

Workshop Report
“Ocean Deoxygenation: Past, Present, and Future”

Organized by the NASA Astrobiology Institute

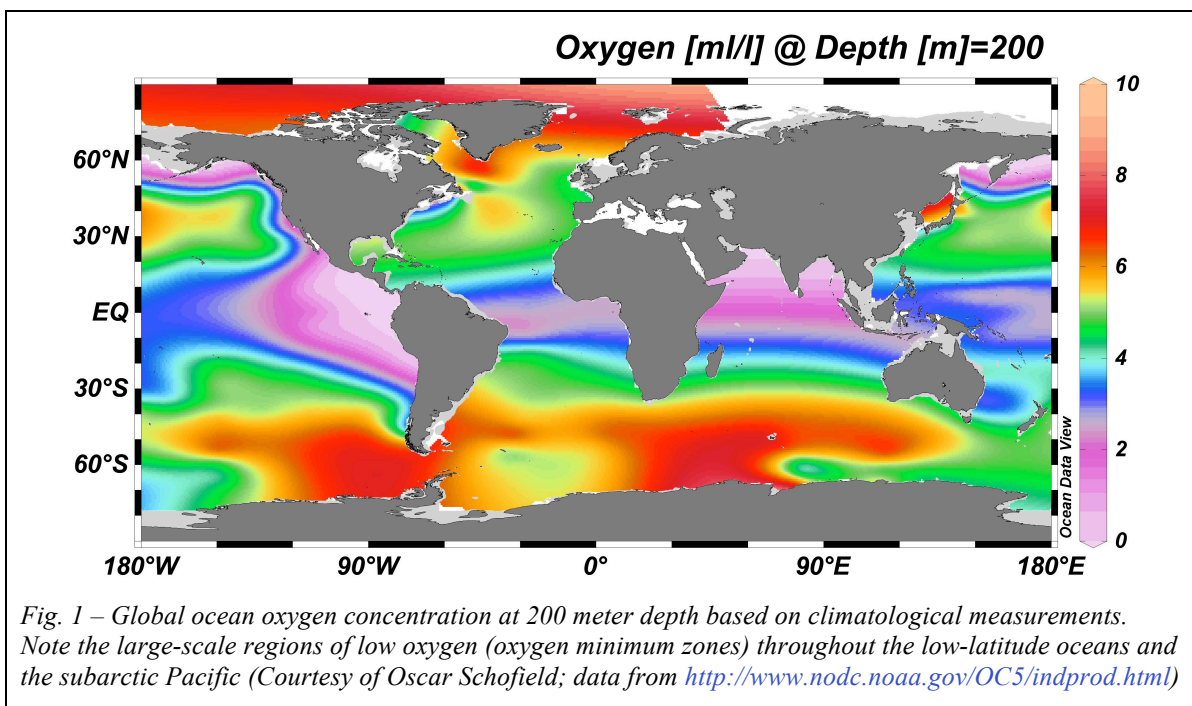
Held at NASA Ames Research Center

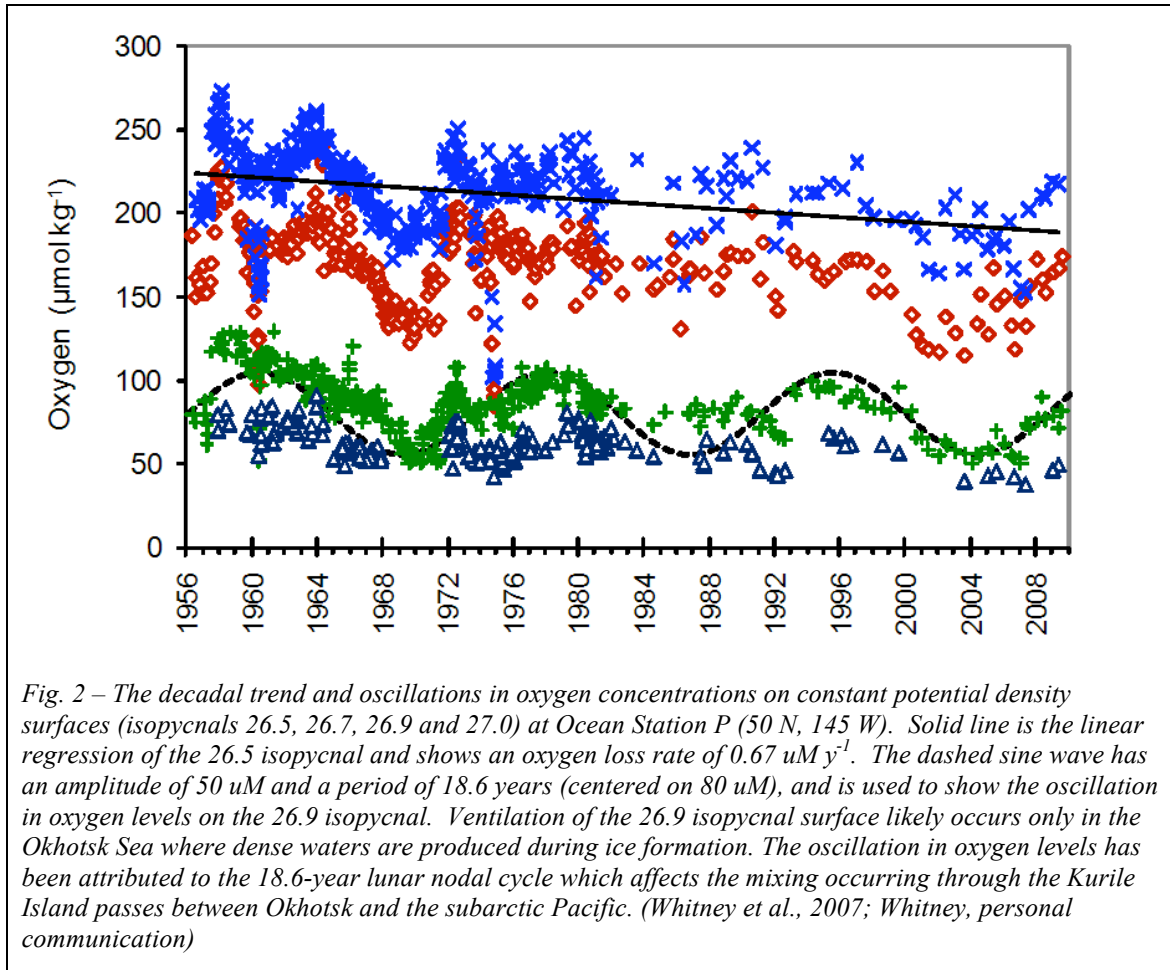
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Introduction

Loss of oxygen from Earth’s oceans has happened repeatedly over at least the last billion years, and is probably occurring today. In the past, major ocean anoxic events (OAEs) have generally been associated with warm climates, high carbon dioxide concentrations, and sometimes large igneous province volcanism. Many of these anoxic events have been regional, but at least some, e.g., OAE-2 (93 million years ago) and the end-Permian mass extinction 252 million years ago, appear to have been global. Much more recently, expansions of oxygen minimum zones (OMZs) occurred during the terminations of ice ages as the ocean emerged from its glacial state.

