Deep-Sea Research I 58 (2011) 1212–1226

Contents lists available at SciVerse ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Hypoxia by degrees: Establishing definitions for a changing ocean

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ARTICLE INFO

Article history:
Received 22 March 2011
Received in revised form
30 August 2011
Accepted 13 September 2011
Available online 8 October 2011

Keywords:
Hypoxia
Low oxygen
Ocean dead zones
Oxygen minimum zone
Dissolved oxygen concentration
Oxygen partial pressure
Limits to aerobic respiration
Limits to marine life
Chemical stress

ABSTRACT

The marked increase in occurrences of low oxygen events on continental shelves coupled with observed expansion of low oxygen regions of the ocean has drawn significant scientific and public attention. With this has come the need for the establishment of better definitions for widely used terms such as "hypoxia" and "dead zones". Ocean chemists and physicists use concentration units such as $\mu molO_2/kg$ for reporting since these units are independent of temperature, salinity and pressure and are required for mass balances and for numerical models of ocean transport. Much of the reporting of dead zone occurrences is in volumetric concentration units of mlO_2/l or mgO_2/l for historical reasons. And direct measurements of the physiological state of marine animals require reporting of the partial pressure of oxygen (pO_2) in matm or kPa since this provides the thermodynamic driving force for molecular transfer through tissue. This necessarily incorporates temperature and salinity terms and thus accommodates changes driven by climate warming and the influence of the very large temperature range around the world where oxygen limiting values are reported. Here we examine the various definitions used and boundaries set and place them within a common framework. We examine the large scale ocean pO_2 fields required for pairing with pCO_2 data for examination of the combined impacts of ocean acidification and global warming. The term "dead zones", which recently has received considerable attention in both the scientific literature and the press, usually describes shallow, coastal regions of low oxygen caused either by coastal eutrophication and organic matter decomposition or by upwelling of low oxygen waters. While we make clear that bathyal low oxygen waters should not be confused with shallow-water "dead zones", as deep water species are well adapted, we show that those waters represent a global vast reservoir of low oxygen water which can readily be entrained in upwelling waters and contribute to coastal hypoxia around the world and may be characterized identically. We examine the potential for expansion of those water masses onto continental shelves worldwide, thereby crossing limits set for many not adapted species.

1. Introduction

The term "dead zone" is now widely used in the media, and often by scientists to describe a situation where dissolved oxygen levels are so low as to pose a threat to marine life but the term appears to have no specific or universal meaning. It appears to be of recent origin as traditional texts (e.g. Sverdrup et al., 1942; Redfield et al., 1963; Richards, 1965; Riley and Skirrow, 1965, 1975) make no use of this wording and the word "dead" is informally assumed to be not absolute. For example the widely described dead zone off the Mississippi delta (e.g. Turner et al., 2008) is not absolutely dead to aerobic life; the nomenclature refers primarily to the important impact on the local shrimp fishery (Lumcon, 2010). Furthermore, various other oxygen thresholds are presented in a bewildering set of units and the resulting confusion impedes useful discussion of genuine limits of various kinds, and inhibits adequate documentation and reporting of significant changes that are now taking place such as apparent long term declines in oceanic oxygen concentrations (Chen et al., 1999; Nakanowatari et al., 2007; Jenkins, 2008; Stramma et al., 2008; Shaffer et al., 2009) associated with ocean warming (Lyman et al., 2010).

A more structured yet not unambiguous approach for a characterization of low oxygen zones is the use of the terms "hypoxia", "suboxia", and "anoxia". Hypoxia was originally meant to describe internal stress on an animal (e.g. Piiper, 1982) but was quickly applied to describe the external ocean medium. Many thresholds for hypoxia in differing units have been used, the most prominent one being 2 mgO_2/l (≈ 61 $\mu molO_2/kg$) (e.g. Gray et al., 2002). Ocean chemical definitions have traditionally used the term "suboxic" (Sillen, 1965) for the situation where dissolved oxygen levels are so low that microbes begin to turn to nitrate as an alternate electron acceptor and a cascade of redox reactions begins to appear (Kamykowski and Zentara, 1990; Rue et al., 1997).

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doi:10.1016/j.dsr.2011.09.004

The suboxic limit is typically set at around 10 $\mu molO_2/kg$ and it represents a quite strict definition; the threshold of 5 $\mu molO_2/kg$ set by Kamykowski and Zentara (1990) was chosen to represent regions where significant nitrate loss was already large and suboxic microbial change is already well underway. However, "suboxic" recently has also been used to define thresholds in connection with macroorganisms (e.g. Shaffer et al., 2009). Even the seemingly unambiguous term "anoxia" is sometimes defined not as the true zero dissolved oxygen state but as $\leq$ 0.2 mlO_2/l (Gooday et al., 2009a). And even under true zero oxygen and sulfide rich conditions some forms of multicellular animals have evolved (Danovaro et al., 2010). There are several problems with definitions based simply upon a concentration limit applied ocean wide with the principal ones being that the same limit appears to be applied over a range of temperature spanning some 30 °C from the tropics to the polar regions, and over a depth range spanning thousands of meters.

Today, dissolved oxygen dead zone or hypoxia thresholds such as the Mississippi delta dead zone threshold of 2 mgO_2/l ($\approx$61 $\mu molO_2/kg$) (Turner et al., 2008), originally defined for species communities in comparatively warm, near shore ecosystems experiencing seasonal oxygen depletion (Gray et al., 2002; Diaz and Rosenberg, 2008; Turner et al., 2008; Gooday et al., 2009a; Kemp et al., 2009; Levin et al., 2009; Middelburg and Levin, 2009; Zhang et al., 2010) are increasingly applied to open ocean permanent oxygen minimum zones (e.g. Shaffer et al., 2009). Those permanent oxygen minimum zones, particularly the Eastern North Pacific and the Indian Ocean, as classically described by Wyrtki (1962), Kamykowski and Zentara (1990), Olson et al. (1993), are inhabited by species communities adapted to low oxygen concentrations (e.g. Childress and Seibel, 1998; Levin, 2003; Diaz and Rosenberg, 2008; Gooday et al. 2009a,b, 2010; Levin et al., 2009) and coastal thresholds have no equivalent meaning. For example the model study of Shaffer et al. (2009) correctly concludes that by the year 2500 up to 61% of the total ocean volume will be "hypoxic", as defined by $\leq$80 $\mu molO_2/kg$ here, compared to 9.1% for the present ocean ($\approx$10% Codispoti, 2010). But there is no widespread knowledge of what the 80 $\mu molO_2/kg$ hypoxia definition implies for species communities spanning a wide range of temperature and depth. For example Seibel et al. (1999) report thriving vampire squid populations in the lowest oxygen levels encountered in the oxygen minimum zone off California ($\leq$15 $\mu molO_2/kg$, e.g. McClatchie et al., 2010), while other authors claim even the conventional hypoxia threshold of 2 mgO_2/l ($\approx$61 $\mu molO_2/kg$) is below the empirical sublethal and lethal O_2 thresholds for half of their tested species (Vaquer-Sunyer and Duarte, 2008).

Two basic mechanisms causing coastal hypoxia are eutrophication due to land and river based nutrient input leading to local microbial oxygen consumption (e.g. Gulf of Mexico, Turner et al., 2008; Hogue, 2010; Lumcon, 2010), and upwelling of oxygen depleted, nutrient rich water from bathyal oxygen minimum zones where deep microbial oxygen consumption occurs (e.g. Oregon coast, Grantham et al., 2004; Chan et al., 2008; Gewin, 2010). While horizontal advection of low oxygen waters should not be neglected (e.g. Bograd et al., 2008; Connolly et al., 2010; Rabalais et al., 2010), here we are primarily concerned with upwelling from the vast reservoir of low oxygen waters in oxygen minimum zones.

The oxygen content of water masses usually is characterized by dissolved oxygen concentration units since these are conservative with respect to the temperature and salinity and can be used for mass balances, mixing calculations, and numerical modeling. This leads to oxygen thresholds also being reported in dissolved oxygen concentration units. However, animals depend on gas exchange across membranes and tissues for critical physiological processes such as respiration and also for controlling gas exchange with the swim bladder of fishes (e.g. Enns et al., 1965; Childress and Seibel, 1998; Pelster and Burggren, 1996; Piiper, 1982); the appropriate thermodynamic property for this is the gas fugacity which is readily approximated by the partial pressure. Experimental work on respiration of marine animals must thus essentially report pO_2 as the critical variable (e.g. Seibel, 2011). Since the partial pressure of a gas is a function of temperature, pressure (Enns et al., 1965), and salinity, thresholds reported as concentration units are not universally applicable but only valid for systems with particular temperature, pressure and salinity. Oxygen thresholds in terms of partial pressure, however, are universally applicable.[1]

In this paper we take steps towards overcoming three of the most fundamental shortcomings of low oxygen science today: (1) we plead for a consistent use of terminology and units by comparing and interrelating existing oxygen thresholds from the literature. (2) We restate that partial pressure of O_2 is required for defining organism needs and stresses and we propose a scale for definition of hypoxic events based on partial pressure. (3) We establish the connection between bathyal oxygen minimum zones and coastal hypoxia by examining how close various coastal ocean regions (without enclosed seas) are, on a yearly averaged basis, to experience significant negative impacts by upwelling-induced hypoxia.

2. Materials and methods

2.1. Oxygen concentration ($[O_2]$) data

Oxygen concentration data[2] in mlO_2/l units from the Ocean Data View version of the global oxygen climatology given in the World Ocean Atlas 2009 (WOA09 Garcia et al., 2010) have been used as primary data source throughout this paper unless stated otherwise. The data are annually averaged one-degree fields, so our analysis here does deal neither with seasonal changes in oxygen content nor with very fine spatial scales. Oxygen concentration[3] values given in the climatology in mlO_2/l have been converted to $\mu molO_2/kg$ using a molar volume for oxygen of 22.392 l/mol and seawater density values calculated with given salinities and in situ temperatures (Millero and Poisson, 1981).

2.2. Conversion of $[O_2]$ thresholds to pO_2 thresholds

While it is simple to produce maps and sections of pO_2 values knowing oxygen concentration $[O_2]$, temperature T, salinity S, and hydrostatic pressure P, the conversion of widely used O_2 concentration limits without T, S, and P data to equivalent pO_2 values requires some assumptions. Oxygen partial pressure[4] threshold values and oxygen saturation states (in %) have been calculated by converting the given coastal oxygen concentration thresholds using a common approximate seawater salinity of 34, and

[1] The much less elegant alternative for using constant pO_2 thresholds would be to use a matrix of $[O_2]$ thresholds with different values for different depths and temperatures. While oxygen saturation state in percentage could be used as an alternative quantity for O_2 thresholds, still a set of multiple values would have to be used for different depths: % O_2 saturation is a ratio between two pressure independent concentrations.

