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Global distribution of naturally occurring marine hypoxia on continental margins

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Abstract

Hypoxia in the ocean influences biogeochemical cycling of elements, the distribution of marine species and the economic well being of many coastal countries. Previous delineations of hypoxic environments focus on those in enclosed seas where hypoxia may be exacerbated by anthropogenically induced eutrophication. Permanently hypoxic water masses in the open ocean, referred to as oxygen minimum zones, impinge on a much larger seafloor surface area along continental margins of the eastern Pacific, Indian and western Atlantic Oceans. We provide the first global quantification of naturally hypoxic continental margin floor by determining upper and lower oxygen minimum zone depth boundaries from hydrographic data and computing the area between the isobaths using seafloor topography. This approach reveals that there are over one million km^2 of permanently hypoxic shelf and bathyal sea floor, where dissolved oxygen is $<0.5\,\mathrm{ml\,l^{-1}}$; over half (59%) occurs in the northern Indian Ocean. We also document strong variation in the intensity, vertical position and thickness of the OMZ as a function of latitude in the eastern Pacific Ocean and as a function of longitude in the northern Indian Ocean. Seafloor OMZs are regions of low biodiversity and are inhospitable to most commercially valuable marine resources, but support a fascinating array of protozoan and metazoan adaptations to hypoxic conditions.

Keywords: Dissolved oxygen; Oxygen minimum zone; OMZ; Continental slope; Hydrography; Pacific ocean; Indian ocean; Ocean floor

1. Introduction

Where upwelling is most intense in the world ocean there is high phytoplankton production. This material sinks and is decomposed in midwater, consuming dissolved oxygen. When high oxygen demand occurs in combination with sluggish circulation and oxygen-poor source waters, massive midwater oxygen minima develop (Wyrtki, 1962; Kamykowski and Zentara, 1990). Such minima are found in large areas of the eastern Pacific Ocean, in the southeast Atlantic off West Africa, and in the northern Indian Ocean. These minima intercept the continental margin at

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the shelf and continental slope (i.e., bathyal depths), creating extensive seafloor habitats subject to permanent hypoxia that persist over thousands of years (Reichart et al., 1998).

There has been much attention to presumed anthropogenically induced hypoxia in shallow and enclosed seas; substantial areas of eutrophication-generated hypoxia occur in the Gulf of Mexico (up to 20,000 km^2), Baltic Sea (84,000 km^2) and parts of the Black Sea ($\leqslant$20,000 km^2) (Rabalais and Turner, 2001; Mee, 2001). However, there are much larger extents of naturally occurring hypoxic seafloor along continental margins (seafloor OMZ) whose areas and distributions have never before been quantified. Due to their high accumulation rates and limited bioturbation, modern OMZs are often the source of valuable high-resolution sediment records used to reconstruct paleoceanographic and paleoclimatic conditions (Behl and Kennett, 1996; Cannariato and Kennett, 1999). Knowledge of the modern distribution of seafloor OMZs will refine our understanding of global biogeochemical cycling (Ward et al., 1989; Law and Owens, 1990), organic matter preservation (Weijden et al., 1999), animal adaptation (Childress and Seibel, 1998), diversity (Levin et al., 2001), and evolution (White, 1987; Jacobs and Lindberg, 1998) in the ocean.

2. Methods

To quantify the area of seafloor OMZs, we selected four target regions for our analysis following the prior work on global hypoxia by Kamykowski and Zentara (1990). These regions are the continental margins of the eastern Pacific, the southeastern Atlantic, the Arabian Sea and the Bay of Bengal (Fig. 1). This includes all the major open-ocean, upwelling-induced OMZs of the world oceans. For each of these areas, dissolved oxygen (DO) data were extracted from the NOAA National Geophysical Data Center global hydrographic dataset of 20,260 hydrocasts (years 1906–1990) using the NEMO server (http://nemo.ucsd.edu) operated by the Physical Oceanography Division of the Scripps Institution of Oceanography. Other areas may occasionally experience hypoxia but do not contribute to the analysis of permanent hypoxic zones reported here. For example, we investigated an additional 6299 hydrocasts in the northwestern region of coastal Africa (from 35°N, 20°W to 0°, 10°E) and found only 8 hydrocasts with dissolved oxygen values of less than 0.5 $ml\,l^{-1}$.