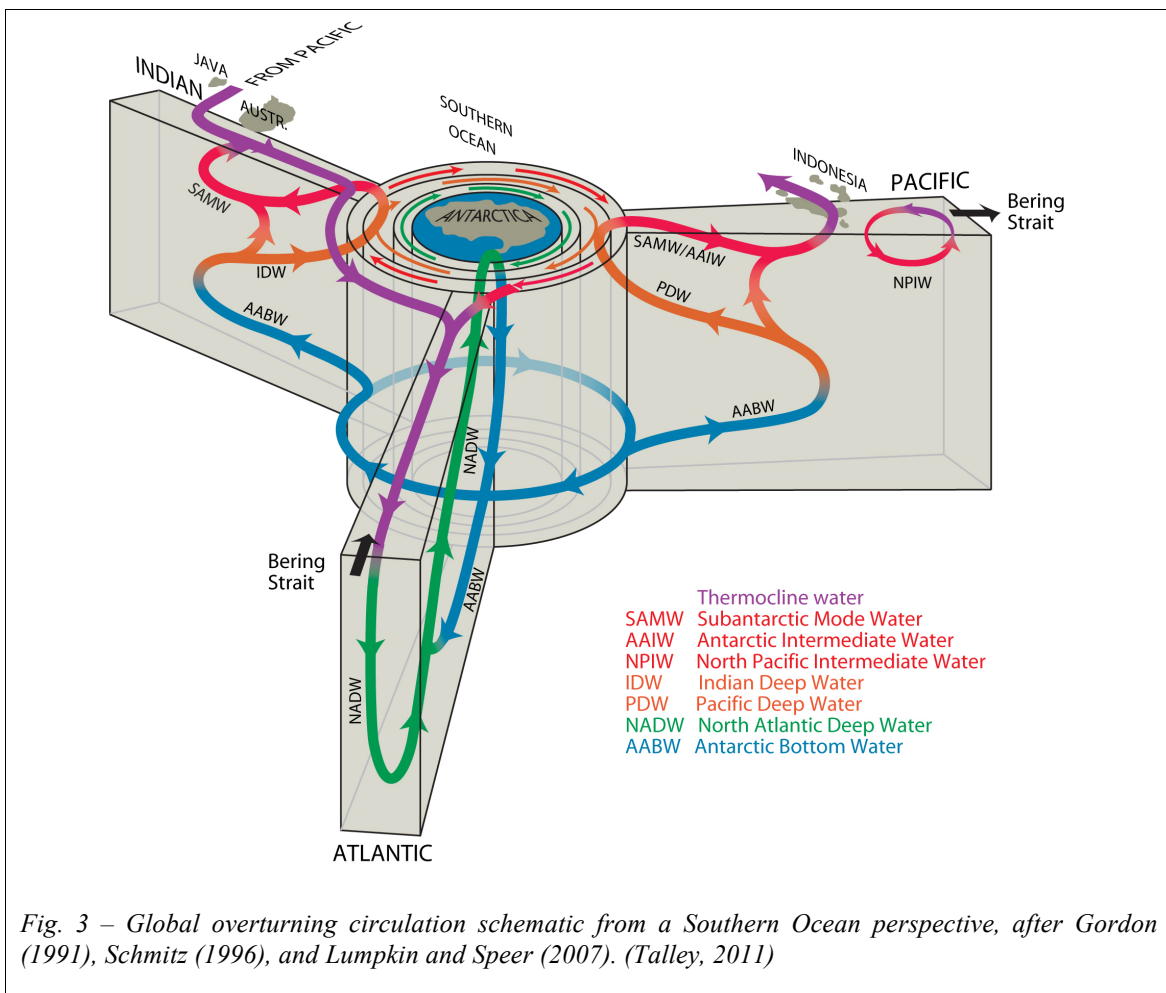
Today, loss of oxygen from the coastal ocean frequently is associated with anthropogenic eutrophication resulting from agricultural runoff and other societal processes. However, it appears that oxygen is also declining from both the North Pacific and the tropical oceans worldwide (Whitney et al., 2007; Keeling et al., 2010; Figures 1 & 2). It is unclear whether the loss throughout the open ocean is a secular trend and related to climate change; the result of natural, cyclical processes; or a combination of both. If related to climate change, a number of important factors may be involved, including the decreasing solubility of oxygen in water with increasing temperature, changes in wind forcing with changes in geographical temperature patterns, and increasing ocean stratification with increasing surface temperature and freshening.





The oxygen content of the oceans is determined by the balance between oxygen supply to the ocean interior, a process called *ventilation*, and the consumption of oxygen by respiring (mostly microbial) organisms and other oxidative processes. Ventilation of the deep ocean interior (> 1000 m) occurs today on time scales of hundreds of years in two principal regions: the North Atlantic and the circum-Antarctic ocean, particularly the Ross and Weddell seas. The locations of these sites of ventilation in the modern oceans are dictated by the current plate tectonic configuration of continental land masses. Hence, the patterns, and possibly the rates, of ventilation in the ancient oceans were inherently different from those of the present. The value of the deep-time paleo-record for understanding the potential for future deoxygenation events therefore lies in the lessons learned about processes and mechanisms rather than as exact analogs for future ocean states.

Digression - Ventilation encompasses all those processes that transfer and transport oxygen into the vast ocean interior. Ventilation happens from a combination of air-sea gas exchange, that makes surface waters dense, causing them to sink (subduct). Subduction of water occurs by a variety of processes, including cooling and salinification, convection, and brine rejection due to seasonal sea ice formation. Arising from a confluence of meteorological and ocean circulation circumstances, these processes tend to occur in specific geographic areas or “ventilation windows” that act as entry points for oxygen into the ocean. Two such windows are the North Atlantic and the Antarctic Oceans. (Fig. 3) Ocean circulation, constrained by a balance between a combination of wind and thermohaline forcing and ocean physics (in particular the geostrophic balance), plays a role in how oxygen is redistributed in the ocean interior. Turbulent mixing, both horizontal and vertical, is superimposed on this circulation and is likely an important, if not dominant, mechanism in oxygen impoverished regions. The key concern is that the processes responsible for ocean ventilation are climate-driven and hence will most likely alter in character in response to global change. This response will have a first-order impact on the oceanic distribution and inventory of oxygen.



The potential consequences of ocean oxygen loss are profound. Long-term declines could lead to reduced biological productivity and diversity, altered animal behavior, declines in fisheries, redistributions of communities, and altered biogeochemical cycles. Environmental feedbacks may also result, potentially including increased production of greenhouse gasses such as N₂O and CH₄. In the past, major shifts in populations and even mass extinctions occurred during periods when ocean oxygen content was low.

Digression – Terms We are concerned about the oxygen content of sea water because of its impact on biological processes as a respiratory electron acceptor. Most of the oceanic water column is well oxygenated with concentrations above 50-100 micromolar. Such waters are commonly referred to as *oxic*. When oxygen concentrations fall below 50-100 μM , many investigators describe such waters as *hypoxic*, but the boundary between oxic and hypoxic waters is variable and depends on the organisms under investigation, among other factors. Oxygen concentrations lower than $\sim 5 \mu\text{M}$ are referred to as *suboxic* by many marine scientists. Waters that are essentially oxygen free (below detection) are termed *anoxic*. In extreme cases of high oxygen demand and low oxygen supply, hydrogen sulfide, the waste product of microbial sulfate reduction, accumulates, and the water is said to be *euxinic*.

In general, hypoxia refers to a situation in which the organism(s) under consideration experience stress due to reduced oxygen. Such stress can occur at levels of about 100 micromolar for large, active animals, such as a tuna, but occurs at concentrations as low as $\sim 5 \mu\text{M}$ for small organisms or microbes. Thus, one cannot give a precise description of hypoxia, and authors should state concentrations ranges when using this term. At the higher range, hypoxic waters comprise $\sim 10\%$ of the oceanic volume.