[2] All data have processed and plotted in the open source data analysis programming language R (R Development Core Team, 2010) using the extension package AquaEnv (Hofmann et al., 2010). Property maps have been created with Ocean Data View 4 (Schlitzer, 2010).

[3] Note that we use "molin": mol per kg *solution* throughout the paper.

[4] Note that the true thermodynamic variable is the oxygen fugacity; however, the difference between fugacity and partial pressure is small, the fugacity coefficient for $O_2 \approx 0.9982$ for T=25 °C, based on Zeebe and Wolf-Gladrow (2001) and Atkins (1996), and we use partial pressure throughout the paper.

temperatures of 25 °C, 17 °C, and 12 °C. 25 °C has been chosen as the primary conversion temperature since the most commonly used hypoxia threshold of 2 mgO_2/l ($\approx$61 μmolO_2/kg) is frequently reported to be equivalent to $\approx$30% saturation (Gooday et al., 2009a; Kemp et al., 2009; Levin et al., 2009; Codispoti, 2010; Ekau et al., 2010; Gilbert et al., 2010; Rabalais et al., 2010; Zhang et al., 2010), implying the standard temperature of 25 °C. 17 °C is roughly the mean sea surface temperature off the coast of Southern California and 12 °C is an approximate mean value for Monterey Bay. Furthermore, a hydrostatic pressure of 10 bar, roughly the value at the center of the 0–200 m depth slice of ocean commonly considered continental shelf or coastal sea, has been used to calculate the pressure dependency according to Enns et al. (1965).

2.3. [O_2] depth profiles of constant pO_2 thresholds and pO_2 profiles of constant [O_2] thresholds

Due to vertical changes in temperature, salinity and pressure, a constant pO_2 value corresponds to different oxygen concentrations along a depth profile, as well as a constant [O_2] value corresponds to different partial pressure values. As an example we calculated the concentration depth profiles resulting from constant pO_2 thresholds and the partial pressure thresholds resulting from constant concentration thresholds using the *S*, *T*, and depth conditions off Southern California (data also from the WOA09 climatology, Garcia et al., 2010). To account for the hydrostatic pressure effect on pO_2 according to Enns et al. (1965), the in situ hydrostatic pressure has been calculated from depth and mean latitude values given in the climatology (Fofonoff and Millard, 1983). Surface oxygen saturation concentrations (Garcia and Gordon, 1992) have been calculated with potential temperature (Bryden, 1973; Fofonoff, 1977), an O_2 mole fraction in air of 0.20946, and a saturation water vapor partial pressure correction according to Weiss and Price (1980) as given in Zeebe and Wolf-Gladrow (2001).

R scripts calculating pressure corrected pO_2 from *T*, *S*, depth, and [O_2] as well as calculating [O_2] from *T*, *S*, depth and pressure corrected pO_2 are given in the file `pO2.R` in the supplementary material.

2.4. Depth of pO_2 thresholds

After calculating pO_2 values for every [O_2] value given in the climatology, we have determined the depth of the upper boundary of the lens of water with pO_2 values below certain hypoxia thresholds. For every position (defined by a unique latitude and longitude value) and every hypoxia threshold (given as pO_2) the depth layer above and below the first occurrence of the threshold from the surface has been determined. The depth value directly at the respective hypoxia threshold has then been linearly interpolated over depth between the two adjacent depth layers.

2.5. Distances in terms of potential density of pO_2 thresholds from the 200 m isobath: "delta–sigma–theta" ($\Delta\sigma\theta$)

In assessing the risk for inundation of certain areas of continental shelf by nearby low oxygen waters, one can examine the depth at which pO_2 values below a certain threshold can be found. While the distance in m of the respective low oxygen waters from the sea surface gives an intuitive indication of how endangered a certain area of coast might be, it is not proportional to the energy it takes for overturning and upwelling the respective water mass onto the continental shelf. Due to ocean stratification, potential density ($\sigma\theta$) is the quantity proportional to the energy needed to vertically displace a parcel of water. As an indicator for the relative likelihood of upwelling-induced hypoxia, we thus calculated the difference in potential density between the upper boundary of the water mass with an oxygen content below the respective pO_2 threshold and the continental shelf, represented as the 200 m depth isobath (for the sake of comparability, a constant depth value of 200 m has been chosen to represent the depth of the start of the continental shelf all over the world).

Potential density has been calculated (Bryden, 1973; Fofonoff, 1977) for every position and depth in the oxygen climatology. For every position (defined by a unique latitude and longitude value) and every hypoxia threshold (given as pO_2) potential density values above and below the threshold have been determined. Those values have been linearly interpolated as functions of pO_2 to determine the $\sigma\theta$ value at the respective hypoxia threshold. Subsequently, the difference between the obtained $\sigma\theta$ value and the $\sigma\theta$ value at 200 m depth has been determined. The so-obtained differences in $\sigma\theta$ have been dubbed "delta–sigma–theta" ($\Delta\sigma\theta$).

Positive $\Delta\sigma\theta$ values express that the upper boundary of the lens of water with an oxygen content below the respective threshold is situated deeper than 200 m, and negative values indicate that the respective hypoxia boundary is already shallower than 200 m. Note that potential density does not scale linearly with depth, so negative $\Delta\sigma\theta$ values often have a higher absolute value than positive values although they only span 200 m depth, where positive $\Delta\sigma\theta$ values span several thousand m. This is a result of the temperature dependency of potential density and the steep temperature gradient in shallow waters.

The list of hypoxia "hot spots" given in this publication is derived based on this difference in potential density ($\Delta\sigma\theta$), approximate depth values are only given for reference.

3. Results

3.1. pO_2 as function of temperature, pressure, and salinity

Fig. 1 illustrates the dependency of oxygen partial pressure on temperature *T*, salinity *S*, and hydrostatic pressure *P*. For a given oxygen concentration of 61 μmolO_2/kg, pO_2 increases from $\approx$50 matm at the surface to 100 matm at $\approx$6000 m depth if the temperature remains constant at 10 °C. At $\approx$4000 m depth, pO_2 would increase from 70 matm to 90 matm when temperature was to rise from 4 °C to 20 °C (left panel of Fig. 1). The effect of salinity *S* on pO_2 is less pronounced (right panel of Fig. 1).

3.2. Categories of "hypoxia" based on oxygen partial pressure

Contemporary scientific literature on hypoxia or low oxygen conditions contains numerous thresholds. Table 1 reproduces a selection of commonly used values. While we stress that a continuum must exist, we find from the literature survey that three categories of hypoxia are in common use: *Category A*: sensitive species show avoidance reactions; *Category B*: the ecosystem is dominated by species communities adapted to low oxygen conditions; *Category C*: mass mortality for most species is induced and only highly specialized species are able to survive. In Table 2 we show suggested threshold values for these three categories, distilled from the literature cited. While we also give pO_2 values in kPa to be comparable to physiological literature (e.g. Childress and Seibel, 1998; Seibel, 2011), we propose the unit milli-atmospheres (matm) be adopted as standard unit for oxygen thresholds and contents to facilitate a later combination of pO_2 fields with pCO_2 fields, which generally are reported on μatm units (e.g. Zeebe and Wolf-Gladrow, 2001; Meehl et al., 2007; IPCC, 2007; Brewer and Peltzer, 2009), for assessment of combined effects of temperature change and ocean acidification.

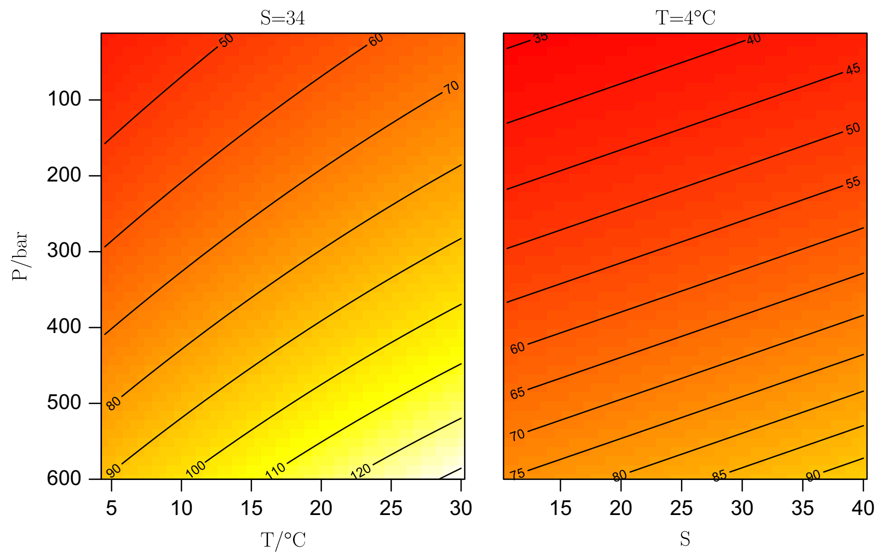

Fig. 1. Temperature T, salinity S and hydrostatic pressure P dependency of partial pressure: the lines indicate pO_2 values in matm for a constant oxygen concentration of $[O_2]=61$ μmol/kg. Left panel: P between 0 and 600 bar, T between 4 °C and 30 °C, $S=34$; right panel: P between 0 and 600 bar, S between 10 and 40, $T=4$ °C.

Fig. 2 shows a hydrographic profile of dissolved oxygen off the coast of Southern California obtained from the WOA09 oxygen climatology (Garcia et al., 2010). The thresholds for hypoxia categories A–C as given in Table 2 in partial pressure units (converted with $T=25$ °C, see caption of Table 2) are superimposed as solid lines, and thresholds in concentration units are superimposed as dashed lines. The right panel shows the traditional view of plotting concentration profiles and using concentration thresholds. Assessment of regions inhospitable to certain animals is made difficult by the fact that the line of constant partial pressure (i.e. the physiologically relevant quantity) is a curved line. This is remedied by plotting partial pressure profiles and using constant partial pressure thresholds (left panel).

3.3. Upwelling induced "coastal hypoxia": hot spots around the world

To indicate the location and extent of bathyal oxygen minimum zones around the world, Fig. 3 shows global maps of minimal pressure corrected in situ pO_2 values (top panel) and the depths at which the minima are attained for each position in the climatology (bottom panel). Contour lines in the top panel show the thresholds for our three categories of hypoxia. For each category, a $\Delta\sigma\theta$ map has been generated.