The data were sorted by cruise, station, latitude, longitude, date and depth to uniquely isolate each hydrocast and were selected to be within a distance from the coasts (Fig. 1) that included the bulk of the stations sampled within the continental margin as estimated by inspection of maps of sample distributions similar to those in Fig. 1. The coordinates for each area analyzed are presented in Table 1. Observations in depths greater than 1500 m were eliminated from the analyses since these are known to be below the world's oxygen minimum zones (Wyrtki, 1962, 1966, 1971, 1973).

From this reduced and sorted dataset of hydrocasts, all DO measurements above the specified oxygen maximum, 0.5 or 0.2 $ml\,l^{-1}$, were discarded leaving only the observations that would be found within an OMZ. From the reduced data set, the shallowest and deepest values of DO in each hydrocast were extracted and plotted with a connecting line to reveal the depth-resolved OMZ as a function of either latitude or longitude (Fig. 2). These plots were used to categorize the water masses into latitudinal (eastern Pacific, southeastern Atlantic) or longitudinal (Arabian Sea, Bay of Bengal) extents. Although there is a data quality parameter for reporting assessment of the quality of measured dissolved oxygen in the NODC data, we find that it is rarely used. Low oxygen values are known to be difficult to measure reliably in situ in the ocean and we have no means of controlling for errors in the data at this time. We are relying on the large number of independent observations in each area to compensate for random errors in the accuracy of the measurements.

For each of these geographical extents, the upper boundary of the OMZ was estimated by the first quartile of observations by depth (25% of the shallowest observations were shallower) and the lower boundary was estimated by the fourth quartile (25% of the deepest observations were deeper). This was done to account for the sampling variation in the top and bottom margins of the estimated OMZ and resulted in a pair of upper and

