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Ocean oxygen minima expansions and their biological impacts

Lothar Stramma^{a,*}, Sunke Schmidtko^{a,b}, Lisa A. Levin^c, Gregory C. Johnson^b^a IFM-GEOMAR, Leibniz-Institut für Meereswissenschaften, Düsternbrooker Weg 20, 24105 Kiel, Germany^b National Oceanic and Atmospheric Administration, Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115, USA^c Integrative Oceanography Division, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, CA 92093-0218, USA

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ABSTRACT

Climate models with biogeochemical components predict declines in oceanic dissolved oxygen with global warming. In coastal regimes oxygen deficits represent acute ecosystem perturbations. Here, we estimate dissolved oxygen differences across the global tropical and subtropical oceans within the oxygen minimum zone (200–700-dbar depth) between 1960–1974 (an early period with reliable data) and 1990–2008 (a recent period capturing ocean response to planetary warming). In most regions of the tropical Pacific, Atlantic, and Indian Oceans the oxygen content in the 200–700-dbar layer has declined. Furthermore, at 200 dbar, the area with $O_2 < 70 \mu\text{mol kg}^{-1}$, where some large mobile macro-organisms are unable to abide, has increased by 4.5 million km^2 . The tropical low oxygen zones have expanded horizontally and vertically. Subsurface oxygen has decreased adjacent to most continental shelves. However, oxygen has increased in some regions in the subtropical gyres at the depths analyzed. According to literature discussed below, fishing pressure is strong in the open ocean, which may make it difficult to isolate the impact of declining oxygen on fisheries. At shallower depths we predict habitat compression will occur for hypoxia-intolerant taxa, with eventual loss of biodiversity. Should past trends in observed oxygen differences continue into the future, shifts in animal distributions and changes in ecosystem structure could accelerate.

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1. Introduction

Climate models run over centuries predict an overall decline in oceanic dissolved oxygen concentration and a consequent expansion of the mid-depth oxygen minimum zone (OMZ) under global warming conditions (e.g. Matear et al., 2000; Bopp et al., 2002; Oschlies et al., 2008). One analysis of oxygen data suggested that most of the expected changes due to decadal-scale perturbation of marine biota occur in shallow water (Keller et al., 2002). Observed oxygen changes in the North Pacific led to apparent oxygen utilization (AOU) increases of $10\text{--}20 \mu\text{mol kg}^{-1}$ since the late 1960s in the subtropical ocean (Emerson et al., 2004). An investigation of the OMZ in the eastern tropical North Atlantic showed that the supply by eastward currents is important for the oxygen budget or changes in the OMZ (Stramma et al., 2008a). Recently, expanding OMZs in all three tropical oceans were documented in a few geographically limited, but well-sampled, areas (Stramma et al., 2008b). Multiple regional analyses of oxygen changes over recent decades and the potential for larger future oxygen declines suggest the need for an improved

observing system to track ocean oxygen changes (Keeling et al., 2010).

While seasonal hypoxia is common on some upwelling-prone shelves, over the past 10–15 years extended low-oxygen events have been observed on normally well-oxygenated shelf areas. Oxygen declines and shoaling of the oxic–hypoxic boundary by as much as 90 m have been observed from 1984 to 2006 on the southern California shelf (Bograd et al., 2008). The California Current system is strongly influenced by subarctic waters, which are losing oxygen. In addition off California, some of the oxygen-poor water appears to originate from the tropical Pacific. This tropical water can be transported north by the California Undercurrent even to the Oregon coast (Pierce et al., 2000). Off the Oregon coast previously unreported hypoxic conditions have been observed on the inner shelf since 2000, with hypoxia being especially severe ($O_2 < 20 \mu\text{mol kg}^{-1}$) in 2006 (Chan et al., 2008).

Water in shallow, oxygen-poor layers frequently upwells onto continental shelves on the eastern boundaries of ocean basins (Diaz and Rosenberg, 2008). Upwelling also injects nutrients onto these shelves, stimulating production and increasing local biological oxygen demand. Coastal upwelling systems support a large proportion of the world's fisheries and play key roles in ocean nutrient cycles. However, many economically and ecologically important mobile macro-organisms are stressed, migrate away, or die under hypoxic ($O_2 < 60\text{--}120 \mu\text{mol kg}^{-1}$) conditions

* Corresponding author. Tel.: +49 431 6004103; fax: +49 431 6004102.

E-mail address: lstramma@ifm-geomar.de (L. Stramma).

(Gray et al., 2002; Vaquer-Sunyer and Duarte, 2008). Therefore, understanding the interactions among ocean oxygen changes driven by climate change, upwelling-driven hypoxia, and ecological perturbations is critical (Bograd et al., 2008).

Anoxic conditions (complete depletion of oxygen) have even greater biogeochemical impacts. For instance, increased marine production of N_2O due to intensifying anoxia was reported on the Indian continental shelf (Naqvi et al., 2000). It was suggested that a global expansion of hypoxic zones may lead to an increase in marine production and emission of N_2O , a greenhouse gas. The oxygen minimum zone-inhabiting microbe SUP05 has the potential to fix CO_2 while simultaneously producing N_2O , and this role will become more visible if habitat range increases with OMZ expansion (Walsh et al., 2009). The OMZs, while spatially limited, also impact nutrient budgets and biological productivity, hence CO_2 cycling within and uptake by the global ocean.

To date most observation-based analyses of large-scale oxygen changes have been regional. Here we investigate oceanic oxygen changes between $40^\circ N$ and $40^\circ S$ around the world at 200 dbar as well as for the layer 200–700 dbar (~ 200 –700 m). We make statistical assessments of oxygen changes and their statistical significance between the period 1960–1974 and the period 1990–

2008. As OMZs expand they impinge increasingly on shelf habitats; hence we discuss the possible biological consequences of increasing oxygen deficits on shelf areas and the mechanisms by which hypoxia may modify shelf ecosystems.