The upper panel of Fig. 4 shows a map of the global ocean indicating the depth of the upper boundary of waters with a concentration below the most commonly used hypoxia threshold (category B, $pO_2=60$ matm $\approx [O_2]=61$ μmolO_2/kg). In the areas where no data are plotted, pO_2 in the whole water column is above the hypoxia cat. B threshold. Top panels of Figs. 5 and 6 show the same for threshold values for hypoxia cat. A and C. The bottom panel of Fig. 4 shows a map of the global ocean indicating the difference in potential density ($\Delta\sigma\theta$) between waters of hypoxia category B and continental shelf depths as represented by the 200 m isobath. Bottom panels of Figs. 5 and 6 show the same for threshold values for hypoxia cat. A and C.

Fig. 4 confirms that large parts of the North Pacific and Northern Indian Ocean, as well as smaller parts of the Western Atlantic off Africa harbor water with pO_2 values below the coastal hypoxia threshold (hypoxia cat. B). Off the West coast of North America, those waters are situated several hundred meters deep and their potential density distance from the continental shelf is about 1 kg/m^3. Off Central and South America, however, hypoxic waters are already at shelf depths or shallower, needing only horizontal displacement to reach the coast. The same holds true for almost the whole Northern Indian Ocean. The situation seems to be the least severe at the Southern Coast of Japan, the Northern Philippines and in the South China Sea: although the bathyal oxygen minimum zones there do contain "hypoxic" water, those water masses are located more than 600 m deep and around 2 kg/m^3 removed in potential density, such that upwelling of these waters onto the continental shelf seems very unlikely.

From Fig. 4 for hypoxia category B, and Figs. 5 and 6 for hypoxia categories A and C, a list of coastal regions in the world can be derived which are particularly in danger of experiencing upwelling induced coastal hypoxia. Table 3 shows a list of such hypoxia "hot spots". Three general endangered areas can be identified: the West coast of Central and South America in the Eastern Pacific, the West coast of Africa in the South-Western Atlantic, and the coasts of Somalia, Yemen, Oman, Pakistan, India, Bangladesh and Myanmar in the Northern Indian Ocean. On the West coast of Ayeyarwady (Myanmar), even hypoxia cat. C water ($pO_2 \leq 22$ matm) is located just below the surface.

Fig. 7 enlarges the Western coast of the Americas and identifies the coasts of Southern Mexico, Guatemala, Honduras, Nicaragua, Costa Rica and Panama as regions where hypoxic water masses are already located shallower than continental shelf depths. Off the coast of Oregon, a well known location of upwelling-induced hypoxia which recently has been receiving intense media coverage (e.g. Grantham et al., 2004; Chan et al., 2008; Gewin, 2010), hypoxic water masses are located less than 100 m below the continental shelf margin with a potential density distance of less than 0.5 kg/m^3. This is a situation similar to that in the Southern half of Chile, but is less severe than the West coast of South America.

Fig. 8 enlarges the West coast of Africa identifying two main hypoxia hot spots along the coast of Mauritania and Southern Angola, Northern Namibia: there, hypoxic waters (cat. B) are already at continental shelf depths. Along the coast between these two hot spots, hypoxic waters are less than 200 m in depth or 0.5 kg/m^3 in potential density away from the continental shelf.

Fig. 9 enlarges the Northern Indian Ocean and Western Pacific. The central coast of Myanmar (Ayeyarwady) can be identified as the main hypoxia hot spot in this area, with hypoxic waters being located shallower than 100 m and 3 kg/m^3 in potential density above the continental shelf depth at the 200 m isobath. While the coast off Myanmar shows as an intense hot spot, all coasts along the Northern Indian Ocean can be seen as threatened by

Table 1
Selection of [O_2] thresholds to describe various low oxygen conditions in the literature. pO_2 and saturation state values are obtained using S=34, T=25 °C, and P=10 bar. Values in bold face are reported in the paper cited. Names not in bold face indicate that the cited paper does not explicitly name the threshold. Bold face values in brackets indicate values given in the cited paper as well which are not the same as the ones calculated with the given S, T, P values here. The values in Childress and Seibel (1998) were given in mlO_2/l concentration and in kPa partial pressure values, no temperature, salinity or pressure was given. When necessary, pO_2 values in kPa where converted to mlO_2/l [O_2] values using a linear relation derived from the given concentration–partial pressure pairs and then, for the sake of consistency, further converted using S, T, P values given here.

µmolO_2/kg	µmolO_2/l	mgO_2/l	mlO_2/l	% sat	pO_2/ matm	pO_2/kPa	Name	Description	Reference
175–131	179–134	5.72–4.29	**4–3**	84–63	173–129	17.5–13.1	Hypoxia	Tolerance of demersal fish predators	Diaz and Rosenberg (2008)
87	89	2.86	**2**	42	86	8.7	**Hypoxia**	Benthic fauna show aberrant behavior	
22	22	0.71	**0.5**	10	22	2.2	**Severe hypoxia**	Mass mortality	
4	4	0.14	**0.1**	2	4	0.41	Oxygen minimum zone	Mass mortality and major changes in community structure during hypoxic events; but benthic fauna is adapted if permanent OMZ extends to bottom	
183	188	**6**	4.2	88	181	18.3	Hypoxia	Growth of actively swimming fish affected	Gray et al. (2002)
61	63	**2**	1.4	29	60	6.1		Most fishes show mortality	
31	31	**1**	0.7	15	30	3.0		Mudskippers show mortality	
15	16	**0.5**	0.35	7	15	1.5		Hydrogen sulphide is released into the water	
122–92	125–94	**4–3**	2.8–2.1	59–44	121–91	12.3–9.2	Hypoxia	Avoidance by fishes, mobile fauna migrates	Cenr (2010)
61	63	**2**	1.4	29	60	6.1		Fishes absent	
46	47	**1.5**	1.05	22	45	4.6		Shrimp & crab absent, fauna unable to escape	
31	31	**1**	0.7	15	30	3.0		Mortality of sensitive fauna	
15	16	**0.5**	0.35	7	15	1.5		Mortality of tolerant fauna, formation of microbial mats	
3	3	**0.1**	0.07	1	3	0.30		Sediment geochemistry drastically altered, hydrogen sulfide builds up in water column	
87	89	2.86	**2**	42	86	8.7	**Geological suboxia**		Gooday et al. (2009a)
64	66 (**65**)	2.1	**1.47**	31	63	6.4	**Coastal hypoxia**	Some animals may exhibit avoidance reactions or even die	
62	64	2.04	1.43	**30**	62	6.3	**Biological hypoxia**		
22	**22**	0.71	**0.5**	10	22	2.2	**Bathyal oxygen minimum zone**		
9	9	0.29	**0.2**	4	9	0.91	**Geological anoxia**		
0	0	0	0	0	**0**	0	**Geological euxinia, biological anoxia**		
5	5	0.16	0.11	2	5	0.51	**Suboxia**	Evidence of nitrate reduction and denitrification	Rue et al. (1997)
61	63	**2**	1.4	29	60	6.1	**Hypoxic (“dead”) zone**	Gulf of Mexico: trawlers cannot catch fish or shrimp on the bottom anymore	Lumcon (2010); Hogue (2010)
22	22	0.71	**0.5**	10	22	2.2	**Severe inner shelf hypoxia**	Complete absence of all fish, near-complete mortality of macroscopic benthic invertebrates, bacterial mats	Chan et al. (2008)
62	64	2.04	**1.43**	30	62	6.3	**Hypoxia**	Fish cannot survive	Gewin (2010)
61	**63**	**2**	**1.4**	29	60	6.1	**Coastal hypoxia**	Significant effect on benthic animals	Middelburg and Levin (2009)
62	63 (**62.5**)	2.03 (**2**)	**1.42**	≈**30**	61	6.2	**Coastal hypoxia**	Responses of benthos depend on the duration, predictability and intensity of oxygen depletion	Levin et al. (2009)
61	63	**2**	**1.4**	29	60	6.1	**Hypoxia**	Avoidance or altered behavior, growth, reproduction or survivorship of many marine organisms	Naqvi et al. (2010)
4	4	0.14	**0.1**	2	4	0.41	**Suboxia**	Reduction of N, I, Mn, Fe, denitrification dominant respiratory process	
0	0	0	**0**	0	0	0	**Anoxia**	Sulphate reduction dominant respiratory process	
62	64 (**62.5**)	2.04 (**2**)	1.43	**30**	62	6.3	**Hypoxia**	Interrupted normal metabolism and behavior of fish and invertebrates causing reduced growth and increased mortality	Kemp et al. (2009)
0	0	0	0	**0**			**Anoxia**	Brief exposure: mortality for many marine animals	

