific (Murata et al. 2007). In the North Atlantic, an O_2 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, Frölicher et al. 2009).

A consistent finding is that the main driver of recent O_2 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 O_2 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, Frölicher 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 O_2 can be noted in **Table 3**. It remains difficult, however, to draw firm conclusions about global trends.

ATMOSPHERIC O_2 MEASUREMENTS

A direct link exists between changes in ocean and atmospheric O_2 inventories. At the global or basin scale, the net air-to-sea flux of O_2 in mol yr^{-1}, F_{O_2}, is related to the change in ocean O_2 inventory, I, according to

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

where C_{org} is the oceanic inventory of organic carbon, including both particulate and dissolved forms, and α is the O_2/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 of atmospheric O_2 concentration (reported as O_2/N_2 ratio) started in 1989 at La Jolla, California, followed by 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 is primarily influenced by the air-sea exchanges of CO_2, O_2, and N_2. It is also impacted 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 varies by fuel type. APO extracts the new information provided by O_2 data beyond that provided by CO_2 data.
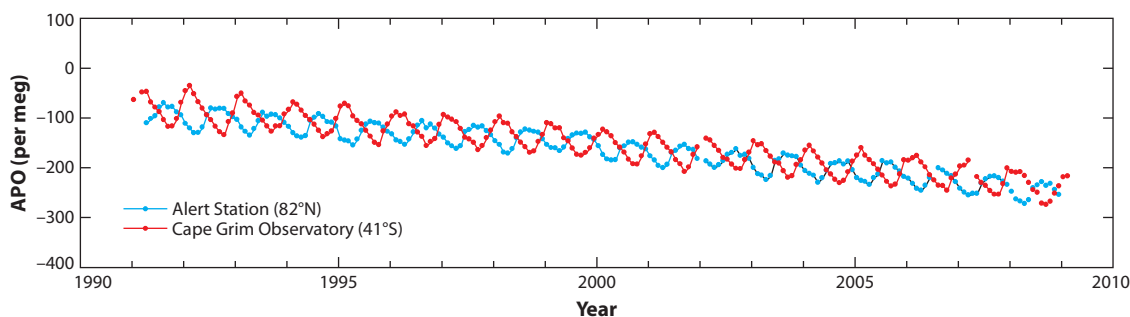

Figure 10

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): δAPO $= \delta(O_2/N_2) + 1.1/(0.2095) X_{CO_2}$, 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.

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 trend results mostly from fossil-fuel burning and ocean uptake of CO_2, with small contributions from long-term air-sea exchanges of O_2 and N_2 (Manning & Keeling 2006). The seasonal cycles in APO are predominantly caused by air-sea exchange of O_2, 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 O_2 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, the gradient is not zero. This annual-mean gradient provides a constraint on the meridonal fluxes of O_2 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 O_2 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 O_2 (Rödenbeck et al. 2008).

A primary application of atmospheric O_2 (or APO) measurements is the partitioning of the total global CO_2 sink into land and oceanic components. The application, however, is sensitive to uncertainties in the long-term fluxes of O_2 between the atmosphere and oceans. The issue can be understood in relation to the downward trend in APO: To resolve the contribution from ocean CO_2 uptake requires accounting for the other terms, including air-sea exchange of O_2. Interestingly, if the air-sea O_2 term is assumed to be zero, the oceanic sink that is obtained is smaller by approximately 0.5 ± 0.5 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 ~40 Tmol O_2 yr^{-1}, which is comparable to the ocean O_2 loss calculated from recent ocean warming of 6×10^{21} J yr^{-1} (Domingues et al. 2008) assuming a scaling of 6 nmol O_2 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 O_2 and C_{org}, the global net air-sea O_2 flux would be determined, thus improving the basis for estimating land (and ocean) CO_2 sinks from atmospheric O_2 data. A key need is thus to develop in situ methods for tracking changes in the O_2 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 O_2 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.