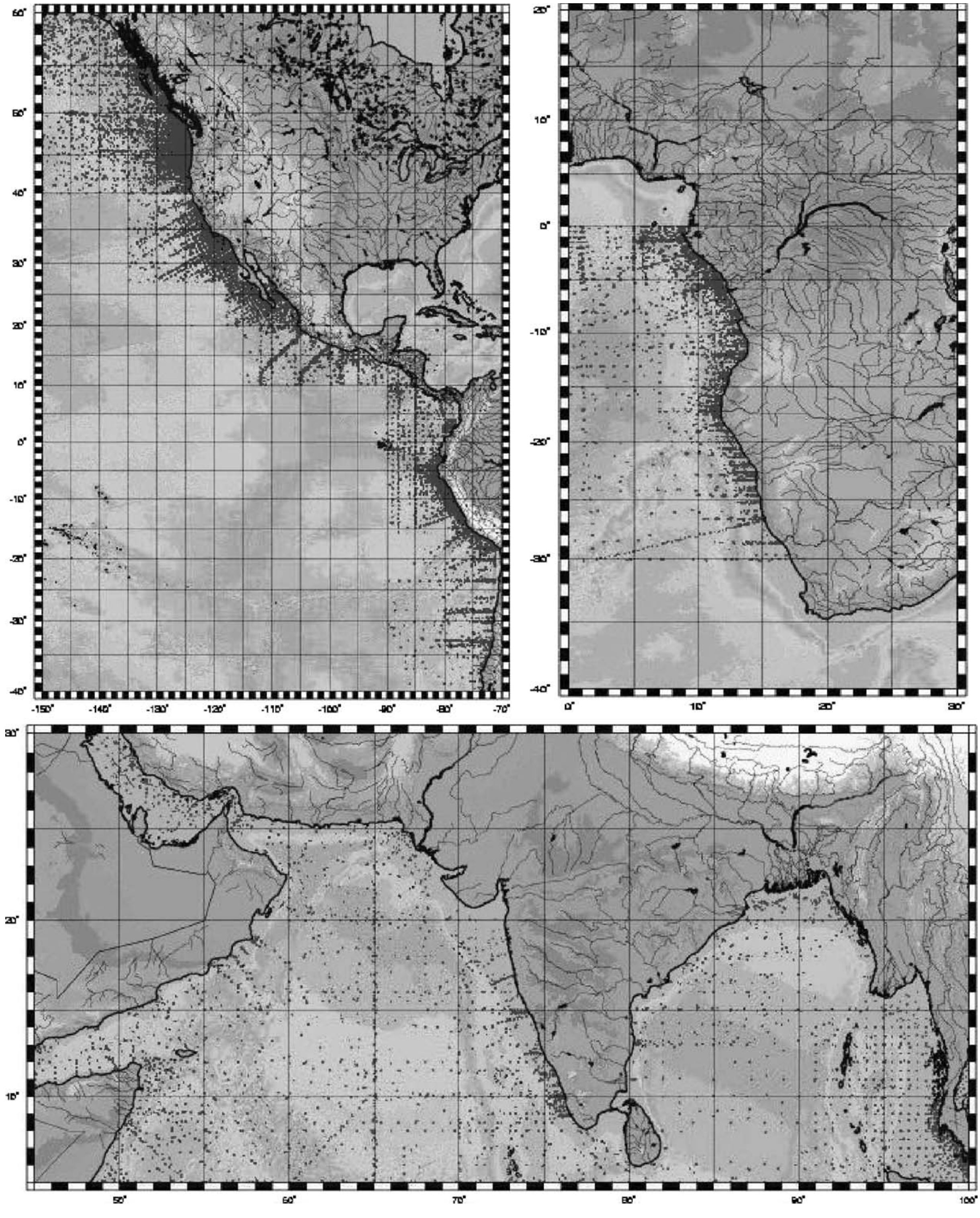

Fig. 1. Gray dots in coastal regions indicate locations of hydrocasts used in this analysis. Number of hydrocasts in each region: eastern Pacific $N = 18,985$, southeastern Atlantic $N = 264$, Arabian Sea and Bay of Bengal, $N = 1011$.

Table 1
Regional OMZ areal estimates defined as DO $<0.5\,\mathrm{ml\,l^{-1}}$

Region, W/E/S/N		Quartile OMZ boundaries ($0.5\,\mathrm{ml\,L^{-1}}$) (depth in meters)		Estimated benthic area ($\mathrm{km^2}$) (computed values in parentheses)
		Upper (25%)	Lower (75%)	
	−150/−120/37/60	−659	−1088	30,000 (29,880)
	−140/−110/28/37	−513	−686	14,000 (14,013)
	−125/−98/23/28	−225	−714	42,000 (41,984)
	−120/−70/6/23	−90	−965	147,000 (146,555)
	−92/−76/0/6	−264	−600	8000 (8,169)
	−92/−76/−6/0	−198	−508	17,000 (16,799)
	−90/−70/−20/−6	−57	−368	77,000 (77,440)
	−90/−70/−40/−20	−113	−378	26,000 (26,434)
	Subtotal			361,000
Arabian Sea	45/73/0/30	−122	−1100	285,000 (284,990)
Bay of Bengal	73/100/0/30	−91	−582	389,000 (389,120)
Southeastern Atlantic	0/30/−15/0	−293	−416	7,000 (6,870)
	0/30/−30/−15	−100	−277	106,000 (105,860)
	Subtotal			113,000
Total	1,148,000			

lower boundary depths for each West/East/South/North (W/E/S/N) region (Tables 1 and 2). Other estimators, such as the mean upper and lower depths, could have been used but the first and fourth quartiles were chosen as conservative estimators to avoid the bias of large or small values. The median (i.e., the second quartile) could also have been chosen to define the upper and lower boundaries, but we observed that this was too conservative in that it failed to capture what appear, graphically (cf. Fig. 2), to be the true shape of the vertical boundaries of the OMZ. Consequently, these geographically categorized, vertical limits were then used to compute the area between the corresponding isobaths of the OMZ using the global seafloor topography data set (Smith and Sandwell, 1997) and the *grdvolume* module in the generic mapping tool (GMT) software system (Wessel and Smith, 1995).