61	63	**2**	1.4	29 (≈ **30**)	60	6.1	**Hypoxia**		Rabalais et al. (2010)
61	**63**	2	1.4	29	60	6.1	**Hypoxia**	Influences biogeochemical cycles; may have severe negative impacts on marine ecosystems, such as mortality of benthic fauna, fish kills, habitat loss, and physiological stress	Pena et al. (2010)
62	64	2.04 (**2**)	1.43	**30**	62	6.3	**Coastal hypoxia**	Has caused a deterioration of a variety of characteristics important to the sustainability of marine ecosystems	Zhang et al. (2010)
61	63 (**60**)	**2**	**1.4**	29 (**30**)	60	6.1	**Low oxygen, hypoxia**	Affects biological systems on different organizational levels: physiological changes, distribution of species	Ekau et al. (2010)
62	64	2.04	1.43	**30**	62	6.3	**Hypoxia**		Gilbert et al. (2010)
87	89	2.86	**2**	42	86	8.7	**Mild hypoxia**	Animals leave shelters, alter activity patterns, expose themselves to higher risk of predation	Haselmair et al. (2010)
44	45	1.43	**1**	21	43	4.4	**Moderate hypoxia**	Triggers changes in inter- and intraspecific interactions	
22	22	0.71	**0.5**	10	22	2.2	**Severe hypoxia**	Sublethal responses, such as discarding of camouflage, ≈ 50% mortality in crustaceans	
87	89	2.86	**2**	42	86	8.7	**Hypoxia**	Loosely associated with ocean “dead zones”	Stachowitsch et al. (2007)
87	89	2.86	**2**	42	86	8.7	**Beginning hypoxia**	Elicits escape patterns	Riedel et al. (2008)
44	45	1.43	**1**	21	43	4.4	**Moderate hypoxia**	Triggers species-specific sublethal responses such as arm-tipping in ophiuroids or extension from the sediment in sea anemones	
22	22	0.71	**0.5**	10	22	2.2	**Severe hypoxia**	Emergence of infaunal organisms and first mortalities	
10	10	0.33	0.23	5	10	1.0	**Suboxia**	Void of fish, other mobile macroorganisms and macrofauna, denitrification and N_2O production	Shaffer et al. (2009)
80	82	2.62	1.83	38	79	8.0	**Hypoxia**	Avoidance by fish stock, mortality events	
193–55	197–56	6.3–1.8	**4.41–1.26**	93–26	190–54	**13–4** (19.3–5.5)	**Hypoxia in shallow habitats**	Critical value for species living in high O_2 environments below which their oxygen uptake rates cannot sustain routine metabolism	Childress and Seibel (1998)
7	7	0.21	**0.15**	3	6	**0.48** (0.66)		Pronounced effects on species distribution and biomass of midwater communities: oxygen uptake rates cannot sustain routine metabolism in adapted species	
62	64	2.04	1.43	**30**	62	6.3	**Hypoxia**		Codispoti (2010)
2	2	0.07	0.05	**1**	2	0.21	**Suboxia**	High N_2O production	
66	67	2.14	**1.5**	31	65	6.6	**Hypoxia**	Impacts on fisheries	McClatchie et al. (2010)
70	71	**2.28**	1.6	33	69	7.0	**Hypoxia**	Median of literature search conducted	Vaquer-Sunyer and Duarte (2008)
61	63	**2**	1.4	29	60	6.1	**Hypoxia**	Severe consequences for marine life, including death and catastrophic changes	
9	9	0.29	**0.2**	4	9	0.87	**Hypoxia**		Kamykowski and Zentara (1990)
8	8	0.26	0.18	4	8	**0.8**		Transition of an ecosystem from diverse midwater fauna to diel migrant biota	Seibel (2011)
50	51	1.63	1.14	24	49	**5.0**		Above this threshold organisms do not have any additional benefit from more oxygen	
10	10	0.33	0.23	5	10	1.0	**Hypoxia**		Matear and Hirst (2003)

Table 2
Commonly used $[O_2]$ thresholds to describe various low oxygen conditions, distilled into three main "hypoxia categories". pO_2 values are obtained for continental shelf depths assuming a hydrostatic pressure of $P = 10$ bar. Salinity is assumed to be 34. The different temperature columns indicate temperatures used to convert thresholds from concentration units to partial pressure units. While the conversion temperature in general should reflect the temperature at which the threshold has been determined, 25 °C is used as the main conversion temperature throughout this paper to be consistent with the literature (e.g. Levin et al., 2009; Rabalais et al., 2010: ≈ 2 $mgO_2/l \approx 61$ µmol/kg is equivalent to 30% saturation which implies $T = 25$ °C; see text for details).

$\mu molO_2/kg$	$\mu molO_2/l$	mgO_2/l	mlO_2/l	pO_2/matm (% sat)			Hypoxia category	Description	References
				$T = 25$ °C	$T = 17$ °C	$T = 12$ °C			
107	109	3.5	2.45	106 ($51 \approx 50$)	93 (45)	84 (40)	**A**	"**Mild hypoxia**", sensitive species show avoidance reactions	Cenr (2010)
61	63	2	1.4	60 ($29 \approx 30$)	53 (25)	48 (23)	**B**	"**(coastal) Hypoxia**", ecosystem dominated by species communities adapted to low oxygen conditions	Gray et al. (2002), Vaquer-Sunyer and Duarte (2008), Gooday et al. (2009a), Kemp et al. (2009), Levin et al. (2009), Middelburg and Levin (2009), Cenr (2010), Ekau et al. (2010), Gewin (2010), Gilbert et al. (2010), Hogue (2010), Lumcon (2010), Naqvi et al. (2010), Pena et al. (2010), Rabalais et al. (2010), Zhang et al. (2010)
22	22	0.71	0.5	22 ($11 \approx 10$)	19 (9)	17 (8)	**C**	"**Severe hypoxia**", mass mortality for most species is induced and only highly specialized species are able to survive	Diaz and Rosenberg (2008), Chan et al. (2008), Riedel et al. (2008), Gooday et al. (2009a), Haselmair et al. (2010)

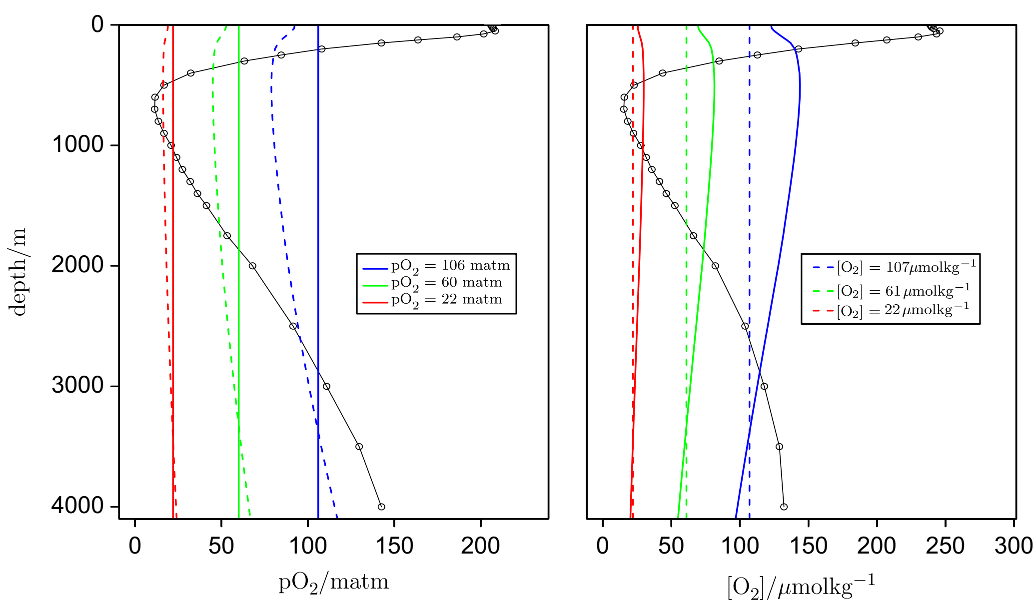

Fig. 2. Dissolved oxygen profiles expressed as pO_2 (left panel) and $[O_2]$ (right panel) for an example station off the coast of Southern California (29.5 °N, 120.5 °W) obtained from the World Ocean Atlas 2009 oxygen climatology (Garcia et al., 2010), overlaid with thresholds for hypoxia categories A–C (blue, green, and red lines). Solid lines: constant pO_2 thresholds, dashed lines: constant $[O_2]$ thresholds. To be consistent with the literature (e.g. Levin et al., 2009; Rabalais et al., 2010: ≈ 2 $mgO_2/l \approx 61$ µmol/kg is equivalent to 30% saturation which implies $T = 25$ °C) $T = 25$ °C has been used to convert thresholds between pO_2 and $[O_2]$ (see Table 3), however, the ambient surface temperatures at the example station are ≈ 17.6 °C, thus the constant pO_2 and constant $[O_2]$ threshold lines do not meet at the surface.

upwelling induced coastal hypoxia since everywhere from Somalia over India to Sumatra, hypoxic (cat. B) waters are located shallower than 200 m.

4. Discussion

4.1. The need for a common language

Without a common language, science is hard if not impossible to communicate either to other scientists or to the general public. Especially when scientific results and definitions are the basis for policies, regulations, and resource management decisions, inconsistent language can lead to misinterpretations with possible unfortunate consequences: oxygen levels that constitute a "dead zone" in one region of the ocean are the norm in others, with the distinction not always clear, possibly resulting in misleading notions of a largely "dead" ocean. We provide here a first step towards a common language in low oxygen science.

4.2. Partial pressure as threshold for physiological reactions

Since the partial pressure of a gas is the thermodynamic driving force for exchange across a membrane, using constant concentration thresholds to determine regions of inhospitability for certain animals might lead to erroneous results. This can

Table 3
Areas particularly endangered by upwelling induced coastal hypoxia (hypoxia ''hot spots''). Areas are grouped by hypoxia category A–C and by potential density distance from the 200 m isobath. Approximate depths of the upper boundary of waters of the respective hypoxia category are given as well. Note that enclosed seas like the Red Sea, Black Sea, Caspian Sea and the Baltic are not discussed here.