This workshop was held to bring together researchers who study the ocean's oxygen content in the past and present. The goal was to identify ways in which one research area could inform the other and to develop collaborative opportunities to advance our overall understanding of the controls on ocean oxygen content.

Current state of knowledge

The Paleo-oceans

There is clear geological evidence that ocean oxygen concentrations have changed over time. In the distant past, the Earth experienced repeated periods of widespread, perhaps ocean-scale, anoxia sometimes lasting millions of years. These episodes, sometimes marked by major biotic extinctions (Figure 4), provide critical windows to the full range of climatic and oceanic extremes possible. Most often, these events occurred during times when atmospheric CO₂ and inferred temperature were both high—periods when there was limited or no ice at the poles—but generally are linked to additional triggers, most commonly large-scale tectonic processes such as volcanism. It becomes increasingly difficult to assess the spatial and temporal persistence of ancient ocean anoxia with greater geologic age because the principal evidence, in the form of “proxies”

such as carbon isotope records, is contained in deep-ocean sediments that are lost through subduction or uplift and erosion. For the most-ancient events (prior to ~250Ma), the geologic record is preserved primarily in sediments from continental margins and epicontinental seas. For the OAEs of the late Mesozoic (occurring mostly between ~140 and 85 Ma), evidence for ocean-scale anoxia is preserved in seafloor not yet lost to tectonic processes. Even more recently, there are detailed records of brief oceanic hypoxia at intermediate water depths accompanying the extreme, but transient global warming at the Paleocene-Eocene (55 Ma) boundary (Thomas, 2007). Despite the limitations, recent years have seen great improvement in our understanding of the patterns of past ocean oxygen deficiency and the drivers and feedbacks that underlie local and global oceanic O₂ budgets.

Digression – Proxies Many environmental variables are difficult or impossible to measure directly, and this is especially true of the ancient world. Thus, our historical knowledge is drawn from ‘proxies’—measurable properties of a sediment or sedimentary rock that scale in a predictable way to some immeasurable parameter of interest. Importantly, the best of these ecological, (bio)geochemical, and mineralogical tracers of transient primary properties are quantitative and preserve their archives deep into the geologic record. For example, O₂ concentrations present in seawater at the time underlying sediment is deposited are obviously not preserved in paleo-systems, but proxy fingerprints within the resulting rock can provide semi-quantitative measures of the initial dissolved O₂ levels.

Ecological proxies include the composition of faunal assemblages and the degree to which animals and unicellular eukaryotes live within and disturb sediment as a function of varying O₂ content. Geochemical proxies for paleo-O₂ concentration are both organic and inorganic and include several within the C-S-Fe system and the distribution patterns of numerous redox-sensitive trace metals (e.g., Mo, Mn, U, Re, and others). These approaches—defined and calibrated in modern O₂-deficient settings such as the Black Sea—have long histories of successful application. Mineralogic proxies include pyrite framboid size relationships, phosphorous distributions and associated C/P relationships, and certain layered silicate minerals (e.g., glauconite). Isotopic proxies (e.g., $\delta^{15}\text{N}$, $\delta^{34}\text{S}_{\text{pyrite}}$, $\delta^{56}\text{Fe}$, $\delta^{98}\text{Mo}$, U-system isotopes) record equilibrium or kinetic controls on processes that are ultimately mediated by molecular oxygen. The best of these can provide estimates of regional or global conditions with only local measurements by capturing seawater compositions that vary as a function of large-scale mass balance relationships. Certain organic molecules (biomarkers) preserved in sediments can be ascribed to microbial taxa with well-known redox-sensitive environmental requirements, including signatures of free hydrogen sulfide conditions within the photic zone of ancient water columns. Multiple proxies measured on the same samples at high stratigraphic resolution provide our most robust records of paleo-O₂ levels and their temporal variations.