2. The data and methods

Hydrobase (Curry, 2008) quality-controlled data available as of 10 October 2008 were augmented with additional recently collected data sets (Table 1) for the world ocean between $40^\circ N$ and $40^\circ S$ for time periods 1960–1974 and 1990–2008 (Fig. 1). The latter time period considered is a little longer than the former, as data for recent years are sparse, and all are not yet archived at data centers. We also added very recently collected data (Table 1). The data distribution for the earlier period shows a focus of station data near the continents with only a few trans-oceanic sections. In contrast, the latter period is dominated by the trans-oceanic sampling pattern of the World Ocean Circulation Experiment (WOCE), augmented by regional experiments.

Profiles within the analysis periods were vertically interpolated to pressure levels at 100-dbar intervals from 200 to 700 dbar.

Table 1

Datasets used to compute the oxygen and temperature differences between 1960–1974 and 1990–2008.

Dataset/cruise	Comments
Hydrobase QC Dataset	Version as online October 2008 with suspect data from Pacific and Gulf of Mexico WMO squares (5012, 5107, 5108, 5109, 7003, 7012, 7013, 7112, 7209, 7300, 7403, 7404) removed
CALCOFI Dataset	1949–2006 bottle data available as of May 2008
NOAA Ship Ka'imimoana Dataset	Tropical Pacific 2000–2006, available cruises with oxygen data. http://tao.noaa.gov/tao/kaimi/ctd/ctd_ndbc.shtml
Melville 1999	October–November 1999 eastern tropical Pacific (see van Geen et al., 2006)
Meteor 28/1	March–June 1994 tropical South Atlantic bottle data
Meteor 47/1	April 2000 tropical Atlantic
Meteor 55	Fall 2002 tropical North Atlantic bottle data
Meteor 68/2	Summer 2006 tropical Atlantic
NACP West Coast Cruise	December 2007–February 2008 northern and tropical eastern Pacific, 13 short cross-shelf sections between Canada and Mexico
Revelle 322	Spring 2007 Indian Ocean
Ron H. Brown 2005	January–February 2005 tropical and South Atlantic
Sonne 89	Summer 1993 Indian Ocean
Sonne 102	May–June 1995 southeastern Pacific, provided by Gary Shaffer and Bo Thomson
Sonne 128	January 1998 Indian Ocean
Thalassa 2000	Summer 2000 tropical Atlantic
WOCE P06e RP	2003 southeastern Pacific, WOCE P06e repeat section

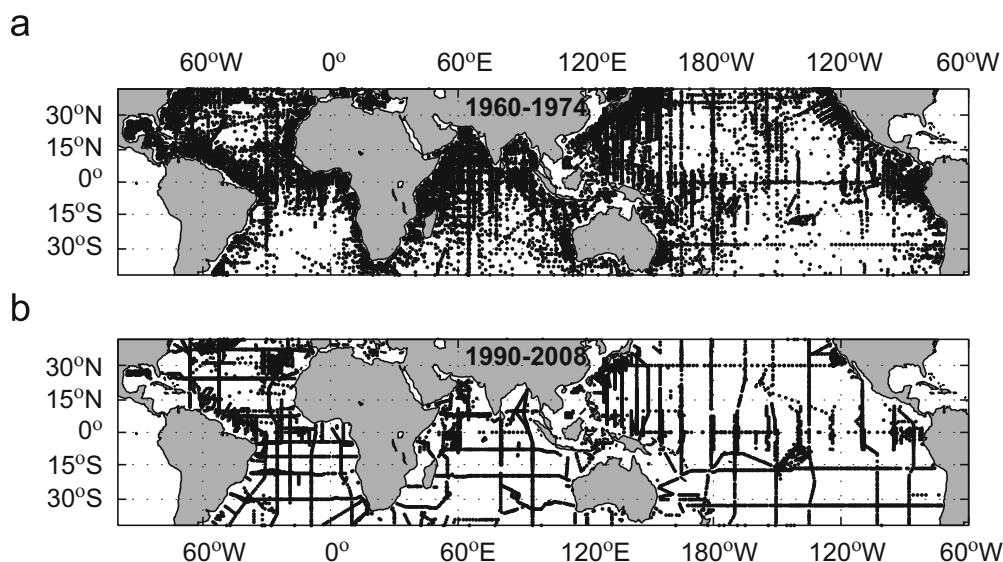


Fig. 1. Distribution of the final data set of quality-controlled oxygen profiles interpolated to 200 dbar for the period (a) 1960–1974 and (b) 1990–2008.

These fixed levels were chosen because they were frequently sampled. No data were used from profiles with constant oxygen or missing temperature. Data for each profile were interpolated using a piecewise cubic spline to each level only if the closest data points both above and below that level were within 25 dbar of it. In instances where all the data points within 25 dbar of a given level were only either above or below that level, the value of the closest data point was used for that level.

After interpolation, dissolved oxygen anomalies were calculated as departures from the monthly World Ocean Atlas 2005 climatology. Mapping anomalies from a seasonal cycle rather than the total fields helps to separate long-term temporal variability from both seasonal and spatial variability. These anomalies were filtered with a local inter-quartile range (IQR—the span between the first and third quartiles of a data set) filter, discarding data points within a running $30^\circ \times 30^\circ$ box that were more than three times the IQR below the first or above the third quartile (often called extreme outliers). All data falling within 1 calendar year

and $0.5^\circ \times 0.5^\circ$ spatial bins were averaged prior to mapping. This step prevents overly strong impact of time series stations, closely-sampled surveys, or often repeated surveys on surrounding sparsely sampled regions.