Region	$\frac{\Delta\sigma\theta}{kg/m^3}$	$\approx\frac{Depth}{m}$
Hypoxia cat. A (pO_2 ***at minimum*** $\leq$ 106 ***matm***):		
Northern East coast of Queensland (Australia) around Cairns, Vanuatu, Fiji, Southern coasts of the Solomon Islands, Northern Coast of Eastern tip of New Guinea, Southern coast of New Britain, Samoa, Tahiti, Mauritius, Reunion	>2	>600
Caribbean (Cuba, Hispanola), Hawaii Islands, Easter Island, South Western Africa (Mozambique, Tanzania), Madagascar, Northern East coast of Queensland (Australia) North of Cooktown, North-Western tip of Western Australia (Kalbarri to Nickol), Northern coast of New Guinea, Northern coast of New Britain, Northern coasts of the Solomon Islands, North Western tip of Maluku Utara and East coast of Pulau Morotai, East coast of the Philippines (Luzon) and Taiwan, Okinawa, Southern tip of Kyushu, South coast of Shikoku, parts of the Southern coast of Honshu	2–1	$>600-300$
Nuku-Hiva (French Polynesia), Guam, Northern Mariana Islands, Southern tip of Hawaii proper, West coast of Aisen and Northern Magallanes, Chile, Northern tip of the Antarctic Penninsula, parts of Baffin Bay, Gulf of St. Lawrence, Northern Gulf of Mexico, Southern Caribbean (Northern Coast of South America, Eastern coast of Central America), Guyana, Suriname, French Guyana, Northern coast of Brazil, Eastern tip of Brazil, coast of Western Sahara, Mauritania, Namibia, Tanzania, Kenya, Northern coast of Western Australia (around South Hedland), parts of Indonesia East of Borneo, South-Western coast of China, Western coast of Kyushu, Southern and Western Coast of Honshu and Hokkaido, Sea of Okhotsk, Bering Sea	1–0	$>600-200$
South coast of Aleutian Islands, West Coast of Canada, USA, Baja California (Mexico), West Coast of South America from the Equator to Aisen (Chile), Cape Verde Islands, West coast of Africa from Mauretania to Namibia, Somalia, Northern coast of Western Australia, East coast of Vietnam, Northern coast of Borneo, Western coast of Luzon (Philippines), Eastern coast of Mindanao (Philippines), Eastern coast of Kamchatka, South-Western Bering Sea, Palau, Micronesia, Galapagos Islands	0 to (-1)	$200--<100$
Southern tip of Baja California, Sea of Cortez, Southern coast of Panama, Western coast of Colombia, Ecuador, Senegal, Guinea, Sierra Leone, Liberia, Arabian Sea, Gulf of Aden, North-Eastern tip of Somalia, Indian Ocean coast of Malaysia, Sulu Sea, Banda Sea	(-1) to (-2)	<100
West coast of Mexico south of Puerto Vallarta, West coast of Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, India, Sri Lanka, central and Northern part of Malayan Indian Ocean coast	(-2) to (-3)	<100
North Eastern part of India, Bangladesh, Myanmar, Andaman and Nicobar Islands, Indian Ocean coast of Thailand	(-3) to (-4)	<100
West coast of Ayeyarwady (Myanmar)	$<(-4)$	<100
Hypoxia cat. B (pO_2 ***at minimum*** $\leq$ 60 ***matm***):		
Northern tip of Luzon (Philippines) and Taiwan, Okinawa, East coast of Kyushu	>2	>600
Hawaii Islands, Nuku Hiva, West coast of Luzon (Philippines), Northern tip of Borneo, Central coast of Vietnam, Southern coast of Honshu	2–1	$>600-300$
Aleutian Islands, Bering Sea, West coast of Northern America from Alaska to central Baja California (Mexico), Aisen (Chile), Galapagos Islands, Cape Verde Islands, Senegal, West coast of Africa from Senegal to Northern Angola, East coast of Africa from central Somalia to Tanzania, Southern coast of Java, Sulu Sea, East coast of Mindanao (Phillipines), North Western coast of Honshu, Sea of Okhotsk, Palau, Micronesia, Marshall Islands	1–0	$>600-200$
Eastern coast of Kamchatka, Southern coast of Eastern Aleuteian Islands, South Coast of Kodiak Island (Alaska), Southern tip of Baja California (Mexico), Sea of Cortez, West coast of central and South America from Panama to Aisen (Chile), Mauritania, Congo, Angola, Northern Namibia, Arabian Sea, Gulf of Aden, North-Eastern tip of Somalia, West coast of Sumatra	0 to (-1)	$200-<100$
West coast of Central America from the Southern tip of Baja California to Panama, West coast if India, Sri Lanka, Northern tip of Sumatra, Indian Ocean Coast of Thailand	(-1) to (-2)	<100
East coast of India, Bangladesh, Myanmar	(-2) to (-3)	<100
West coast of Ayeyarwady (Myanmar)	$<(-3)$	<100
Hypoxia cat. C (pO_2 ***at minimum*** $\leq$ 22 ***matm***):		
Kauai (Hawaii)	>2	>600
Hawaii Islands, North Eastern tip of Somalia	2–1	$>600-300$
Aleutian Islands, Bering Sea, West coast of North America from Alaska to Baja California (Mexico), Colombia, Ecuador, Galapagos Islands, Central Chile, Northern Namibia, Gulf of Aden, East coast of Kamchatka, Sea of Okhotsk, Northern tip of Sakhalin	1–0	$>600-200$
West coast of Central America from the tip of Baja California (Mexico) to Northern Colombia, West Coast of South America from Peru to Central Chile, Southern Angola, Arabian Sea, India, Sri Lanka, Southern Myanmar	0 to (-1)	$200-<100$
Central Mexico, North Eastern India, Bangladesh, Northern Myanmar	(-1) to (-2)	<100
West coast of Ayeyarwady (Myanmar)	<-2	<100

be illustrated by a simple example. Assume an animal has been investigated in the laboratory at temperature $T=25\,^{\circ}C$ and hydrostatic pressure $P=0$ bar, and an oxygen threshold of $[O_2]=107\ \mu molO_2/kg$ has been found. However, as long as there is enough oxygen, the animal's habitat off the coast of California (see Fig. 2) stretches from the surface down to the bottom below 4000 m depth where the temperature decreases from $\approx 17.6\,^{\circ}C$ at the surface to $\approx 1.6\,^{\circ}C$ at 4000 m. To determine the depth range between the surface and the bottom that is inhospitable for the animal due to oxygen limitation, one would now traditionally turn to the right panel of Fig. 2 and find that this range stretches over 2355 m from 260 m to 2615 m depth, as this is the range in which the ambient $[O_2]$ is below 107 $\mu molO_2/kg$. However, if the oxygen threshold the animal experiences in the lab experiment is expressed in terms of pO_2 at lab conditions (≈ 106 matm for $T=25\,^{\circ}C$ and $P=0$ bar), which is the quantity that is actually measured, and this pO_2 is used as constant threshold (Fig. 2, left panel), then the 2671 m between 204 m and 2876 m depth can be considered inhospitable to the animal as the ambient pO_2 in this range is below 106 matm. The difference between the two approaches of more than 300 m is due to the fact that partial pressures of oxygen for a given concentration are smaller due to decreased temperatures at depth. However, if one was to assume that the ambient oxygen concentration at depth does not increase past 107 $\mu molO_2/kg$ while going down, but remains constant at for example 100 $\mu molO_2/kg$ all the way to the bottom, then the inhospitable region obtained using a constant $[O_2]$ would extend all the way to the bottom, while the inhospitable region obtained with a constant pO_2 threshold would end at 3873 m, since the increasing partial pressure of oxygen for a given concentration with increasing hydrostatic pressure (Enns et al., 1965) becomes dominant over the temperature effect at greater depths. This effect of hydrostatic pressure decreasing the extend of inhospitable zones is more pronounced at even greater depths and in seas with less counteracting temperature decrease with depth. For example in the warm Mediterranean, the pO_2 for a given $[O_2]$ is usually higher at 4000 m depth than it is at the surface, which means there is a possibility of inhospitable zones

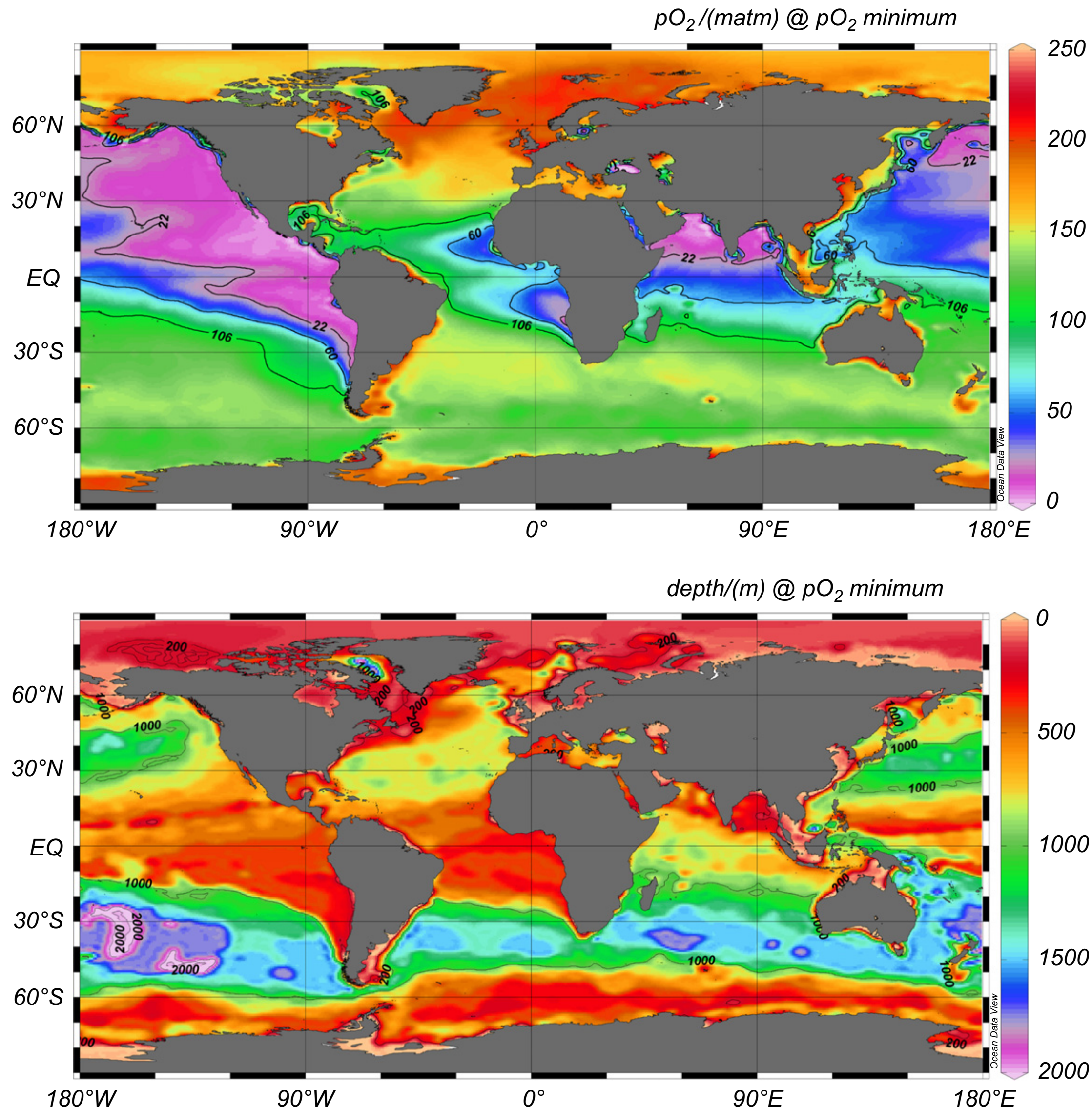

Fig. 3. Bathyal oxygen minimum zones: pO_2 minimum values (top panel), and depth at which pO_2 minimum is attained (bottom panel). Data from the World Ocean Atlas 2009 oxygen climatology (Garcia et al., 2010).

for certain animals at the surface while they can live at greater depths. This issue is dealt with in greater detail in Hofmann et al. (submitted for publication).

The critical value in pO_2 that animals minimally need to survive is ultimately set by the efficiency with which animals can transport the oxygen from the outside water to their mitochondria (Childress and Seibel, 1998), which is ultimately limited by the diffusive boundary layer. Besides temperature, salinity and hydrostatic pressure, the water velocity over gas exchange surfaces plays a vital role in this respect, the higher the velocity (ambient current velocity, swim speed, or pumping speed across gas exchange surfaces), the thinner the boundary layer and the more efficient the oxygen transport. Hofmann et al. (submitted for publication) examine this in detail.