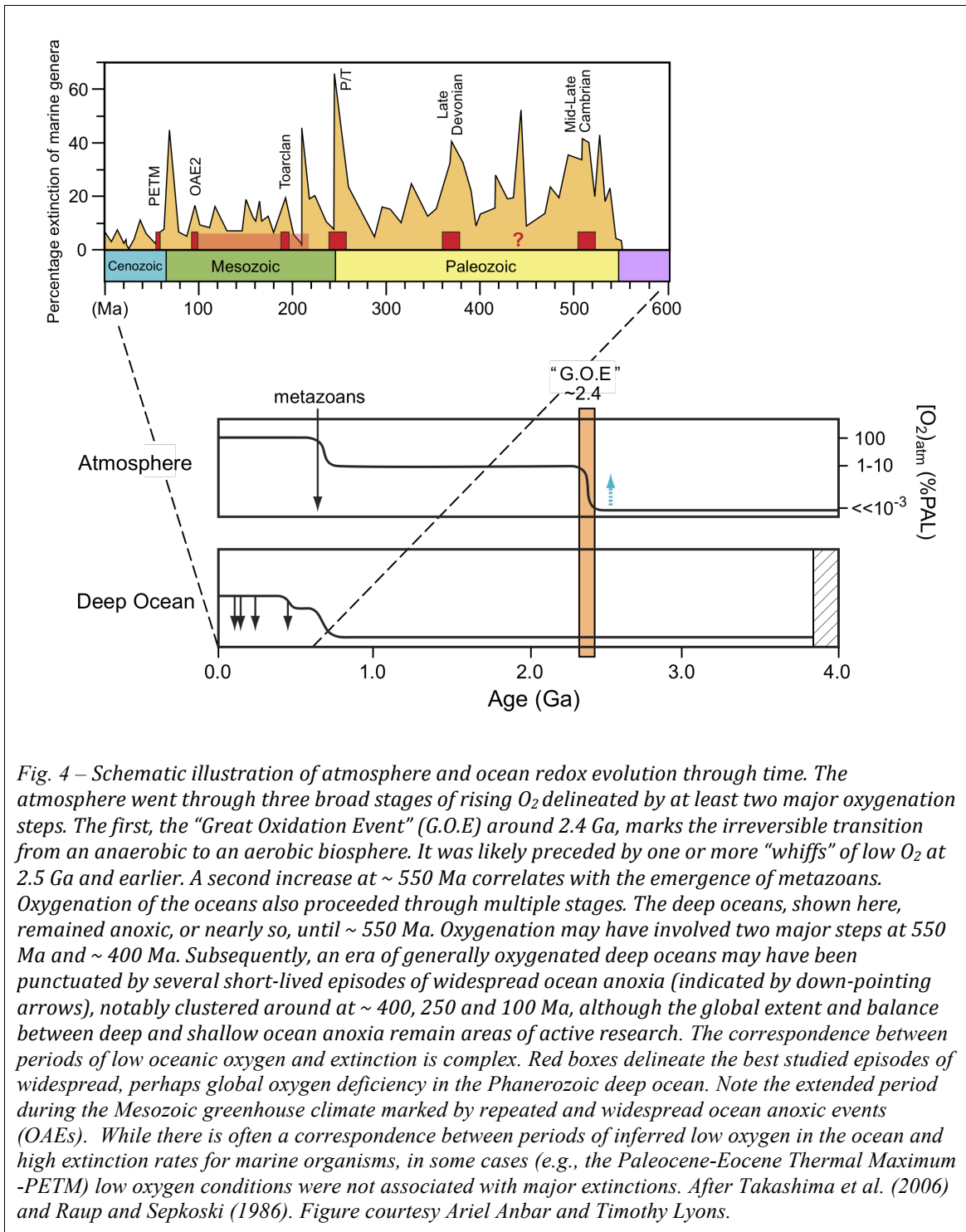


Fig. 4 – Schematic illustration of atmosphere and ocean redox evolution through time. The atmosphere went through three broad stages of rising O_2 delineated by at least two major oxygenation steps. The first, the “Great Oxidation Event” (G.O.E) around 2.4 Ga, marks the irreversible transition from an anaerobic to an aerobic biosphere. It was likely preceded by one or more “whiffs” of low O_2 at 2.5 Ga and earlier. A second increase at ~ 550 Ma correlates with the emergence of metazoans. Oxygenation of the oceans also proceeded through multiple stages. The deep oceans, shown here, remained anoxic, or nearly so, until ~ 550 Ma. Oxygenation may have involved two major steps at 550 Ma and ~ 400 Ma. Subsequently, an era of generally oxygenated deep oceans may have been punctuated by several short-lived episodes of widespread ocean anoxia (indicated by down-pointing arrows), notably clustered around at ~ 400, 250 and 100 Ma, although the global extent and balance between deep and shallow ocean anoxia remain areas of active research. The correspondence between periods of low oceanic oxygen and extinction is complex. Red boxes delineate the best studied episodes of widespread, perhaps global oxygen deficiency in the Phanerozoic deep ocean. Note the extended period during the Mesozoic greenhouse climate marked by repeated and widespread ocean anoxic events (OAEs). While there is often a correspondence between periods of inferred low oxygen in the ocean and high extinction rates for marine organisms, in some cases (e.g., the Paleocene-Eocene Thermal Maximum -PETM) low oxygen conditions were not associated with major extinctions. After Takashima et al. (2006) and Raup and Sepkoski (1986). Figure courtesy Ariel Anbar and Timothy Lyons.

Multi-proxy elemental, mineralogical, isotopic, molecular, and paleontological records preserved in Phanerozoic sedimentary rocks (542 million years [Ma] old to the present) point to numerous anoxic events (Fig. 4), including evidence for free hydrogen sulfide extending into the photic zone—the ocean’s surface layer where photosynthesis occurs.

There is strong evidence that some of these anoxic events were global in scale. The inventory and spatial distribution of continental crust was a critical variable, dictating the relative rates of weathering and burial of organic matter, both of which impacted O₂ content of the oceans and atmosphere, as well as the patterns of ocean circulation. Weathering rates also controlled the fluxes and spatial patterns of nutrient delivery to the ocean (e.g., P and Fe). An associated phenomenon, also under tectonic influence, was the emplacement of large igneous provinces that seem to have fostered, or at least accompanied, low-O₂ conditions in the ocean.

A complementary geological window is provided by the ice age world, when the continental configuration was the same as today, but the oceans were colder. Multiple proxies, measured in a large number of globally distributed marine sediment records, show coherent patterns of contraction for oxygen minimum zones (OMZ) during cold periods (Galbraith et al., 2004) and dramatic expansions of OMZs during intervals of rapid warming (Zheng et al., 2000). The most recent warming occurred at the end of the last ice age, when the large modern OMZs blossomed throughout intermediate depths of the Indian and Pacific Oceans, as physical oxygen supply decreased and export production patterns shifted. Recent work has revealed that these OMZ expansions were not synchronous between the northern and southern hemispheres but instead progressed in lockstep with atmospheric warming in the respective hemispheres, as recorded in ice core records (Robinson et al., 2007). The overwhelming message from this recent cold-to-warm climate transition is that the extent of oxygen-depleted waters is very sensitive to climate.

Changes in ocean oxygen levels have been an important factor in major bio-evolutionary events, including the advent of animals and episodic mass extinctions (Figure 4). Rising oxygen levels starting over 2 billion years ago were caused by, and in turn contributed to, the evolution of life, including the first appearance and proliferation of animals roughly 600 million years (Ma) ago (Canfield et al. 2007; Knoll and Carroll, 1999; Narbonne and Gehling, 2003). Subsequent intervals of low atmospheric oxygen levels contributed to oceanic hypoxia and marine biotic crises during the Phanerozoic (Huey and Ward, 2005). For example, widespread anoxia in shallow continental seas coincided with an extended biotic crisis during the Middle Devonian to Early Carboniferous periods (385-360 Ma), with maxima in extinction rates at times of peak anoxia (Algeo and Scheckler, 1998). Marine anoxia was widespread in both shallow-marine and deep-ocean environments during the Permian-Triassic boundary crisis (~252 Ma), the largest mass extinction event in Phanerozoic history—marked by the loss of ~90% of marine taxa (Benton 2003; Erwin 2006; Wignall and Twitchett, 1996; Grice et al., 2005). The extinction of benthic foraminifera during the Paleocene-Eocene (55 Ma) thermal maximum provides a clear example of how abrupt global warming (on a scale similar to that predicted for the future) affected ocean oxygen levels and biota (Thomas 1998, 2007).

During the warming of the last deglaciation, oxygen-poor waters expanded rapidly throughout the upper 1 km of the oceans, with dramatic de-oxygenation occurring locally on millennial timescales (Higginson et al., 2004, De Pol Holz et al., 2006). It is clear that the marine biosphere was impacted by these changes, with greater loss of fixed nitrogen

(Altabet et al., 1995, Ganeshram et al., 1995) and more nitrous oxide production during warm periods (Suthhof et al., 2001, Schmittner and Galbraith, 2008, Agnihotri et al., 2006).

The association of oceanic deoxygenation and marine biotic crises reflects a combination of effects linked directly and indirectly to low levels of dissolved seawater O₂. For example, an immediate consequence of reduced oxygen levels is to constrain organisms with high respiratory demands. An additional consequence is to provide greater ecospace for anaerobic communities, which frequently leads to elevated concentrations of compounds (e.g., CO₂ and H₂S) that are toxic to the vast majority of animal taxa (Knoll et al., 1996; Grice et al., 2005). Biotic responses to changing ocean O₂ levels, as captured in the deep-time record, thus provide an essential predictive window to the future impacts of ocean deoxygenation.

The Modern Oceans

The number of research papers about changes in oxygen concentrations in the contemporary ocean has increased rapidly in the last decade because there are now enough reliable measurements at the same location to make temporal comparisons. These comparisons come from all ocean basins (Keeling et al., 2010), but they are most numerous in the subarctic North Pacific, where oxygen transport to the interior ocean is weak. Observations of oxygen decrease in the open ocean thermocline between the 1970s and 1990s (e.g., Emerson et al., 2004) captured much attention because it was suggested that declining oxygen levels might be an early indicator of human impact on oceanic ecosystems through global warming. Model reproductions of these trends indicated that they were primarily induced by changes in ocean ventilation and circulation (Deutsch et al., 2006). However, subsequent measurements in the first decade of the new millennium (Mecking et al., 2008) indicated that the declines in oxygen levels were not secular but rather part of a decadal scale cycle. A recent comparison of data from global databases indicates a statistically significant decrease in oxygen concentration between the 1960/70's and 1990-2000 in the equatorial ocean and suggestive changes, both increases and decreases, in other regions (Stramma et al., 2010).