The seafloor topography was projected into the Universal Transverse Mercator (UTM) representation and the area calculated in square kilometers ($\mathrm{km^2}$). The UTM zone for each region was selected as centermost for each area: the Arabian Sea (zone 42), Bay of Bengal (zone 43), eastern Pacific (zones 9,10,13,17,18) and southeastern Atlantic (zones 32, 33). There are uncertainties associated with the topographic dataset (Smith and Sandwell, 1997), especially in shallow water, but this is generally regarded as the best currently available global dataset. The areal estimates presented in Tables 1 and 2 have been rounded to the nearest $10^3\,\mathrm{km^2}$ to account for uncertainties in the global topographic data set, however, the computed values are also reported parenthetically to facilitate reproduction of these results. Our calculations omit seamounts or other topographic features that might penetrate OMZs away from the continental margin, but the area of these features within the OMZ is expected to be $<1\%$ of the total estimate.

3. Results

We have calculated that the OMZ (dissolved oxygen $<0.5\,\mathrm{ml\,l^{-1}}$) covers $1,148,000\,\mathrm{km^2}$ of sea

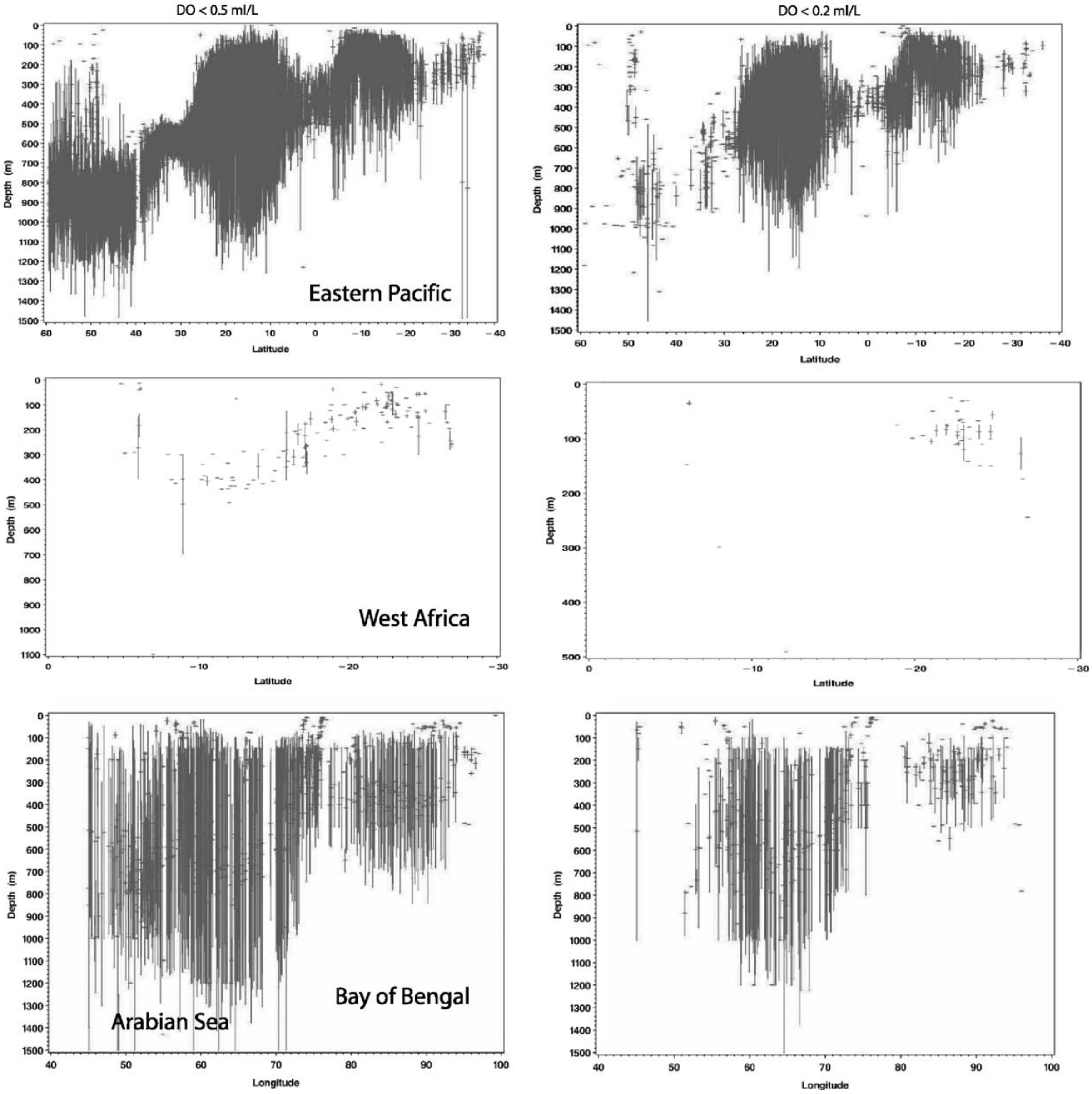

Fig. 2. Depth range of the OMZ for $0.5\,\mathrm{ml\,l^{-1}}$ DO (left) and $0.2\,\mathrm{ml\,l^{-1}}$ DO (right) for each of the study areas. Each vertical bar connects the upper and lower OMZ value for a given hydrocast.