Because the available oxygen data for the two periods analyzed are sparsely and differently sampled (Fig. 1), we estimated experimental variograms of the data, a procedure somewhat uncommon in ocean sciences but common in several fields of geostatistics that analyze sparse or uneven sampled data (e.g. Deutsch and Journel, 1992; Cressie, 1993). To take the regional variations of the spatial correlations of oxygen data into account for the mapping, we estimated anisotropic experimental variograms separately for the equatorial and mid-latitude regions using the anomaly data from the first period. We chose this period for its superior spatial sampling. We fitted four models to the experimental variograms, for both latitude and longitude in both the equatorial and the mid-latitude regions. Exponential models provided a good fit with length scales of 5.7° longitude and 2°

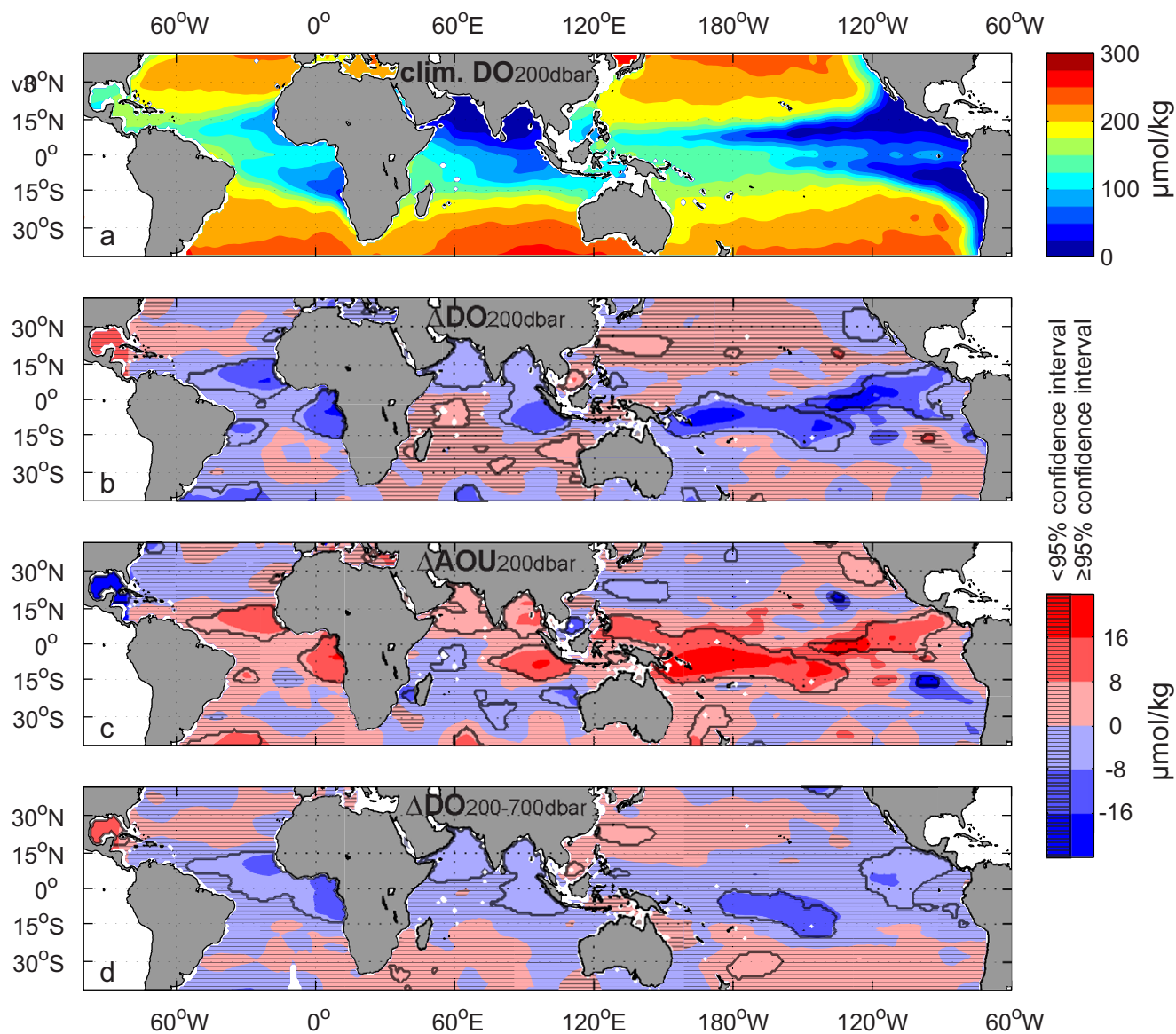


Fig. 2. Dissolved oxygen (DO) distributions (in $\mu\text{mol kg}^{-1}$) between 40°S and 40°N for (a) the climatological mean (World Ocean Database 2005) at 200 dbar, as well as changes between 1960–1974 and 1990–2008 of (b) dissolved oxygen (ΔDO) at 200 dbar, (c) apparent oxygen utilization (ΔAOU) at 200 dbar and (d) ΔDO vertically-averaged over 200–700 dbar. In (b)–(d) increases are red and decreases blue, and areas with differences below the 95% confidence interval are shaded by black horizontal lines.

latitude in the equatorial region and 3.4° for both latitude and longitude in the mid-latitude region. Because of narrowing meridians at higher latitudes, these length scales result in a predominantly zonal filter in the equatorial region and a slightly meridional one at higher latitudes. To accommodate the sparse spatial sampling in some parts of the globe, data within a 15° radius of a given grid point were used in mapping the estimates at that point.

The model length scales were interpolated versus latitude so that they vary smoothly from equator to mid-latitudes. Hence each 1° latitude band has its own length scales. For each time period and each $1^\circ \times 1^\circ$ grid point between 40°S and 40°N the local length scales and exponential model were used to map a model-weighted oxygen anomaly value using dissolved oxygen anomaly data within a 15° radius. The difference of the anomaly maps for the two periods gives an oxygen change over that period (e.g. Fig. 2b).