There are two longer time-series observations in the North Pacific with high-quality measurements in the open ocean over periods of about 50 years (Ono et al., 2001; Whitney et al., 2007). These data indicate a roughly 20-year cycle of varying oxygen concentration superimposed on a monotonic oxygen decrease of $\sim 0.5 \mu\text{mol kg}^{-1} \text{yr}^{-1}$. The cycle in oxygen concentration has been correlated with an 18.6-year periodic fluctuation of the diurnal tide of the ocean due to lunar precession (Whitney et al., 2007; Keeling, 2010). This process is believed to affect ocean ventilation by increasing mixing across the density gradient near the Kuril Islands at the mouth of the Sea of Okhotsk (Yasuda et al., 2006), a key area for ventilation of the North Pacific (Figure 2). The monotonic decrease could be the limb of a longer cycle or it may be the ocean's response to more restricted ventilation because of anthropogenically induced global warming.

Deoxygenation on ocean margins is in some places more dramatic than in the open ocean because of anthropogenic eutrophication (e.g., the Mississippi plume described by Rabalais and Turner, 2001, among others) of semi-enclosed coastal waters (e.g., Gooday et al., 2009). There have also been observations of extreme oxygen depletion on open continental shelves that appear to have been driven by natural ocean biogeochemical processes (e.g., Falkowski et al., 1980; Grantham et al., 2004; Hales et al., 2006; Chan et al., 2008). Continental margin upwelling systems are particularly prone to deoxygenation because their source waters are already low in O₂ and high in nutrients. The high nutrient levels fuel elevated production rates of photosynthetic organic matter. When this matter sinks and is respired at depth, oxygen concentrations are further reduced, with more severe effects when the water column is also stratified.

The relative roles of on-shelf biogeochemical cycling and source-water secular trends are unclear. Off the U.S. west coast, upwelled waters carry sufficient nutrient loads to induce extreme deoxygenation when photosynthetic products are trapped and respired locally. Such conditions are observed only intermittently, however, suggesting that a pathway of organic carbon export to the adjacent deep ocean must be playing a role in avoiding these conditions in many other years (Hales et al., 2006). The necessity of this deep-ocean export suggests a reason for the proximity of ocean interior OMZs and continental margin upwelling systems (e.g., Stramma et al., 2010). If a majority of the organic matter produced in upwelling systems is exported to the adjacent ocean-interior OMZ, the respiratory consumption in these areas will be increased relative to other similarly ventilated ocean interior waters.

Recent analysis of relatively long-term databases indicates trends of deoxygenation in waters that are sources for margin upwelling systems and shoaling of the depths of critical O₂ concentration iso-surfaces (Bograd et al., 2008). These O₂-lean waters are associated with migration of impacted fish stocks in the California Current System (F. Whitney, unpublished results). Even moderate long-term trends in declining source-water O₂ and increasing nutrient concentrations will cause currently intermittent but extreme deoxygenation conditions to become more frequent, intense, and persistent.

Our best tools for assessing future anthropogenic influence on ocean oxygen concentrations are global circulation models that succeed in reproducing observed changes over the past 50 years and include forcing due to future global warming. In nearly every case, the predicted concentrations decrease in the open ocean because of decreased ventilation due to stronger stratification (Oschlies et al., 2008; Hofmann and Schellnhuber, 2009). Presently, global ocean models (coupled 3-D general circulation models) do not resolve near-shore waters well enough to predict future trends in these regions. Future measurements should focus on determining the validity of the predicted open-ocean trends and the intensity of nearshore deoxygenation and its biological consequences.

Research needs

Improved Models

Ocean models are crucial tools for integrating the variety of processes that govern the distribution of O₂ in the modern ocean and for exploring its changes on a wide range of time scales. In addition, they serve to identify which processes might have driven large-scale changes in ocean oxygen content during historic greenhouse and super-greenhouse conditions, including periods of mass extinction. In order to better address changes in ocean oxygenation, model development is needed to improve the simulation of O₂ in current General Circulation Models (GCMs) as well as to establish model hierarchies that leverage the high-resolution capabilities of current GCMs and the more efficient but lower-resolution Earth System Models of Intermediate Complexity (EMICs).

Simulations of biogeochemical cycles in the modern ocean reproduce reasonably well the observed large-scale O₂ distributions. However, several processes of O₂ supply and consumption are only crudely represented, and, as a result, there are significant discrepancies between models and observations in some key areas. For example, most (if not all) models predict much larger anoxic zones in the contemporary ocean than those observed, suggesting that we lack the information to parameterize all the critical processes. Some of the uncertainties may result from our poor characterization of (1) the dependence of oxygen utilization rate on environmental parameters such as organic carbon flux, temperature, and oxygen concentration, especially in the low-O₂ regions; (2) the role of coastal margins and mixing and stirring by eddies in the supply of oxygen to zones that are not directly ventilated by the mean flow; (3) the role of equatorial/poleward undercurrent systems in supplying O₂-poor water to OMZs; and (4) the physical processes that determine properties such as the nutrient and O₂ content of newly ventilated water.

These problems should be addressed with the use of models that explicitly resolve the narrow currents and eddies that help to ventilate low-O₂ regions. In addition, such models need to include more biologically based representations of organic matter respiration. The combined development of eddy-resolving and biologically mechanistic models of O₂ cycling will permit the testing of such models against observations at the spatial and temporal scales now being achieved with measurements.

Models can also benefit from advances by the paleoceanographic community in investigating radically different ocean conditions in the geological past. To the extent that oxygen-deficient and fully anoxic zones may expand in the future, a stronger collaboration between modern- and paleo-oceanographers, involving model-model and model-data comparisons for modern and ancient data sets, will be highly beneficial to both communities.

Remote Sensing

A number of remote sensing observations have relevance to the ocean deoxygenation question. All are indirect, with ocean observables used as proxies for relevant forcings that drive both ventilation and respiration processes. Satellite-derived records of sea surface temperature, altimetry, wind stress, and curl and salinity allow us to characterize the scale of variability of physical processes driving ocean ventilation from regional to global scales. In addition, remotely sensed measurements of the ocean provide us with information that can help us constrain respiration rates in the ocean interior. For example, new ocean color products can provide estimates of the concentrations of particulate organic carbon (Stramski et al., 1999) and calcite (Balch et al., 2005), net primary production (Behrenfeld et al. 2005), and estimates of the particle size spectrum (Kostadinov et al., 2009). Ongoing developments also include estimates of phytoplankton functional group abundances (Alvain et al., 2005), which are important for estimating ballast effects and levels of chromophoric dissolved organic matter (CDOM, a proxy for biological oxygen consumption in the interior, Nelson et al., 2010; Fig. 5). From these datasets the sinking rate of organic carbon and thus particulate carbon export can be estimated, leading to estimates of oxygen utilization rate (Martin et al., 1987). However, in order to maximize the utility of these datasets, we need to develop integrated remote sensing/field observation/modeling approaches toward linking the surface to subsurface ocean for deoxygenation assessment.