4.3. "Hot spots" for upwelling induced hypoxia

Table 3 and Fig. 5 show regions of the world that are in close proximity to waters below the hypoxia category A threshold. Upwelling of those waters to shelf-depths could impact fisheries via changes in species composition as a result of evasive reactions of key species. Table 3 and Fig. 4 represent areas around the world in close proximity to waters with hypoxia category B (and for some areas even category C: Fig. 6), where upwelling can have more severe consequences. For parts of Japan and the Phillipines, the West Coast of North and South America, the African West Coast and parts of its East coast south of Somalia the respective low oxygen water masses are less than 1 kg/m^3 away from continental shelf depths. However, along the West Coast of Central America, the whole coast of the Northern Indian Ocean and parts of the African West Coast, the respective oxygen water masses start already even shallower than shelf-depths. The Northern Bay of Bengal represents the prime hot spot in this respect: cf. the East Coast of India and the coasts of Bangladesh and Myanmar in Fig. 9. For the South-Western African coast, including Mauritania, Angola, and Namibia (Fig. 8), the close proximity of bathyal oxygen minimum zones to shallow ecosystems adds to the threat of periodic oxygen consumption due to oxidation of methane and hydrogen sulfide erupting from the sediment (Weeks et al., 2004). We confirm the coast off Oregon for which upwelling-induced hypoxia has already been reported (Grantham et al., 2004; Chan et al., 2008; Gewin, 2010) to be a

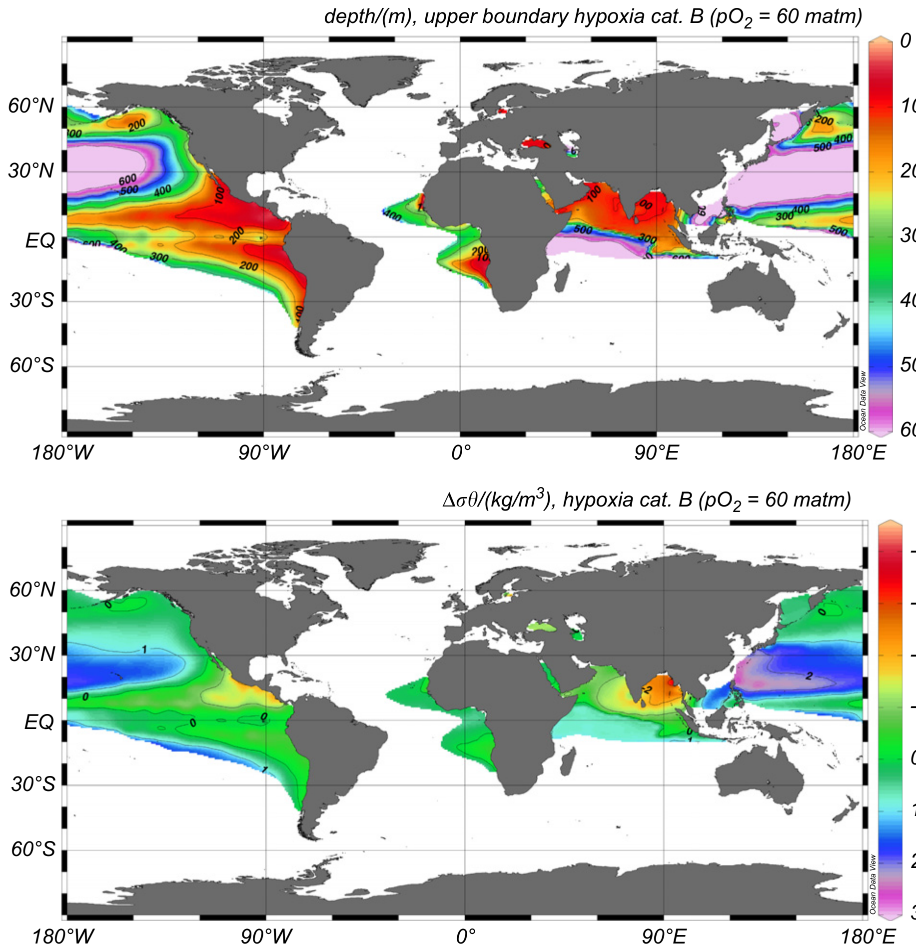

Fig. 4. Depth of the upper boundary of waters with concentrations below the hypoxia cat. B oxygen partial pressure threshold (pO_2 = 60 matm): top panel. Difference in potential density ($\Delta\sigma\theta$) between the isosurface of the upper boundary of waters with concentrations below the hypoxia cat. B oxygen partial pressure threshold and the 200 m isobath: bottom panel. $\Delta\sigma\theta$ values express the potential energy distance of the respective low oxygen waters to the continental shelf and represent a relative measure for the likelihood of upwelling events inducing coastal hypoxia in the respective regions. Negative $\Delta\sigma\theta$ represents hypoxic waters shallower than 200 m.

hypoxia hot spot. Furthermore, our treatment reveals that off the coast of Central America, from Southern Mexico to Panama, such an event is even more likely to occur (Fig. 7). The coast off Peru, usually less media covered while being known for upwelling induced hypoxia (Chavez, 2008), shows up as a hot spot in our map.

The picture painted in Fig. 4 is generally similar to the previous assessments of danger of upwelling-induced coastal hypoxia (Fig. 1, top panel Rabalais et al., 2010). While those authors similarly identify the West Coast of the American continent, two parts of the African West Coast, the Northern Coast of the Indian Ocean, and the Sulu sea as being endangered by expansion of the oxygen minimum zone and upwelling, their treatment lacks an indication of the relative likelihood of the occurrence of an upwelling event. This entails the failure to mention regions in the Western North Pacific, where upwelling events of low oxygen waters are possible but less likely. More importantly, it does not allow for a ranking of all the shown areas due to the severity of their endangerment by upwelling induced hypoxia. Our study provides such a ranking.

The upwelling-induced hypoxia hot spots found in this study are in good agreement with areas exhibiting hypoxic bathyal sea floor and shelf slope as identified by Helly and Levin (2004). While Helly and Levin (2004) identify regions with permanently hypoxic benthic communities and elude to the effects of variability of the oxygen minimum zone on local species communities, their study does not yet provide a relative measure of the likelihood of hypoxic waters being transported up in the water-column as it is given here.

4.4. Future prospect

There is still no complete consensus in the scientific community if anthropogenic forcing already lead to a decline in global ocean oxygen content. There are both modeling studies (Froelicher and Joos, 2009) and observations (Mecking et al., 2008) that suggest that over recent decades natural variability in oxygen content might have masked anthropogenic influences, while other authors suggest that due to ongoing global ocean warming (Lyman et al., 2010), the oxygen concentration in the ocean is already declining (Chen et al., 1999; Nakanowatari et al., 2007; Jenkins, 2008; Stramma et al., 2008). In spite of those uncertainties and the fact that our capability to predict the exact location of oxygen content changes is still rudimentary (Keeling et al., 2010), there is a rather high confidence that oxygen is bound to decline further in the coming century (e.g. Matear and Hirst, 2003; Shaffer et al., 2009) due to reduced oxygen solubility and increased stratification/reduced ventilation at higher temperatures.

Here we propose to use oxygen partial pressure pO_2 instead of the oxygen concentration $[O_2]$ as thresholds. As mentioned, $[O_2]$ decreases with increasing temperature, but pO_2 at constant $[O_2]$ increases with increasing temperature. Thus, both

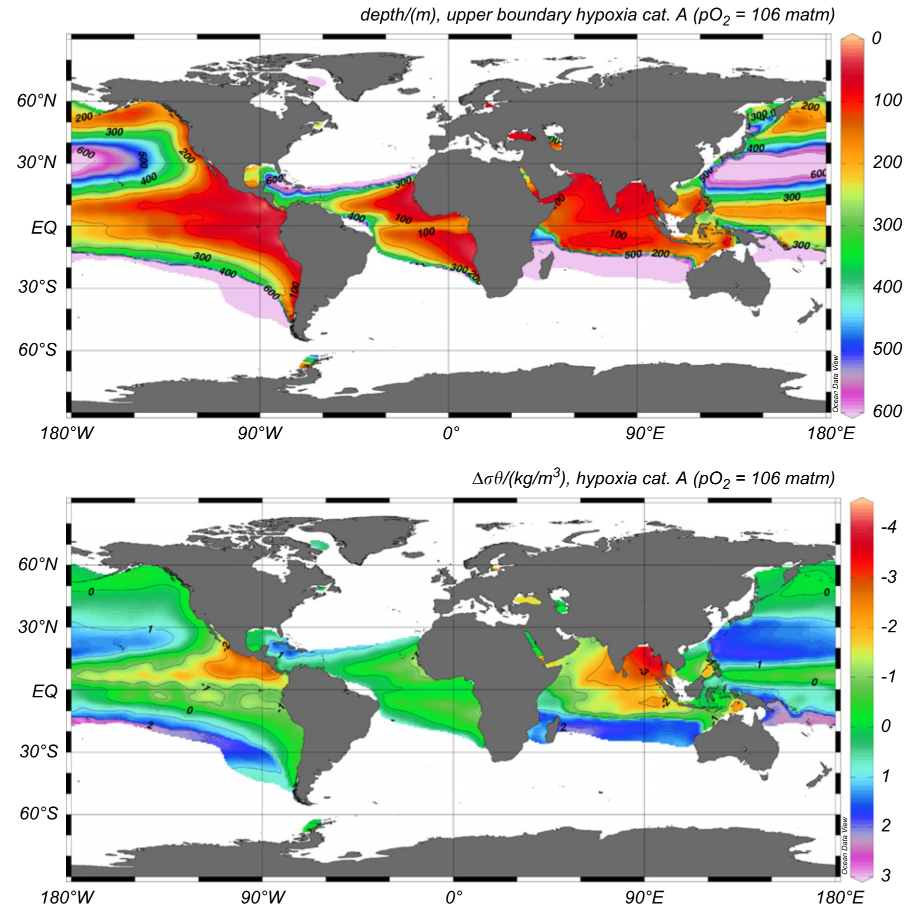

Fig. 5. Depth of the upper boundary of waters with concentrations below the hypoxia cat. A oxygen partial pressure threshold ($pO_2 = 106$ matm): top panel. Difference in potential density ("$\Delta\sigma\theta$") between the isosurface of the upper boundary of waters with concentrations below the hypoxia cat. A oxygen partial pressure threshold and the 200 m isobath: bottom panel. $\Delta\sigma\theta$ values express the potential energy distance of respective low oxygen waters to the continental shelf and represent a relative measure for the likelihood of upwelling events inducing coastal hypoxia in the respective regions.

temperature effects counteract each other. As a consequence, pO_2 is bound to change less strongly than $[O_2]$ in projections for the future ocean. However, these differences will be negligible: for a temperature change from 5 °C to 7 °C with $S=34$ and an initial oxygen concentration of 20 $\mu molO_2/kg$, pO_2 will change 1.3% less than $[O_2]$, considering $[O_2]$ changes due to reduced oxygen solubility only and including the effect of increased saturation water vapor pressure at higher temperatures. (Note that only in this particular case, which is basically looking at a 2 °C change in temperature at constant pressure, the effect of considering partial pressure instead of concentration is rather small. When using constant partial pressure instead of concentration for thresholds determined in the laboratory and applied to the deep ocean, as eluded to above, this transition has a much larger effect (see Figs. 1 and 2) as one looks at temperature changes of ≈ 20 °C associated with pressure changes of several hundred bars.)