Toward an Ocean O_2 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 as part of the joint World Ocean Circulation Experiment (WOCE) Joint Ocean Flux Study (JGOFS) survey. 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 O_2 trends that impact ecosystems and complicate carbon budgeting. Prior studies of O_2 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 O_2 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 O_2 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 O_2 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 O_2 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 $\mu mol\ kg^{-1}\ decade^{-1}$, requiring high long-term stability and accuracy. To date, several Argo floats with O_2 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 $\mu mol\ kg^{-1}\ decade^{-1}$ 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 assessible long-term accuracy and the latter resolving scales of natural variability, knowledge of which is important in deconvoluting observations.

Determining Ocean CO_2 Uptake

A central goal of the CLIVAR Repeat Hydrography Program is to quantify the global CO_2 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 O_2 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 CO_2," i.e., the uptake driven by rising atmospheric CO_2 but excluding contributions from internal ocean processes, such as changes in the biological pump. Concurrent measurements of dissolved O_2 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 CO_2 input despite internal variability (Peng et al. 1998). But this raises questions when systematic changes in O_2 also occur: To what extent does the resulting estimate of CO_2 uptake include contributions from changing circulation and biology? Are corrections needed for changes in ocean O_2 inventory (Keeling & Garcia 2002)? The challenge posed by systematic changes in O_2 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 CO_2 sink to climate changes is to determine the total CO_2 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 O_2 from profiling floats suggests a possible way forward. The first step is to combine measurements of DIC and O_2 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

$$OPO = O_2 + \alpha(DIC - \tfrac{1}{2}ALKn) \qquad (2)$$

where ALKn is the nitrate-corrected total alkalinity and α is the O_2/C ratio for formation/destruction of marine organic matter. OPO is conserved with respect to marine photosynthesis/respiration, which produces compensating effects on O_2 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 O_2 and CO_2 across the air-sea interface. OPO is a close analog of APO, being conservative with respect to marine rather than terrestrial photosynthesis/respiration but responding to air-sea fluxes of both O_2 and CO_2. (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, O_2, and alkalinity (ALKn). The sum of ALKn and DIC terms can easily be shown to be a measure of the total CO_2 uptake from the atmosphere, whether "anthropogenic" or otherwise. The O_2 term is a measure of the net air-sea O_2 exchange per Equation (1). The change in OPO inventory thus provides a measure of the combined air-sea exchanges of O_2 and CO_2 over the basin.

The final step is to use float-based O_2 measurements in the upper ocean, with high spatial and temporal coverage, combined with the ship-based measurements of O_2, to provide an independent measure of the change in O_2 inventory. Correcting the change in OPO inventory allows the net CO_2 uptake to be calculated. Although this last step must await the development of an expanded

ocean O_2 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 CO_2 in the ocean in the face of a changing climate. The need for such an ambitious O_2 observing system is thus made even more compelling. Developing such an observing system may be the key to determining the total oceanic CO_2 uptake, whether using atmospheric O_2 measurements or ocean DIC measurements.

Other Challenges

Improving our ability to predict changes in ocean O_2 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 coupled physical/biological ocean general circulation models (OGCMs) 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 O_2 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 O_2 variability (Deutsch et al. 2006; Rödenbeck et al. 2008; P. Brandt, V. Hormann, A. Körtzinger, M. Visbeck, G. Krahmann, 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 O_2 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 O_2 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 O_2 depletions at depth (Lohan & Bruland 2008). Low O_2 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 $\sim$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 CO_2. 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 O_2 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 O_2 (Van Mooy et al. 2002). Rising CO_2 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 O_2 utilization. All remain poorly understood (Riebesell et al. 2009).

SUMMARY

The realization that future global warming might significantly impact ocean O_2 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 O_2 changes already seem to be occurring, most notably in the North Pacific and tropical O_2 minimum zones. Changes in the North Pacific are tied to increased stratification in the subarctic region. O_2 declines are consistent with the predicted response to global warming in global ocean models, and the patterns of observed O_2 change can be reproduced with higher-resolution models driven by observed forcings. The relative rapidity of O_2 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 O_2 declines in the tropics is unclear. Exiting global models do not have the resolution or accurate parameterizations to adequately describe the controls on O_2 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 O_2 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 O_2 is changing will also improve our ability to document the uptake of CO_2 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.

DISCLOSURE STATEMENT

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

ACKNOWLEDGMENTS

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**Annual Review of
Marine Science**

Volume 2, 2010

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Errata

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