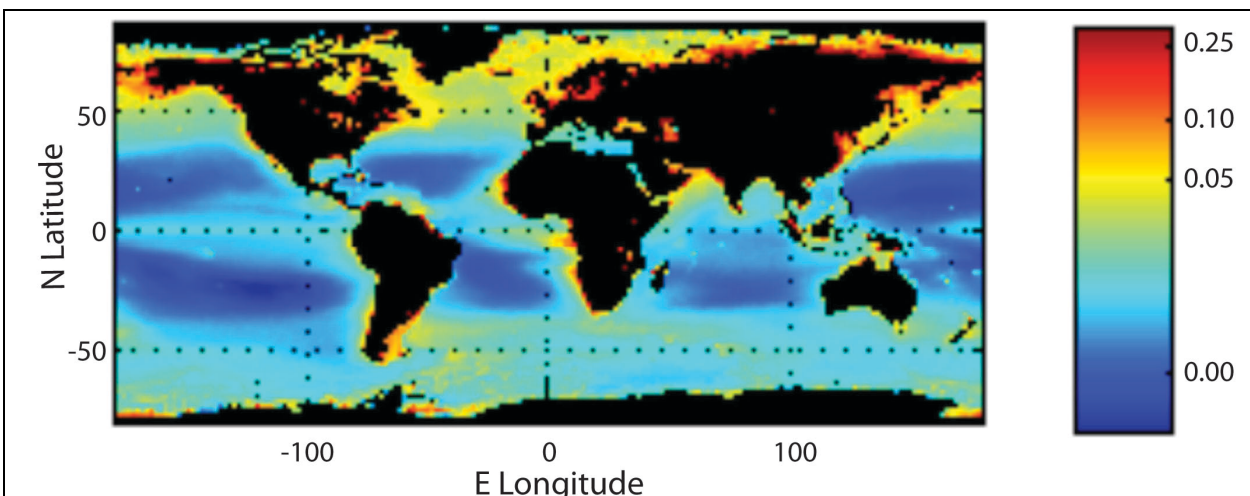


Fig. 5 – Global mean distribution of CDOM and particulate detrital material (as absorption coefficient at 443 nm, m^{-1}) estimated from SeaWiFS mission ocean color data (from Nelson et al., 2010, used by permission of the author). CDOM abundance in the ocean interior has been linked to remineralization processes including apparent oxygen utilization.

Improving the Historical Record

Our ability to quantify ocean oxygen concentrations in the geological record is critically dependent on geochemical proxies. The C-S-Fe system has long been used as a redox proxy (e.g., Raiswell et al., 1988), with Fe partitioning within sediments standing out as our best inorganic measure of local O₂ conditions (e.g., Lyons and Severmann, 2006; as reviewed in Lyons et al., 2009). Routinely constrained temporal variations in C and S isotope compositions of the ocean mirror the relative burial rates of organic matter and pyrite, which can be linked through simple modeling to the prevailing O₂ conditions in the ocean. Elemental concentrations of redox-sensitive trace metals (e.g., Mo, U) in marine sediments can be used to constrain both local dissolved O₂ levels and deepwater ventilation rates (Algeo and Lyons, 2006; Algeo and Tribovillard, 2009) and, through inventory relationships, the global extent of low O₂ levels in the oceans and atmosphere (Scott et al., 2008).

Recent innovations in analytical instrumentation have permitted accurate determinations of isotopic variation in high-mass elements such as Fe, Mo, and U, all of which are redox sensitive and thus potentially useful recorders of paleo-redox conditions. Iron isotope distributions, for example, can be diagnostic of iron cycling patterns unique to anoxic basins and oceans (Rouxel et al., 2005; Johnson et al., 2008; Severmann et al., 2009; Duan et al., 2010). Sediments deposited from anoxic waters thus provide a mechanism for tracking the isotopic composition of the ocean and its balance of oxic versus anoxic deposition through time. The long residence times of Mo (~800 kyr) and U (~450 kyr) in seawater make them potentially useful as proxies for global-scale variations in ocean redox conditions (Anbar and Rouxel, 2007).

Organic molecules, most of which are derived from lipids, record paleo-redox conditions in several ways. They can be diagnostic of the metabolic physiologies of diverse microbes; their preservation pathways can be determined by paleo-redox conditions (Brocks and Summons, 2004; Knoll et al., 2007); and they carry oceanographic carbon, hydrogen, and nitrogen isotope signals with great fidelity (Hayes, 2001). Combined, organic and inorganic methods allow us to infer the presence and specifically the depth of anoxic conditions in the ancient ocean (e.g., Anbar and Knoll, 2002; Lyons et al., 2009). Our confidence in these inferences would be greatly enhanced by improved knowledge of the phylogenetic distributions, biosynthesis, and physiological roles of geostable molecules. This gap is an important area of ongoing and future research.

Biological proxies based on fossil remains can also be valuable sources of information on past events. The chemical composition of animal shells; mollusk statoliths; or fish otoliths, bones, teeth, jaws, or scales may provide clues about exposure to hypoxia (as well as other environmental perturbations). Understanding the signatures in hard parts of animals exposed to hypoxic, suboxic, or anoxic waters may help us interpret O₂ in the sedimentary archive over short and long time scales, and microsampling provides resolution of subannual variation over the lifetime of an organism.

Despite recent progress with paleo-O₂ proxies and our greatly refined view of the temporal and spatial variations in early ocean redox conditions (reviewed, for example, in Lyons et al., 2009), the paleoceanographic frontier is defined by our need for improved proxies that speak specifically to global conditions. Also needed is further drill core sampling of fresh, unweathered materials on land, collected without trace element and organic contamination, and further ocean drilling along depth transects to enable reconstruction of the vertical extent of oxygen minimum zones in the past.

Understanding the geologic record of ocean anoxia would also be aided by stronger integration of paleobiological and geochemical investigations of past oceanic anoxic intervals at even higher stratigraphic resolution. Studies of the Cenozoic (65 Ma to the present), for which there is an extensive record of open ocean to continental margin environments, are of obvious value, as are investigations of sediments deposited below modern-day oxygen minimum zones as important analogs for ancient systems.

Oxygen Observational Records for the Modern Ocean

The best modern records of ocean oxygen concentration show ~bi-decadal oscillations superimposed on a slow ~50-year record of decrease. Unfortunately, many of the data archived over this time frame are of poor quality. The overall quality improved circa 1965 with the publication of papers by Carpenter (1965a,b) and Carritt and Carpenter (1966), which codified the methodology. Nevertheless, some post-1965 data are poor, and some groups obtained high quality data much earlier than 1965. A quality assessment of the archived data is essential to gain the maximum possible information from these historical observations—as backdrops for assessing current and future change.

Even the highest quality historical observations were not collected with the goal of resolving the low-period oscillations and longer-term trends of interest here. Future observations must strive for improved spatial-temporal resolution. Ships, moorings, floats, gliders, and the expanding international network of ocean observatories will all be important infrastructure for developing a robust data set. Standardized protocol and calibration procedures will also be important for ensuring high quality data that are readily compared. Sampling resolution should reflect the characteristic spatial and temporal scales of variability for the particular system under study, such that comparisons can be made without bias over long temporal and spatial scales. This goal will require a multi-platform sampling strategy. Emphasis should be placed on regions deemed to be the most sensitive recorders of changes in oxygen concentrations, such as OMZs and low-O₂ regions.

Experimental Research

A barrier to understanding changes in contemporary ocean oxygen content is an incomplete understanding of anoxia in the geological record. Although modern circulation models are able to accurately simulate the locations of oxygen minimum zone boundaries, they tend to produce excessive drawdown of oxygen and nitrate within those zones (c.f., Sarmiento et al., 2010). It is unclear whether this problem is due to a failure

to properly simulate the physics governing vertical and lateral exchange in the OMZs or whether there are biogeochemical controls on remineralization that cause it to occur at shallower depths over the OMZs.