For error estimates we then further computed residuals of the interpolated profile anomaly data relative to the anomaly maps and used the results to estimate maps of the model-weighted residual variances in a manner similar to the estimation of the anomaly maps. The sums of the weights were also computed at each grid point for each period to obtain the effective number of observations. We estimated 95% confidence intervals for the anomalies by applying Student's *t*-test to the model-weighted residual variances and numbers of observations for each period. Hence we assumed that the residuals were normally distributed and statistically independent. The latter assumption may be somewhat optimistic for densely sampled WOCE (World Ocean Circulation Experiment) sections within the second period. The square roots of the summed squared confidence intervals for both periods were used at each grid point to determine the error of the difference maps and hence statistical significance of oxygen differences (Fig. 2 shading).

Apparent oxygen utilization (AOU) provides an estimate of the oxygen consumed in subsurface waters after they leave the mixed layer. AOU is defined as the solubility of oxygen at its temperature *T* (adiabatically adjusted to a surface value) and salinity *S* minus the measured oxygen concentration. By definition AOU removes the effect of oxygen solubility, which is primarily driven by temperature (Garcia et al., 2005), although AOU ignores any super- or under-saturation when water is formed. Hence, AOU removes the direct influence of changing temperature on the changes in ocean oxygen. To examine this direct temperature influence, changes in AOU between 1960–1974 and 1990–2008 and their statistical significance were computed in the same manner as the oxygen differences, using AOU anomaly and interpolated profile temperatures (Fig. 2c). Vertically averaged oxygen changes for 200–700 dbar (Fig. 2d) and their statistical significance are also calculated from the individual layer maps.

3. Changing oxygen conditions

3.1. Spatial changes and time series

We construct and analyze horizontal maps of ocean oxygen differences between the earliest time period with reliable data (1960–1974) and a recent period (1990–2008), as detailed in the previous section. Our focus is on the tropical and subtropical ocean from 40°S to 40°N (Fig. 1), the region containing the predominantly tropical OMZs and their poleward eastern boundary extensions. We further focus on the ocean from 200 to 700 dbar, a range encompassing the central core of the tropical OMZs.

The climatological distribution of dissolved oxygen at 200 dbar (Fig. 2a) shows the lowest oxygen at this depth in the northern Indian, the eastern tropical Pacific and the eastern tropical Atlantic Oceans. In the subtropical oceans within the subtropical gyres, the climatological oxygen content is much higher at 200 dbar. Declining oxygen concentrations between the two time periods at 200 dbar are found in all three tropical oceans (Fig. 2b). However, there are also regions in which oxygen content in this layer increases between the two time periods, especially from 30°S to 20°S and from 20°N to 30°N , on the equatorward sides of the subtropical gyres. The regions where we estimate oxygen differences are statistically significantly different from each other at 95% confidence are located mainly in all three tropical oceans, at least partly because of higher data densities in the tropical areas. Inclusion of the CALCOFI data set (Table 1) off California at $30\text{--}34^\circ\text{N}$ results in a statistically significant oxygen decrease at 200 m, concordant with the oxygen decrease after 1984 reported there (Bograd et al., 2008).

Spatial patterns of the vertically averaged oxygen differences between the two time periods for the 200–700 dbar layer (Fig. 2d) are largely similar to those at 200 dbar (Fig. 2c). At many locations, especially in the equatorial regions, near or in the OMZs, observed differences are statistically significant at 95% confidence. A comparison of cruise data in the Pacific north of 24°N along 152°W reveals an AOU decrease at 250–600-m depths at $24\text{--}25^\circ\text{N}$ from 1980 to 2006 and a large AOU increase north of 30°N (Mecking et al., 2008) in agreement with our results (Fig. 2d). In the Indian Ocean mean differences between two cruises on six isopycnal surfaces located between 300 and 1000 m depth along 80°E between 5°N and 20°S show an oxygen increase of up to $3.2 \mu\text{mol kg}^{-1}$ from 1978 to 1995 on two surfaces but a large oxygen decrease of up to $11.7 \mu\text{mol kg}^{-1}$ on four surfaces (Peng et al., 1998). This pattern agrees with the oxygen decrease we find at this location (Fig. 2d). In the South Pacific oxygen on the isopycnal $\sigma_\theta=26.7 \text{ kg m}^{-3}$ (about 700 m depth) along 32°S increases by $6\text{--}9 \mu\text{mol kg}^{-1}$ east of 180°W between 1992 and 2003 cruises with almost no changes west of 180°W (Murata et al., 2007). This comparatively recent short-period trend is congruent with the longer-term oxygen increase we find in the subtropical South Pacific. Surprisingly, we find oxygen increases in the deep Gulf of Mexico (Fig. 2d), distinct from the growing anthropogenic hypoxia reported in the shelf regions (Rabalais et al., 2007). However, we have few data in the deep Gulf during our latter period.

Comparison of the $70\text{-}\mu\text{mol kg}^{-1}$ oxygen isopleths at 200 dbar (Fig. 3a) for the two time periods shows an overall increase in the area of the hypoxic zone, particularly a westward expansion in the equatorial Pacific, but also expansions in the tropical eastern Indian Ocean and the eastern South Atlantic. The regions where $\text{O}_2 \leq 70 \mu\text{mol kg}^{-1}$ increased by 4.5 million km^2 from 1960–1974 to 1990–2008—an area about half the size of the USA (including Alaska and Hawaii). The region where $\text{O}_2 \leq 70 \mu\text{mol kg}^{-1}$ shows the largest expansion in area at 200 dbar compared with other thresholds, but areas with oxygen concentrations between 10 and $150 \mu\text{mol kg}^{-1}$ also increase by similar magnitudes (Fig. 3b).