floor. Of the total OMZ area, approximately 31% occurs in the eastern Pacific Ocean, 59% in the Indian Ocean (Arabian Sea and Bay of Bengal) and 10% in the southeastern Atlantic (Table 1). When we use a much stricter definition of hypoxia (dissolved oxygen $< 0.2\,\mathrm{ml\,l^{-1}}$) (Kamykowski and Zentara, 1990), we calculate that $764{,}000\,\mathrm{km}^2$ of shelf and bathyal seafloor are hypoxic. Under this definition, the southeastern Atlantic contributes only 3% of the total area, 63% occurs in the

Table 2
Regional OMZ areal estimates defined as DO $<0.2\,\mathrm{ml\,l^{-1}}$

Region, W/E/S/N		Quartile OMZ boundaries ($0.2\,\mathrm{ml\,l^{-1}}$) (depth in meters)		Estimated benthic area (km^2) (computed values in parentheses)
		Upper (25%)	Lower (75%)	
Eastern pacific	−150/−120/48/60	−204	−958	N/A
	−140/−115/36/48	−699	−984	11,000 (10,780)
	−140/−115/26/36	−472	−650	12,000 (11,646)
	−140/−100/20/26	−230	−640	35,000 (34,620)
	−110/−80/8/20	−207	−796	51,000 (51,219)
	−90/−75/2/8	−302	−498	63,000 (63,440)
	−90/−70/−4/2	−304	−426	5,000 (5,078)
	−90/−70/−8/−4	−188	−500	6,000 (5,646)
	−90/−70/−10/−8	−56	−378	27,000 (27,390)
	−90/−70/−20/−10	−75	−312	35,000 (34,935)
	−90/−70/−24/−20	−120	−261	4,000 (4,196)
	−90/−70/−40/−24	−121	−247	14,000 (13,592)
	Subtotal			263,000
Arabian Sea	45/73/0/30	−150	−988	230,000 (230,440)
Bay of Bengal	73/100/0/30	−104	−389	251,000 (250,700)
Southeastern Atlantic	10/20/−30/−15	−70	−111	20,000 (20,340)
Total	764,000			

Indian Ocean and 34% in the eastern Pacific Ocean (Table 2). With both definitions, the Indian Ocean exhibits a disproportionately large fraction of the open ocean hypoxic area relative to its size (21% of the sea floor).