One way to potentially address this issue is by conducting an experiment in the field. The question of whether physical exchange was properly simulated could be addressed by a tracer release experiment—with patches deployed on both sides of the physical front that marks the western edge of the OMZ, as well as by high resolution measurements of tracers in the oxycline above and below the OMZ (particularly CFCs but potentially including others). Because mixing above the OMZ has potentially interesting feedbacks to climate through ocean color (Anderson et al., 2009; Gnanadesikan and Anderson, 2009) as well as through controls on biological productivity, bio-optical measurements of color and solar absorption should be a part of this effort as well. The question of biogeochemical feedbacks on remineralization would require measurements of particle fluxes as well as detailed examination of the processes (remineralization rate, zooplankton abundance) controlling how material is reprocessed as it moves into the OMZ. It is possible that Lagrangian floats and gliders could play an important role in characterizing both the particle fluxes and the horizontal currents involved in setting the biogeochemical structure of this region, but in-situ characterization of the bacterial and zooplankton communities would still be required to generate a properly mechanistic understanding. NASA could play a key role both in supporting characterization of ecosystem structure and particulate dynamics on the biological side and altimetry and winds in data-assimilative models on the physical side.

Implications for Technology Development

NASA and other agencies can catalyze major advances in ocean instrumentation by fostering new sensor technologies aimed at characterizing both the oceanic response to deoxygenation and the processes that promote or mitigate change. Although oxygen sensor technologies have improved over recent years, further advances in sensitivity and stability are required. Moreover, new sensor methodologies (e.g., those based on membrane-inlet mass spectrometry and/or precision barometry) aimed at characterizing the solution state of other gases (e.g., Ar and N₂) in near-surface waters have potential for diagnosing details of air-sea oxygen exchange at a level useful for establishing regional mass balance constraints on ventilation and biological production. Advances in infrared and electrode technology could also enable us to enhance observations of nitrous oxide production and denitrification in hypoxic and suboxic zones underlying high production regions. Molecular and physiological technology is now expanding rapidly and soon will include development of indicators of O₂-stress or adaptation to low-O₂ environments.

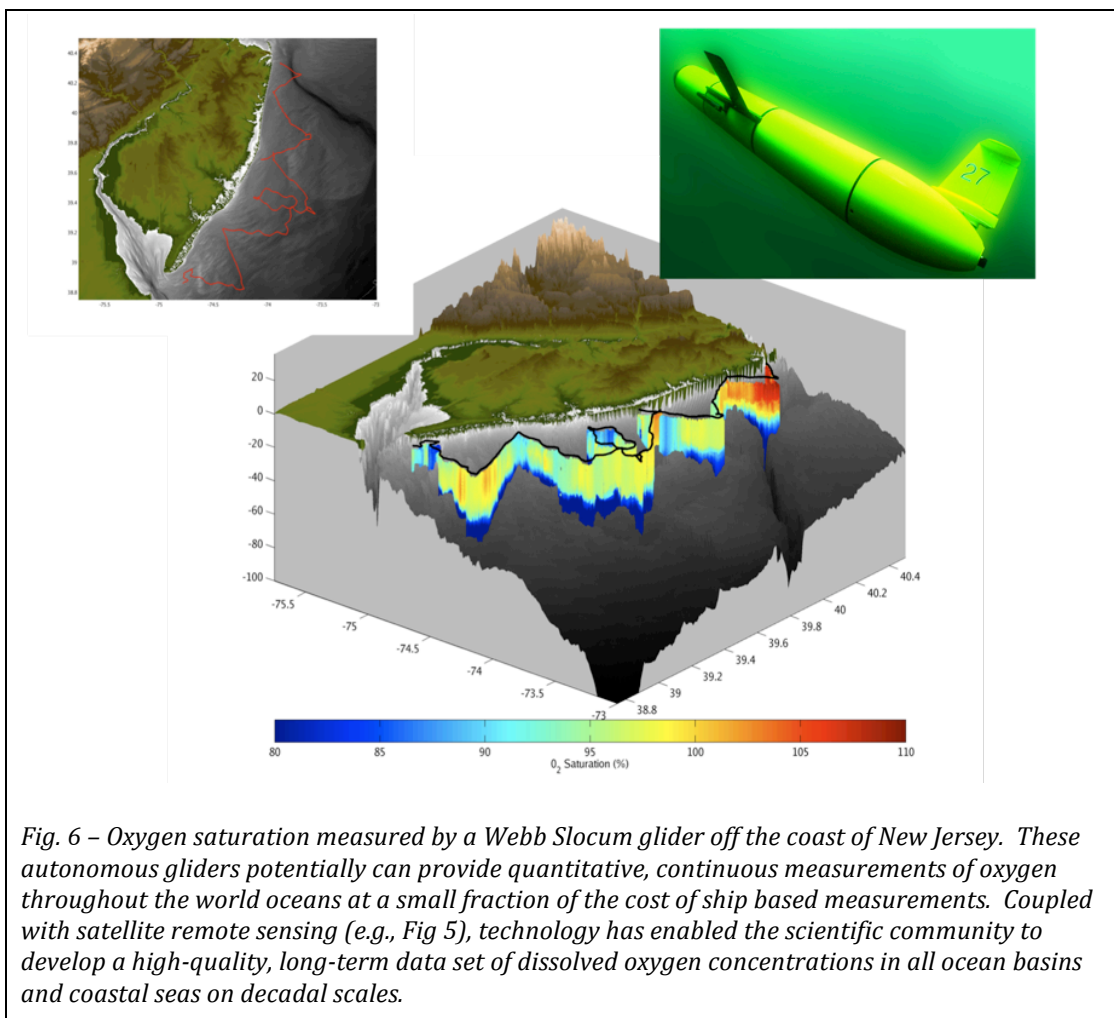
Our capacity to predict and address biotic responses to oxygen changes requires knowledge of animal exposures to oxygen and their tolerances. Due largely to inaccessibility, such information is scarce for deep-margin and open-ocean biota. Improved imaging through optical, acoustic, or satellite-based tagging approaches can enhance understanding of animal distributions, behavior, size structure, and diversity in relation to oxygen level and its variability over time. Integration of tools—such as time-

lapse video cameras, optical plankton recorders, and hydroacoustic backscatter signals—with new technologies in autonomous vertical profiling or Lagrangian drifters and long-duration underwater gliders has great potential for mapping the distribution of organisms within oxygen minima zones. Such characterizations are critical, since oxygen minima function as strong barriers to some species and refuge to others, with interfaces and transition areas having heightened biotic activity (Levin, 2003; Levin et al., 2009).

A critical need in oceanographic instrumentation is access to biological rate measurements. Indeed, despite the importance of aerobic respiration to the overall oxygen budget in the oceans, measurements of respiration are sparse and based primarily on methods and technologies from the early 20th century. Guided by basic scientific principles of gas exchange, heat production, and biologically altered redox reactions, there exists a possibility to develop novel instrumentation to access real-time rates of oxygen consumption, nitrous oxide production, and other critical microbial metabolic processes *in situ*.