Here, we identify hot spots for upwelling-induced hypoxia based on long term oxygen concentration averages as given in an oxygen climatology. Oxygen minimum zones, however, are not only expected to expand and shoal in the future (e.g. Codispoti, 2010), but also shoaling of the location of hypoxia thresholds in the water column can already be observed (e.g. Bograd et al., 2008). This trend makes our treatment a lower estimate of threat levels and the situation will most likely worsen in the future. Adverse effects of decreasing oxygenation not only imply the growing of "dead zones" and areas that are threatened by low oxygen deep water, but also less dramatic but still severe effects like changes to local species communities (see also Chavez, 2008; McClatchie et al., 2010), major loss in biodiversity, sublethal stresses, and disruption of life cycles of key fishery species (Vaquer-Sunyer and Duarte, 2008). Also commercially interesting fishes might be out-competed by low oxygen tolerant species such as the jumbo squid *Dosidicus gigas* (Field, 2008; Chavez, 2008; Rosa and Seibel, 2010). In the face of the prospect of decreasing future oxygenation of the world ocean and potential severe consequences, freely available oxygen data from the Argo floats http://www.argo.ucsd.edu would greatly facilitate much needed monitoring efforts.

Our treatment here is based on a static assessment of ocean stratification as given in the World Ocean Atlas 2009 oxygen climatology. An upwelling event is needed to actually displace low oxygen waters onto the shelf. This makes our $\Delta\sigma\theta$ values only relative measures of the likelihood of the occurrence of upwelling-induced hypoxia as the frequency of such upwelling events is variable and not very well known. However, there is a chance that, due to global warming and intensified atmospheric turbulences, wind-driven upwelling might increase in the future (e.g. Bakun and Weeks, 2004). This would increase the overall frequency and likelihood of upwelling events and thus upwelling induced hypoxia in our hot spot areas in the future.

Declining oxygenation is not the only threat that coastal ecosystems will face in the near future. As atmospheric anthropogenic CO_2 is taken up by the oceans, organisms will not only face the effects of resulting ocean acidification (e.g. Royal Society, 2005), but increasing pCO_2 will also reduce the energy yield of the oxic respiration reaction (Brewer and Peltzer, 2009) due to

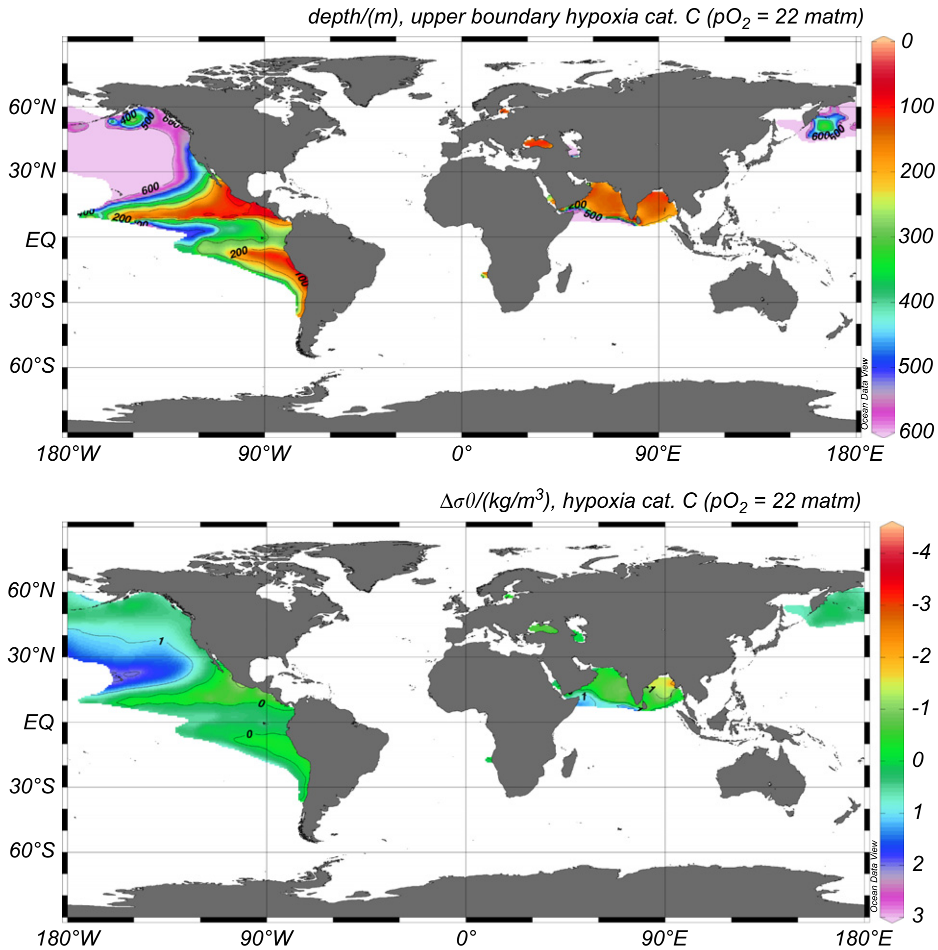

Fig. 6. Depth of the upper boundary of waters with concentrations below the hypoxia cat. C oxygen partial pressure threshold ($pO_2=22$ matm): top panel. Difference in potential density ("$\Delta\sigma\theta$") between the isosurface of the upper boundary for isosurface of waters with concentrations below the hypoxia cat. C oxygen partial pressure threshold and the 200 m isobath: bottom panel. $\Delta\sigma\theta$ values express the potential energy distance of respective low oxygen waters to the continental shelf and represent a relative measure for the likelihood of upwelling events inducing coastal hypoxia in the respective regions.

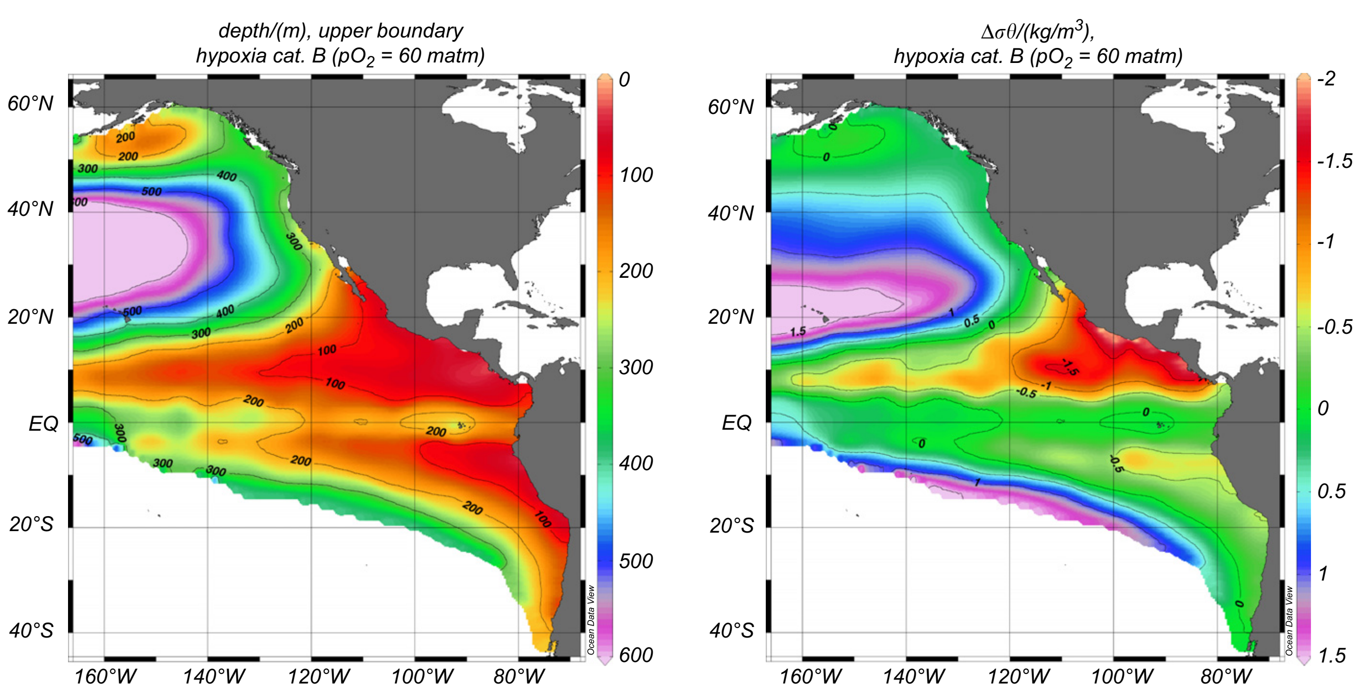

Fig. 7. Eastern Pacific: depth of the upper boundary of waters with concentrations below the hypoxia cat. B oxygen partial pressure threshold ($pO_2=60$ matm): left panel. Difference in potential density ("$\Delta\sigma\theta$") between the isosurface of the upper boundary of waters with concentrations below the hypoxia cat. B oxygen partial pressure threshold and the 200 m isobath: right panel. $\Delta\sigma\theta$ values express the potential energy distance of respective low oxygen waters to the continental shelf and represent a relative measure for the likelihood of upwelling events inducing coastal hypoxia in the respective regions.