The vertical changes in dissolved oxygen between the periods 1960–1974 and 1990–2008 between 200 and 700 dbar at 10°N , the equator, and 5°S (Fig. 4) show deoxygenation predominant in all three tropical oceans. Only a few regions show weak oxygen increases. The $\text{O}_2=70 \mu\text{mol kg}^{-1}$ contours for 1960–1974 (Fig. 4, dashed line) and 1990–2008 (Fig. 4, solid line) from 200 to 700 dbar show that the expansion of the low-oxygen zones takes place over the entire depth. This pattern is most prominent at the equator in the Pacific, the Atlantic Ocean at 10°N and the Indian Ocean at 5°S . The vertical oxygen change distribution at 10°N (Fig. 4) shows the expanding oxygen minimum zone in the

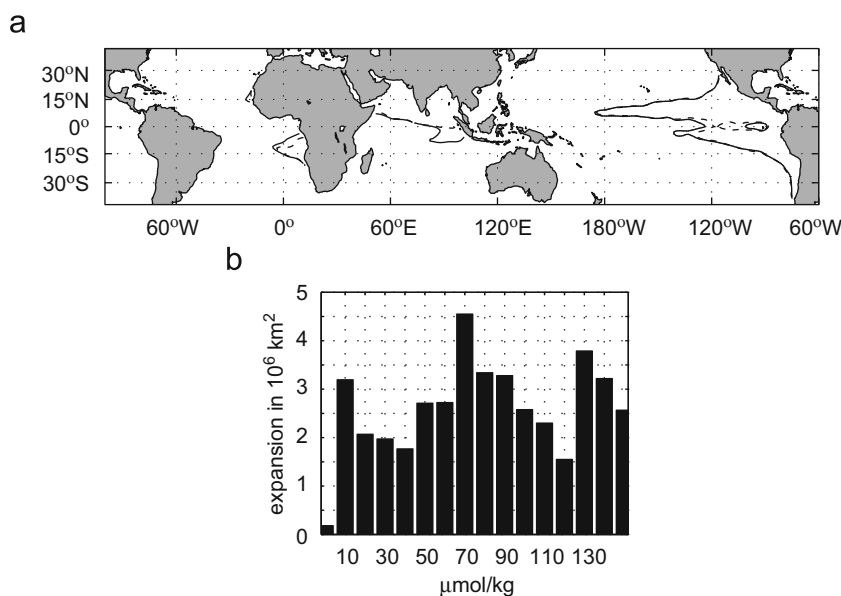


Fig. 3. Contours of (a) $\text{O}_2 = 70 \mu\text{mol kg}^{-1}$ at 200 dbar for the period 1960–1974 (dashed line) and the period 1990–2008 (solid line) indicate the growth and change of the spatial extent of the hypoxic region. The global areal expansion of the OMZs (b) at 200 dbar in $10\text{-}\mu\text{mol kg}^{-1}$ steps reveals a slight maximum at $70 \mu\text{mol kg}^{-1}$.

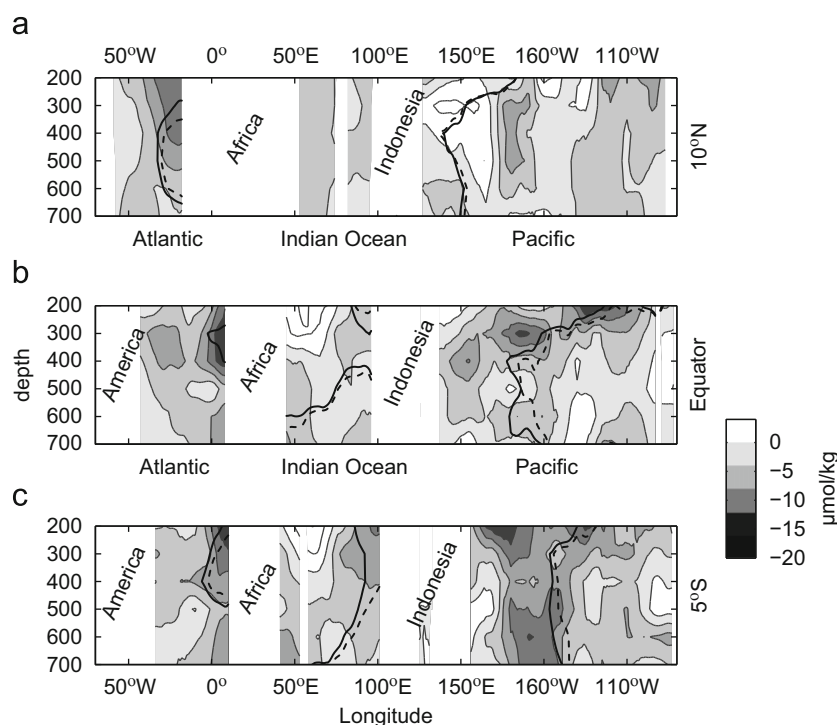


Fig. 4. Vertical changes in dissolved oxygen between the periods 1960 to 1974 and 1990 to 2008 between 200 and 700 dbar at (a) 10°N , (b) the equator and (c) 5°S . Areas of dissolved oxygen decreases are contoured and shaded gray. The small areas with positive trends are contoured but left unshaded. The $70 \mu\text{mol kg}^{-1}$ oxygen isopleths for the period 1960–1974 (dashed line) and the period 1990–2008 (solid line) are included.

tropical North Atlantic better than do the $70 \mu\text{mol kg}^{-1}$ oxygen isopleths at 200 m in that region (Fig. 4).