Changes in ocean oxygenation are often accompanied by changes and interactions involving temperature, pH, salinity, nutrient levels, and inorganic compounds. These physical and chemical interactions alter key physiological processes in complex ways that are not currently well understood. Experiments that manipulate multiple environmental factors in concert, not individually, will elucidate how changes in modern ocean environments alter organismal survival and physiology and also inform paleophysiological patterns. Experiments that document differences in physiological tolerances of representatives from various taxonomic groups and from areas differing in oxygen content will indicate which organisms are acutely vulnerable to deoxygenation and other environmental change. Multi-generation laboratory experiments can monitor genetic responses to altered oxygen, temperature, and pH levels and thus elucidate the potential for organisms to adapt rapidly to oxygen change. A strategic search for molecular, morphological, physiological, geochemical, or ecosystem-level indicators of exposure to hypoxia is needed to track current or past changes. Observations in environments with oxygen near biotic thresholds can clarify how deoxygenation alters community composition, species interactions (predation, competition, symbiosis), as well as biologically driven geochemical feedbacks that are critical to maintaining an oceanic environment that is sustainable for human exploitation.

To better understand the feedbacks between climatic changes and ocean oxygen concentration will require long term ocean observing networks, models, and analyses of historical data. To this end, the Ocean Observing Network, with its focus on *in situ* sensors on gliders and mooring (Figure 6), and remotely sensed data of upper ocean phenomena including color, sea surface temperature, wind speed, and sea surface height, will provide an invaluable set of data for the coming decades. The resulting time series of ocean oxygen and physical, chemical and biological phenomenon requires interagency cooperation and commitment to this critical issue facing the health of the oceans.



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Appendix A – Workshop Agenda

Wed., March 31

0800 – 0845 Welcome, introductions, and charge to the workshop
Pete Worden, Ames Center Director
Paul Falkowski, Science Organizing Committee Chair
Carl Pilcher, NASA Astrobiology Institute Director

Session 1: Processes

Chair: Steve Hipskind, Ames Research Center
Rapporteur: Steve Emerson, Univ. Washington

0845 – 0930 Bill Jenkins (WHOI) -- **How the Ocean Ventilates**
0930 – 1015 Lynne Talley (SIO) -- **Climate Change and Ventilation Processes**

1015 - 1045 Break

Session 2: The Phanerozoic

Chair: Jeff Kiehl, National Center for Atmospheric Research
Rapporteur: Lee Kump, Pennsylvania State University

1045 – 1130 Tim Lyons (UCR) -- **Geochemical Evidence of Ocean Anoxic Events**
1130 – 1200 Ellen Thomas (Yale) – **PETM Ocean Oxygen - Biogeochemical Proxies**

1200 – 1300 Lunch

Session 3: Climate Effects

Chair: Paul Falkowski, Rutgers University
Rapporteur: Roger Summons, MIT

1300 – 1330 Tom Algeo (U. Cinn.) – **The Pleistocene and Ocean Oxygen Content**
1330 – 1400 Steve Emerson (U. Wash.) -- **Evidence of Modern Ocean Deoxygenation**
1400 – 1430 Curtis Deutsch (UCLA) -- **Biogeochemical Feedbacks between Climate and Ocean Oxygen Content**
1430 – 1500 Burke Hales (Oregon State) -- **Processes Controlling Oxygen Minimum Zones in the Modern Ocean**

1500 -- 1530 Break

Session 4: Biological Effects and Remote Sensing

Chair: Ricardo Letelier
Rapporteur: Ray Huey, Univ. Washington

1530 – 1600 Lisa Levin (SIO) -- **Ocean Deoxygenation: Responses of Metazoans**

1600 – 1630 Ray Huey (U. Wash.) -- **Respiratory Physiology**
1630 – 1700 Lou Codispoti (U. Maryland) -- **Interactions between Oxygen and the Nitrogen Cycle**
1700 – 1730 Norm Nelson (UC Santa Barbara) – **Chromophoric Dissolved Organic Matter as a Proxy for Dissolved Oxygen**

1730 – Adjourn

Thurs., April 1

0830 – 0930 Reports from rapporteurs
0930 – 1000 General discussion and breakout group structure/participants/questions
1000 – 1015 Break
1015 – 1130 Breakout sessions
1135 – 1215 Reconvene in plenary – brief reports from breakout chairs – identify key questions and process for rest of day
1215 – 1315 lunch
1315 – 1530 Breakout sessions
1530 – 1600 Each participant writes ~2 paragraphs about their key issues, questions, priorities, etc.
1600 – 1730 Reconvene in plenary – reports from breakouts to plenary – prioritize key issues and areas that require research investments.
1730 Adjourn

Friday, April 2

0830 – 1200 The speakers from Wednesday and 4 rapporteurs remain to develop ~7 to 10 page White Paper (with appendices, as appropriate). Other participants are free to leave. White Paper should identify the basic issues of controls of oxygen in the ocean and its effect on life in the geological past, at present, and in the future (time scale to be defined by participants), as well as remote sensing of ocean oxygen content - proxies and models.
1200 – 1300 lunch
1300 – end of meeting

Appendix B – Science Organizing Committee

Paul Falkowski, Chair	Rutgers University
Mark Altabet	Univ. Massachusetts, Dartmouth
Ariel Anbar	Arizona State University
Steve Emerson	Univ. Washington
Mick Follows	Massachusetts Institute of Technology
Ray Huey	Univ. Washington
Ralph Keeling	Scripps Institution of Oceanography, UCSD
Dennis Kent	Rutgers University
Jeff Kiehl	National Center for Atmospheric Research
Lee Kump	Pennsylvania State University
Ricardo Letelier	Oregon State University
Tim Lyons	University of California, Riverside
Roger Summons	Massachusetts Institute of Technology

Appendix C – Workshop Participants

Algeo	Tom	U. Cincinnati
Altabet	Mark	U. Mass. Dartmouth
Anbar	Ariel	ASU
Behrenfeld	Mike	Oregon State
Bristow	Laura	U. Mass. Dart.
Codispoti	Lou	U. Maryland
Deutsch	Curtis	UCLA
Emerson	Steve	U. Washington
Falkowski	Paul	Rutgers
Galbraith	Eric	McGill
		NOAA GFDL
Gnanadesikan	Anand	Princeton
Goolish	Edward	NASA Ames/NAI
Hales	Burke	Oregon State
Hayes	John	Berkeley
Hipskind	Steve	NASA Ames
Huey	Ray	U. Washington
Jenkins	Bill	WHOI
Jewett	Libby	NOAA
Kendall	Brian	ASU
Kiehl	Jeff	NCAR
Kirven-Brooks	Melissa	NASA Ames/NAI
Kryc	Kelly	Moore Foundation
Kump	Lee	Penn State
Letelier	Ricardo	Oregon State
Levin	Lisa	SIO
Lipschultz	Fred	NASA HQ
Lyons	Tim	UC Riverside
Manizza	Manfredi	SIO
Meyer	Katja	Stanford
Nelson	Norm	UCSB
Pilcher	Carl	NASA Ames/NAI
Planavsky	Noah	UC Riverside
Reinhard	Chris	UC Riverside
Robinson	Rebecca	URI
Romaniello	Steve	ASU
Rothschild	Lynn	NASA Ames
Schmittner	Andreas	OSU
Scofield	Christine	NASA Ames
Sepulveda	Julio	MIT
Summons	Roger	MIT
Sundquist	Eric	USGS/Woods Hole
Talley	Lynne	SIO
Thomas	Ellen	Yale

van de Schootbrugge
Voytek

Whitney
Worden
Zornetzer

Bas
Mary

Frank
Pete
Steve

Goethe
Univ/Frankfurt
NASA HQ
Fisheries/Oceans,
Canada
NASA Ames
NASA Ames