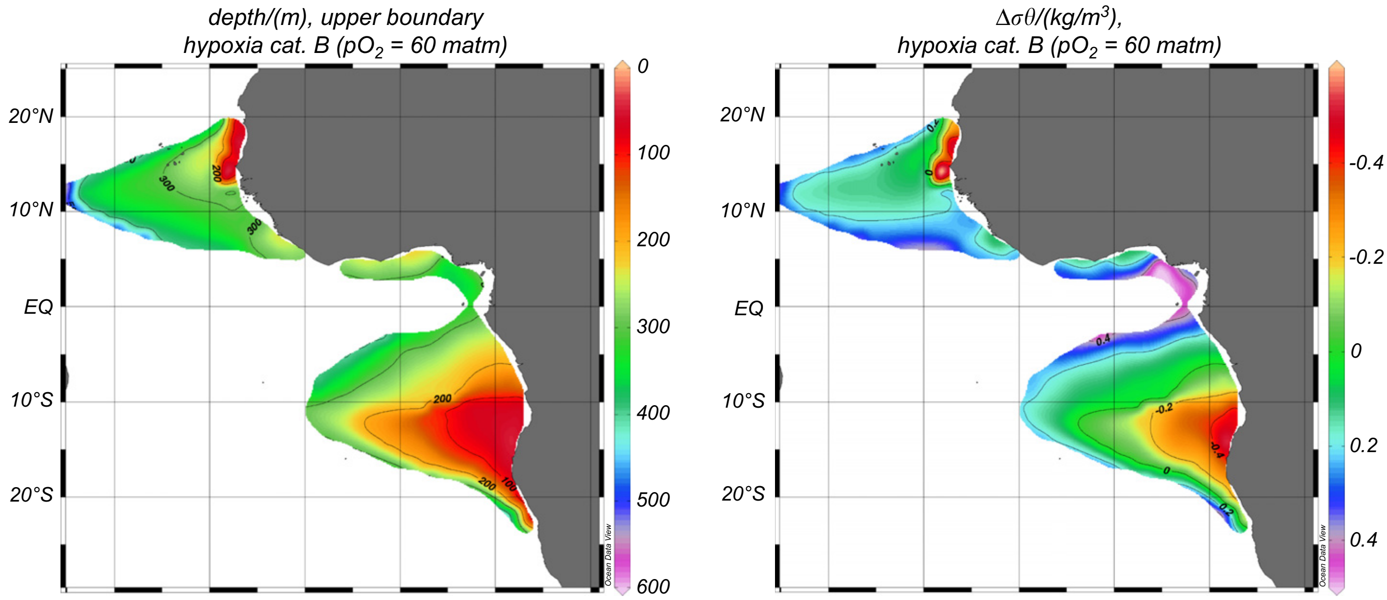

Fig. 8. Eastern Atlantic: depth of the upper boundary of waters with concentrations below the hypoxia cat. B oxygen partial pressure threshold ($pO_2=60$ matm): left panel. Difference in potential density ("$\Delta\sigma\theta$") between the isosurface of the upper boundary of waters with concentrations below the hypoxia cat. B oxygen partial pressure threshold and the 200 m isobath: right panel. $\Delta\sigma\theta$ values express the potential energy distance of respective low oxygen waters to the continental shelf and represent a relative measure for the likelihood of upwelling events inducing coastal hypoxia in the respective regions.

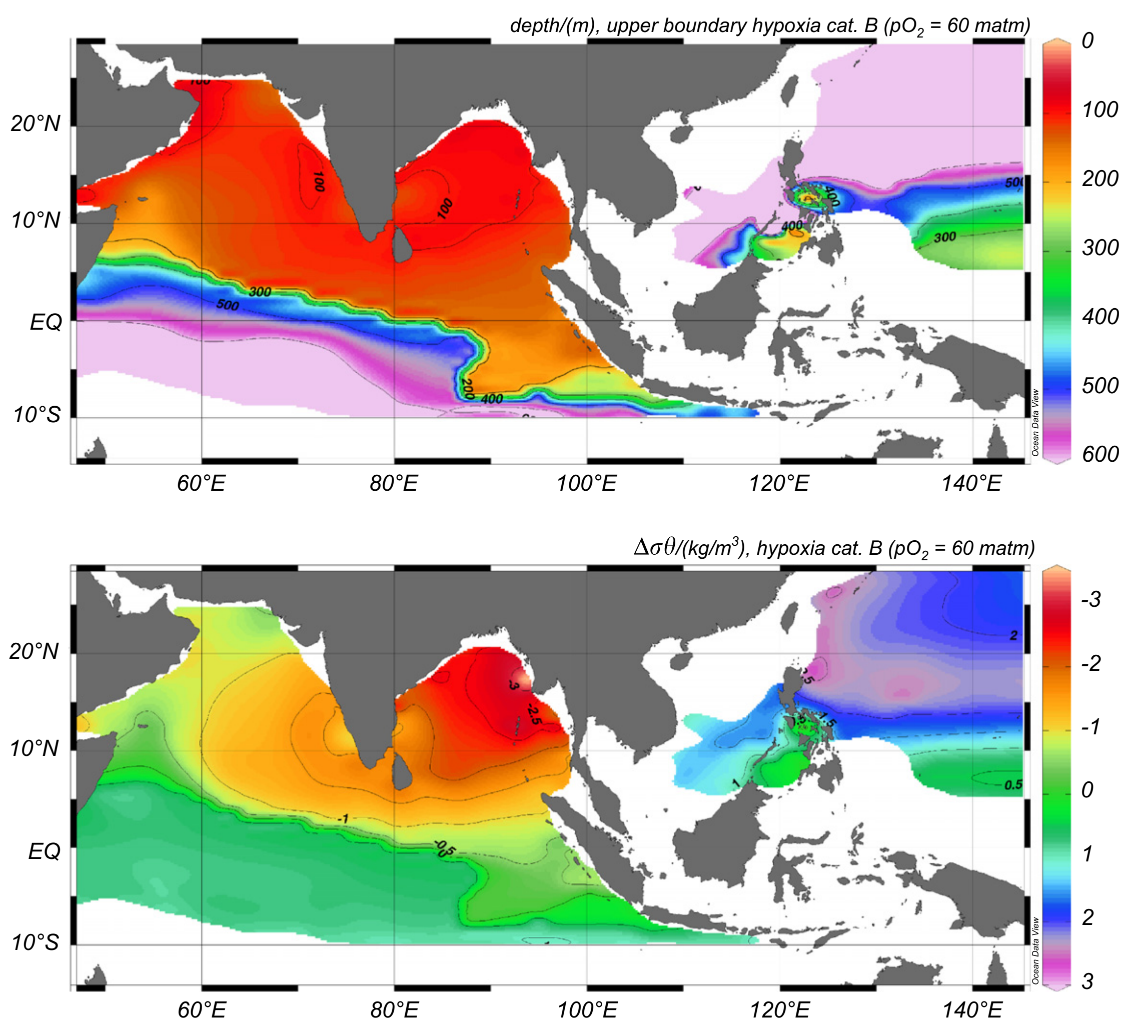

Fig. 9. Northern Indian Ocean: depth of the upper boundary of waters with concentrations below the hypoxia cat. B oxygen partial pressure threshold ($pO_2=60$ matm): top panel. Difference in potential density ("$\Delta\sigma\theta$") between the isosurface of the upper boundary of waters with concentrations below the hypoxia cat. B oxygen partial pressure threshold and the 200 m isobath: bottom panel. $\Delta\sigma\theta$ values express the potential energy distance of respective low oxygen waters to the continental shelf and represent a relative measure for the likelihood of upwelling events inducing coastal hypoxia in the respective regions.

changes in the chemical equilibrium of reactants and products as expressed by the Le Chatelier–Braun principle. This combined oxygen and carbon dioxide stress for aerobic life has only just begun to be understood and investigated (e.g. Mayol et al., 2010) and clearly needs further attention.

5. Conclusions

Within the field low oxygen research, widely different thresholds with different units are used. A unified set of thresholds and a common language, as proposed here, will greatly benefit the field.

Ultimately limiting oxic respiration is the gradient in oxygen partial pressure pO_2. Therefore, and due to the strong dependency of pO_2 on temperature and hydrostatic pressure, any low oxygen threshold describing effects on animals should be reported as partial pressure not as concentration. Partial pressure incorporates the effects of T and P profiles into one single number and makes thresholds universally applicable. This is a conclusion that is also strongly supported by authors like Seibel (2011) who approach the problem of defining oxygen thresholds from the biological side rather than the oceanographical side as it is done here. Using correct pO_2 thresholds instead of concentrations is a professional necessity, even if there are cases where the resulting differences are small. An absolute pO_2 threshold below which aerobic life is not sustainable anymore remains yet to be determined.

Coastal hypoxia caused by land based coastal eutrophication (like in the Gulf of Mexico case) and open ocean oxygen minimum zones are ultimately formed by the same process, decomposition of organic matter, but should not be confused: thresholds for coastal hypoxia are different to open ocean oxygen minimum zone thresholds since the involved timescales are different: coastal hypoxia is a seasonal phenomenon while oxygen minimum zones are a permanent feature allowing for the evolution of species communities adapted to low oxygen.

Oxygen minimum zones are permanent features, but their upper boundaries are highly dynamic (Woulds et al., 2007): to the point that upwelling can cause low oxygen water to reach areas on the continental shelf which do not regularly experience low oxygen conditions and where species communities are not adapted: upwelling-induced coastal hypoxia occurs. Here, we have identified "hot spots" for this type of coastal hypoxia around the world. Among those hot spots there are not only regions which have received much media attention recently, like the Oregon Coast, but also regions which are less known for upwelling induced coastal hypoxia, e.g. the coasts of Mauritania, Angola, Namibia, India, Bangladesh, and Myanmar. Scientists, policy makers and the general public in those areas need to be aware of the danger. Especially since our analysis does not include seasonal variability of oxygen content, which might let a system cross thresholds seasonally when the yearly averaged value is already close.

Oxygen minimum zones seem to be shoaling and expanding, and the overall oxygen concentration in the world ocean is most likely declining due to global warming and associated reduced oxygen solubility and ocean ventilation. Even without creating "dead zones", declining oxygen concentrations in the future can have grim socio-economic impacts by destroying fisheries via species composition shifts as low oxygen tolerant species might out-compete commercially important species.

Acknowledgments

This work was supported by a grant to the Monterey Bay Aquarium Research Institute from the David & Lucile Packard Foundation.

Appendix A. Supplementary materials

Scripts in the programming language R to calculate pO_2 from common hydrographical data can be found in the online version at doi:10.1016/j.dsr.2011.09.004.

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