The mechanisms responsible for oxygen decreases in climate models under global warming scenarios vary with depth (Bopp et al., 2002; Shaffer et al., 2009). Decreased oxygen solubility from surface-layer warming accounts for most of the enhanced oxygen depletion in the upper 500 m of the model tropical oceans. Weakening of ocean overturning and convection further contribute to oxygen depletion (Shaffer et al., 2009). In warming waters lower oxygen solubility will team with higher metabolic

rates to place additional stress on resident organisms. Observed oxygen decreases at 200 dbar (Fig. 2b) are co-located with temperature increases (not shown) in some areas, especially the tropical North Atlantic where this relation has been observed previously (Garcia et al., 1998). However, the distribution of AOU changes (Fig. 2c) is very similar to that of dissolved oxygen changes, even at 200 dbar (Fig. 2b), where effects of temperature changes on oxygen solubility would be expected to be largest. Hence in the 200–700 db layer, the observed oxygen changes are not driven predominantly by temperature-induced solubility

changes. The reduced oxygen solubility in warmer water may contribute slightly to observed oxygen reductions at 200 dbar, but there are clearly other effects in play.

Variations in ocean dynamics contribute strongly to deeper oxygen changes, below 150 m. The mid-depth tropical OMZs are located in the “shadow zone” regions (Luyten et al., 1983), which are relatively isolated from subduction and hence ocean ventilation. Oxygen-rich water is supplied to the OMZs mainly from the west by zonal equatorial currents. In addition, modeled North Pacific oxygen changes between the 1990s and the 1980s on $\sigma_\theta = 26.6 \text{ kg m}^{-3}$ (~300–400-m depth) have been attributed to circulation changes (Deutsch et al., 2005). Notably, a southward expansion of the model subtropical gyre explains a modeled subtropical oxygen increase similar to that detected here. These, as well as other processes that could cause oxygen changes, such as a reduction in chlorophyll density and productivity in the subtropical gyres (Polovina et al., 2008) or remineralization (Paulmier et al., 2006), have been discussed in the literature. However, their relative roles cannot be determined from our limited data set.

Time series of oxygen concentrations for two selected areas are presented (Fig. 5). The linear trends and their 95% confidence interval were estimated (e.g. Wunsch, 1996), using annual 200–700-dbar averages of the objectively mapped fields. Degrees of freedom for the confidence intervals were determined from integral time scales (von Storch and Zwiers, 1999). The time series show large interannual variability. Nevertheless, these data also exhibit fairly robust trends, statistically significantly different from zero at 95% confidence, over roughly the last half century. The area with negative trends is similar to the area A used in Stramma et al. (2008b), although for an extended depth layer, while the area with positive trends (Fig. 5b) is new. The time series area in the Atlantic at 10–14°N, 20–30°W (Fig. 5a) with a statistically significant trend of oxygen decrease at 95% confidence is located in a region where the 200–700 dbar differences between 1990–2008 and 1960–1974 show a statistically significant decrease. The region 15–20°S, 65–70°E in the Indian Ocean (Fig. 5b) with statistically significant oxygen increase is located in a larger region where the difference between the two time periods is positive, but not statistically significantly at 95% confidence.

Frequent ocean surveys are required to distinguish long-term trends from interannual variations, especially in Pacific Ocean eastern boundary regimes, where El Niño exerts a strong influence on ocean circulation and water properties (Morales et al., 1999). Unfortunately, for some areas where oxygen appears to have increased (e. g. off Chile), we could not locate data for recent years, making it difficult to tell whether the increase persists into the most recent decade or was related to the stronger and frequent El Niños connected to higher oxygen (Shaffer et al.,

2000) in the 1980s and the 1990s compared with the 1960s. Higher oxygen concentrations were seen in the upper ocean off northern Chile in December 1997 (during a strong El Niño) compared with cruises in the 1980s (Morales et al., 1999). In contrast stations at 28°S off Chile in 1995 compared with 1967 displayed an oxygen decrease near 500 m and an oxygen increase near 750 m due to vertical displacements of isopycnals (Shaffer et al., 2000).

3.2. Potential biological impacts

Biological consequences of reduced oxygen concentrations are likely to be most notable for the 200–300-m layer, as these waters impinge on the euphotic zone and the outer continental shelf, where these oxygen-depleted waters may be upwelled into productive eastern boundary currents (Chhak and Di Lorenzi, 2007). Near the eastern shelf-breaks, poleward undercurrents such as the California and Peru–Chile Undercurrents carry oxygen-poor water from the expanding OMZs toward the subtropics. The upwelled OMZ waters may interact with natural or eutrophication-induced hypoxic zones on the inner shelves; this occurs for example off Peru and Chile, Namibia and the western Indian margin (Fig. 6). In the eastern Pacific these oxygen-poor upwelled waters are corrosive and undersaturated with respect to aragonite, exacerbating the stress imposed on the exposed ecosystems (Feely et al., 2008).

Shoaling of the tropical OMZ restricts the depth distribution of tropical pelagic fishes such as marlins, sailfish, and tuna by compressing their habitat into a narrow surface layer (Prince and Goodyear, 2006). Larger sizes of these fish over the OMZs compared with those in the western basins may reflect enhanced foraging opportunities afforded by the closer proximity of predator and prey in a vertically compressed habitat. However, restriction of these fishes toward the surface could also make them more vulnerable to over-exploitation by surface fishing gear (Prince and Goodyear, 2006). Increased fishing pressure has been associated with a decline of 10–50% in open-ocean predator diversity (Worm et al., 2005), making it difficult to isolate the influence of expanding OMZs on ecosystems.

Expanding hypoxia may cause jelly plankton to become more prevalent in the water column, especially nearshore. Recent increases in jellyfish blooms (Purcell et al., 2007) have been linked to eutrophication and hypoxia (Purcell et al., 2001) and lowered pH (Attrill et al., 2007). Jellyfish and their polyps are broadly tolerant to hypoxia at oxygen levels $< 1 \text{ mg L}^{-1}$; $\sim < 60 \mu\text{mol kg}^{-1}$; this tolerance appears related to their capacity to store and use intragel (mesoglea) oxygen (Thuessen et al., 2005). In addition, increasing jellyfish populations may promote hypoxia by preying on zooplankton, leaving unconsumed phytoplankton to sink and degrade (Purcell et al., 2001).