Graphical representation of the OMZ vertical extent within the water column (Fig. 2) reveals that it is far thicker and more homogeneous in the Northen Indian Ocean than along the eastern Pacific margin. The eastern Pacific OMZ exhibits significant latitudinal variations in depth, thickness, and intensity (Fig. 2). In the northern Indian Ocean the OMZ is notably thicker (and deeper) in the Arabian Sea than in the Bay of Bengal.

4. Discussion

4.1. OMZ boundaries

Latitudinal variations in the eastern Pacific upper and lower OMZ boundaries reflect combined effects of surface productivity, water mass age, and circulation. Increased upwelling, higher productivity, and greater oxygen demand along with sluggish circulation will contribute to a thicker OMZ with lower oxygen concentration. The water masses and currents exert additional influence. For example, the eastward moving Equatorial Undercurrent, which drives a belt of high oxygen water across the Pacific from 150°E to Equador at the equator (Tsuchiya, 1968), probably accounts for depression of the upper OMZ boundary from 5°S to 5°N (Fig. 2). To the North and South, the upper OMZ boundary exhibits distinct dips and OMZ thinning occurs where the Peru Chile current (20–30°S) and the California Current (28–45°N develop along the coastline. An additional influence near 30°N may be a tongue of better oxygenated water that moves across the ocean from the Southwest Pacific to the eastern Pacific margin (Reid and Mantyla, 1978). Deep water in the North Pacific remains low in oxygen (Fig. 2) because the water is very old and there is no substantial replenishment (Reid and Mantyla, 1978). Near the surface, the subarctic and subtropical gyres carry better oxygenated waters shoreward. The depth of the lower OMZ boundary also shows strong latitudinal variation, reflecting the water-mass age and the influence of circulation in the southeastern Pacific.

Differences in the thickness of the Arabian Sea and Bay of Bengal OMZs are probably not due to differences in oxygen demand, as these two regions have similar productivity and particle flux (Ramaswamy and Nair, 1994). The difference appears to result in part from flow of high salinity, low oxygen water from the Red Sea over the sill into the Arabian Sea. This water sinks along the continental slope and continues to lose oxygen as it spreads through the Arabian Sea at mid-water depths to 1200 m (Wyrtki, 1971; Warren, 1994).

4.2. The biology of OMZs

Investigations of modern OMZ biota (Levin, 2003) lag far behind the hydrographic measurements, although foraminifera in historical OMZ sediments are better known (Bernhard and Sen Gupta, 1999). The biota of some OMZ areas such as the Bay of Bengal or Central American margin have not been studied at all, despite the extensive coverage of hypoxic habitat. Many countries with well-developed OMZs along their coasts have not had the resources or ship facilities to conduct deep-water oceanographic investigations of the hydrology or biota. Levin (2003) has synthesized information about benthic faunas for those OMZ areas that have been studied. General trends are that foraminifera and meiofaunal nematodes are widespread at the lowest oxygen levels ($<0.2\,\mathrm{ml\,l^{-1}}$; $<9\,\mu\mathrm{M}$), whereas other meiofaunal, macrofaunal and megafaunal size organisms are scarce. Diversity among all taxa is very low (Levin et al., 2001). Massive mats of sulfide-oxidizing bacteria may cover the sediments (Jorgensen and Gallardo, 1999) and symbiont-bearing invertebrates can occur (Cary et al., 1989; Levin et al., 2002, 2003). Many OMZ species are new to science (Levin, unpublished) and some have exhibited unusual evolutionary novelty. An inconspicuous gutless oligochaete discovered in the Peru OMZ for example, supports more types of nutritional bacterial symbionts (3 for certain and possibly 5) than reported from any other invertebrate (Giere and Krieger, 2001; Dubilier, 2003). There is growing evidence that chemosynthesis may fuel secondary production in OMZ transition zones where sulfide oxidation can occur (Levin, 2003). An understanding of OMZ distributions can help guide further exploration of potentially unusual habitats.