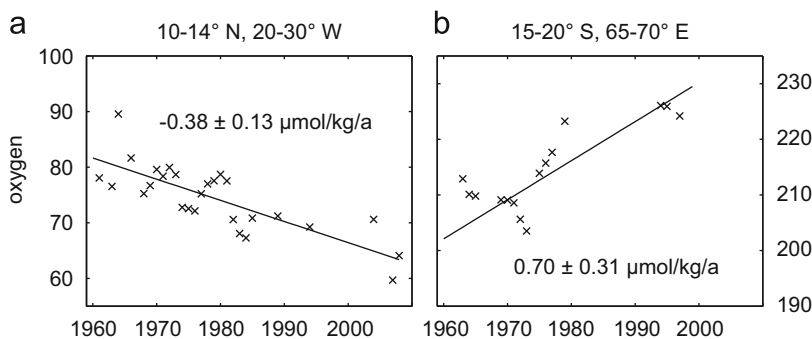


Fig. 5. Annual mean 200–700-dbar dissolved oxygen concentration time series ($\mu\text{mol kg}^{-1}$) with fitted linear trends and their 95% confidence intervals for selected areas (geographical limits in panel headers) for (a) the tropical North Atlantic and (b) the southwestern Indian Ocean.

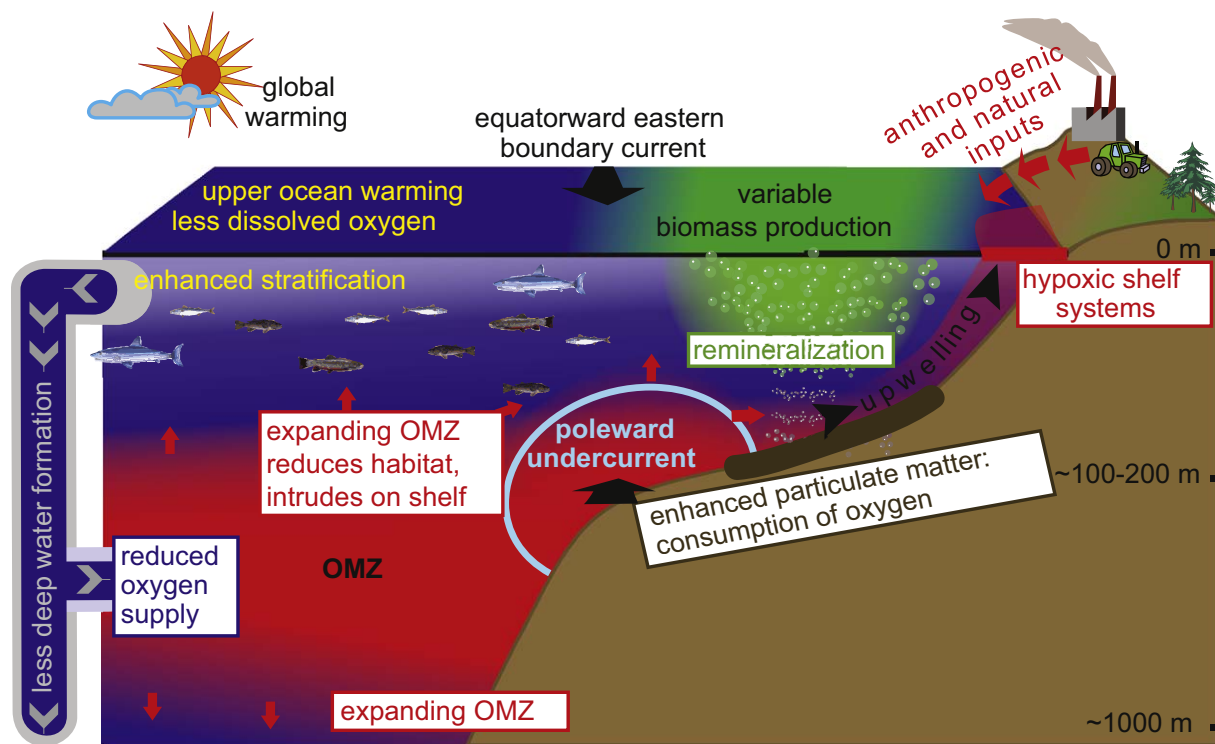


Fig. 6. Schematic of interactions of open ocean oxygen minimum zones (OMZ, red) with hypoxic shelf systems and dead zones (Diaz and Rosenberg, 2008) on continental shelves of eastern ocean boundaries.

Mounting evidence suggests that expanding hypoxia on continental shelves could cause state changes in the structure and function of marine ecosystems. Oxygen depletion affects biogeochemical processes in the sediments and water column. Metagenomic analyses have revealed abundant but uncultivated OMZ microbes capable of autotrophic carbon assimilation, sulfide oxidation and nitrate respiration (Walsh et al., 2009). Thus it is not surprising that hypoxia alters the rate and mechanisms of organic matter and metal recycling (Andersson et al., 2008; Middelburg and Levin, 2009), with influence on the efficiency of the biological pump. Increasing anaerobic diagenetic pathways and reduced efficiency of organic matter remineralization lead to increased accumulation and burial of high-quality organic matter (Cowie, 2005). Experiments to assess seafloor fates of ^{13}C -labeled phytodetritus at (a) Pakistan margin stations across the OMZ and with differing oxygen content in overlying water and (b) on a 140-m shelf experiencing seasonal, monsoon-driven hypoxia, have revealed strong oxygen control on the amount of C processed and the relative C-processing roles of protozoans (foraminifera) versus metazoans (macrofaunal invertebrates) (Woulds et al., 2007). Thresholds of $5\text{--}7\ \mu\text{mol L}^{-1}$ have been identified as critical on the Pakistan margin. Below these levels, bacteria and protozoans dominate and consume most organic matter.

The oxygen concentrations causing mortality in animals vary as a function of organism taxon and mobility; these range over an order of magnitude with a mean value of $\sim 64\ \mu\text{mol kg}^{-1}$ (Vaquer-Sunyer and Duarte, 2008) for estuarine and shelf taxa. Differential tolerance of major taxa yields dominance of specific copepods, pyrosomes, salps, and jellyfish in the hypoxic water column (Childress and Siebel, 1998; Wishner et al., 2008) and dominance of nematodes and small annelids in hypoxic sediments (Levin, 2003). Within and near OMZs, animal communities change rapidly across small oxygen gradients, suggesting threshold responses (Wishner et al., 2008; Levin et al., 2009b). Sampling

at 50-m depth intervals in water with oxygen concentrations of $5\text{--}10\ \mu\text{mol L}^{-1}$ revealed that metazoan communities on the Pakistan margin shift from single-species, surface-dwelling assemblages at 800 m to more diverse, bioturbating faunas at 1100 m (Levin et al., 2009a). ENSO cycles, which cause fluctuating oxygenation on the Peru and Chile shelves, are also associated with the appearance and disappearance of large, deeper-dwelling, burrowing and bioturbating organisms (Gutiérrez et al., 2008).

For many fish and crustacean species, larvae are less tolerant of hypoxia than adults, and thus expansion of hypoxic waters may create or enlarge dispersal barriers. Rapidly growing larval fish are especially susceptible to stress from hypoxic conditions as they shift from oxygenation by diffusion to active ventilation of gills. Among adults, reproducing females might also be more likely to experience oxygen limitations, as gonads have elevated oxygen demand (Pörtner and Farrell, 2008).

Ocean warming also limits oxygen delivery by creating a mismatch between oxygen demand and tissue oxygen supply (Pörtner and Knust, 2007). This mismatch could be exacerbated by declining oxygenation, particularly for animals with high metabolic rates like jumbo squid or marlin, which are forced to spend all or part of their time in inhospitable, warm, shallow, increasingly acidified waters. Such exposure can reduce activity rates and locomotory functions in fishes (Vagner et al., 2008) and squid (Rosa and Siebel, 2008), causing lost capabilities for prey capture or predator avoidance.

In most marine systems hypoxia alters physiological and metabolic rate processes, organism abundance, lifestyles, composition, complexity, diversity, and size structure (Childress and Siebel, 1998; Levin, 2003). Persistent hypoxia can foster morphological, physiological, and behavioral adaptations among some taxa, but seasonal, episodic, or unprecedented hypoxia often causes impaired functions (Levin et al., 2009a). On the sea floor these changes are manifested in altered trophic pathways and reduced rates of seafloor bioirrigation and bioturbation, with

feedback to rates of remineralization, preservation, and burial (Middelburg and Levin, 2009). In the future we expect to observe range expansions of hypoxia-tolerant taxa (Gilly et al., 2006) but overall reduced biodiversity associated with avoidance, mortality, or lowered growth and reproductive rates of hypoxia-sensitive species. We hypothesize that expanding OMZs will cause changes in plankton and nekton assemblages, with reduced vertical migration depths and increased species encounters due to compression of hypoxia-intolerant species into surface layers.

4. Conclusion

The results presented here reveal that large areas of the subsurface tropical oceans have experienced decreasing oxygen levels during the past few decades, although sparse data limit the number of regions where the decreases are statistically significant at 95% confidence. This confidence limit is a high statistical hurdle, so even differences not designated as statistically significant here may be realistic indicators of oxygen changes in the ocean. The observed changes between the two time periods could be influenced by slow fluctuations sometimes linked to modes of climate variability as observed in time series (Garcia et al., 2005; Whitney et al., 2007; Stramma et al., 2008b) and frequently repeated hydrographic sections (Johnson and Gruber, 2007); however, statistically significant trends for the last 50 years at some locations (Fig. 5) point to possible long-term trends. Our results show expanding low-oxygen-minimum zones in all three tropical oceans between the time periods 1960–1974 and 1990–2008. The low oxygen zones expand both horizontally and vertically. There are large areas in the subtropics with weak increases in oxygen, but subsurface oxygen generally decreases offshore of most continental shelves.

The ocean could undergo major shifts in nutrient cycling and trophic structure triggered by the expansion of tropical OMZs, should past trends in observed oxygen differences continue into the future. The multiplicative effects of oxygen stress on shelf systems are predicted to yield ecosystem-level changes. Increases in jellyfish blooms are likely to be part of this response. Long-term consequences may include impacts on ocean CO₂ uptake and commercial fisheries.

In addition to temperature-driven changes in solubility and in ocean circulation rates, changes in preformed oxygen values, changing Redfield ratios, warming-induced changes in biological production, variations in respiration rates and remineralization have been offered as possible explanations for oxygen changes in different regions (Keeling and Garcia, 2002). Increased thermal stratification might also play a role in mid-depth oxygen declines (Keeling and Garcia, 2002). At shelf depths the biotic systems experiencing oxygen stress are also subject to overfishing, pollution, species invasion, and corrosive waters with lowered pH. While the multiplicative effects of these influences are unknown, there is a potential for continued degradation of ecosystems and coastal fisheries, should past oxygen trends continue. From our limited data set it is not possible to estimate whether the observed changes are a trend continuing into the future and the relative roles of the processes involved in the changes are unresolved, especially as the relative importance of these factors is expected to vary with time for different regions.

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