4.3. Implications of OMZ variability

By visualizing the vertical distribution of the OMZ as a function of latitude or longitude (Fig. 2), we can identify those regions whose outer continental shelves and upper slopes are severely impacted by natural hypoxia: the margins of Mexico, Peru, Chile, Namibia, Pakistan, and India. In the eastern Pacific it is subtropical latitudes that exhibit the greatest hypoxic area (Tables 1 and 2). In these regions, changes in the OMZ will inevitably redistribute or alter the distribution of marine resources, often with significant economic impacts, both positive and negative (Arntz et al., 1991). We have not yet attempted to analyze these data temporally; our present estimates are integrated over time. Although we would not expect the lower boundary of the OMZ to shift significantly over seasonal to decadal intervals, the upper boundary may experience seasonal fluctuations (e.g., of 25 m off Chile) and interannual shifts of up to 65–100 m. During the 1997–8 El Niño event there was large-scale oxygenation of the Peru margin caused by circulation changes, with depression of the OMZ by 100 m (Sanchez et al., 1999). Under these circumstances a strong El Niño could reduce the OMZ area off Peru and northern Chile (6–20°S) by 61% (from 77,000 to 30,000 km^2). Fig. 3 depicts the estimated variation in the areal extent of the OMZ in this region under these assumptions.

Fluctuations in the extent of the OMZ can have significant environmental, ecological and economic impacts. For example, Peruvian hake and scallop fisheries are greatly expanded but pelagic species are reduced during El Niño events off Peru

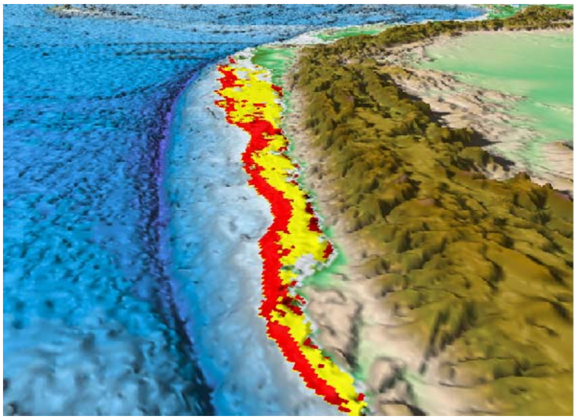

Fig. 3. The coast of Peru and northern Chile looking north. Central and North America are in the distant background. The red area is the estimated area of the OMZ during an extreme El Niño event while the union of red and yellow indicates the extent during non-El Niño periods.

(Arntz et al., 1988). When the OMZ moves up the shelf during the southwest monsoon in the Indian Ocean (Banse, 1984) there is a notable drop in catches of fishes and prawns (Sankaranarayanan and Qasim, 1968). Expansion of hypoxia off Namibia, sometimes associated with hydrogen sulfide gas release (Weeks et al., 2002), causes redistribution of biota with negative consequences for fish such as hake, shellfish (e.g., lobsters) and humans (Bailey et al., 1985; Hamukuaya et al., 1998; Woodhead et al., 1998).

Global warming may lead to lowered oxygen content of the world oceans (Keeling and Garcia, 2002), and expansion of OMZs in selected areas. Because OMZs are inhospitable to many species, they serve as biogeographic barriers, limiting cross-slope movements of populations (White, 1987; Etter et al., 1999; Rogers, 2000; Weeks et al., 2002). OMZ expansion or shrinkage may promote the evolution of species and genetic diversity maxima at mid-slope depths (Jacobs and Lindberg, 1998; Etter et al., 1999; Ulloa et al., 2001). The extent and severity of OMZs will change with alteration of ocean circulation, temperature and productivity (Reichart et al., 1998; Keeling and Garcia, 2002). Our methods can be used to readily estimate the hypoxic seafloor added or lost by a change in OMZ boundaries. The regional quantification of hypoxic seafloor given here provides the baseline information necessary for estimating the geological, ecological and economic impacts of shifts in OMZ distributions.

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