The role of open ocean boundary forcing on seasonal to decadal-scale variability and long-term change of natural shelf hypoxia

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Received 12 November 2010  
Accepted for publication 7 April 2011  
Published 11 May 2011  
Online at stacks.iop.org/ERL/6/025002

Abstract

In this study we investigate the possible reasons for the widespread differences between the seasonal cycles of carbon production and export compared to those of hypoxia in eastern boundary upwelling systems. An idealized model is proposed that qualitatively characterizes the relative roles of physics and biogeochemical fluxes. The model is tested on three contrasting upwelling systems: the Benguela (from relatively aerated to interannual anoxic), the Humboldt (sub-oxic and interannually anoxic) and the Cariaco (permanently anoxic). Overall we propose that shelf hypoxia variability can be explained on the basis of the interaction between ventilation by ocean boundary forcing through ocean–shelf exchange and the role of shelf geometry in the retention of shelf-based particulate organic carbon (POC) fluxes. We aim to identify the hypoxia regimes associated with low ventilation—wide-shelf systems and high ventilation—narrow-shelf systems, considering them as extremes of conditions controlled by the two factors. We propose that this may help to explain differences in the seasonal cycles of the biogeochemical drivers and responses as well as difference between upwelling systems and within individual upwelling systems. It is suggested that when seasonal hypoxia emerges it does so preferentially at a wide-shelf part of a system.

Keywords: natural shelf hypoxia, seasonal cycle, ocean, shelf, exchange

Online supplementary data available from stacks.iop.org/ERL/6/025002/mmedia

1. Introduction

Natural shelf hypoxia is relatively common in eastern boundary upwelling systems apparently because such systems all share the common property of high productivity (Bailey 1991, Chavez and Toggweiler 1995, Levin 2002, Levin and Gage 1998, Brüchert et al 2000, Carr 2002, Bakun and Weeks 2008, Weeks et al 2004, Monteiro 2010). However, the extent and scales of variability of hypoxia in these systems are far larger than is reflected by differences in production carbon export fluxes to sub-thermocline waters and sediments (figure 1; table 1). Seasonally integrated net production fluxes in upwelling systems vary by a factor of 2–3 (table 1) whereas the spatial and temporal extent and variability of hypoxia show much larger contrasts, both within the boundaries of a single...

The role of equatorward wind stress in driving productivity, POC export fluxes and hypoxia has been an important basis in understanding hypoxia in coastal upwelling systems (Bakun 1990, Chavez and Toggweiler 1995). This has become an important basis for the discussion around their vulnerability to intensification of wind stress associated with global warming (Grantham et al 2004, McGregor et al 2007, Bakun and Weeks 2008). However, upwelling systems range from the relatively aerated southern Benguela and Canary systems to the seasonally hypoxic northern California, from the interannually anoxic Central Benguela and Humboldt systems to the permanently anoxic deep Cariaco basin (Monteiro and van der Plas 2006, Gutierrez et al 2008, Scranton et al 2001). Moreover, in the Benguela system, hypoxia strengthens during the Benguela Niño, whereas in the Humboldt upwelling system, hypoxia tends to weaken during ENSO periods (Monteiro et al 2008). Furthermore, the temporal characteristics of hypoxia variability in the Humboldt and Benguela systems (Gutierrez et al 2008, Monteiro et al 2006, 2008), the appearance of seasonal hypoxia where it was not previously evident (Grantham et al 2004), the emergence of long-term trends in hypoxia in the Gulf of St Lawrence (Gilbert et al 2005) and differences in denitrification rates between the Arabian sea and the Bay of Bengal (Naqvi et al 2000, 2010) cannot be easily explained in this way. The variability and long-term trends of natural sub-thermocline shelf hypoxia have come to be understood as the result of the dynamical interaction between ventilation, advection of water mass properties by ocean boundary conditions, and shelf-based biogeochemical fluxes of carbon (Helly and Levin 2004, Escribano et al 2004, Gilbert et al 2005, 2010, Monteiro et al 2005, 2006, Mohrholz et al 2008, Bograd et al 2008, Rabalais et al 2010, Zhang et al 2010).

These suggest that the variability of natural hypoxia can be a response to intensified upwelling or enhanced buoyancy fluxes linked to global warming (Grantham et al 2004, Chan et al 2008, Bograd et al 2008) or to underestimated changes to the oxygen concentration in the ocean interior adjoining shelf systems (Keeling et al 2010, Emerson et al 2004, Matear and Hirst 2003, Whitney et al 2007, Stramma et al 2008, Shaffer et al 2009). In this study, using the two most productive systems (the Humboldt or HUS and the Benguela or BUS; table 1) and marginal basins as examples, we examine the factors that appear to influence temporal and spatial characteristics of hypoxia variability to help understand natural shelf hypoxia dynamics. The study examines these systems in a complete way (tropical to temperate) but the details of the temperate sectors of the Benguela and the Humboldt as well as the California borderlands basins can be found in the supporting material on the web (available at stacks.iop.org/ ERL/6/025002/mmedia). We aim to do so at system-scale by integrating the physical and biogeochemical processes that characterize the variability. We seek to examine why shelf hypoxia is decoupled from the seasonal cycle of upwelling-driven POC fluxes in some instances but not in others. We start by proposing three contrasting conceptual flux balance models to identify and characterize the key process fluxes and then examine how each interacts with ocean boundary ventilation by analysing case studies in terms of this framework.

Table 1. Comparison of mean primary production rates and estimated mean annual POC export fluxes at five different upwelling systems which show that production rates differ by relatively small factors (~2.5) relative to the spatial extent of regional hypoxia (see figure 1) from: Carr (2002) and data from the CARIACO site are from Varela (2010) (http://www.imars.usf.edu/CAR/Master.txt).

<table>
<thead>
<tr>
<th>System</th>
<th>Mean daily net primary productivity rates (g C m$^{-2}$ d$^{-1}$)</th>
<th>Annual productivity derived carbon flux for entire system (Gt C y$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Benguela</td>
<td>2.49</td>
<td>0.37</td>
</tr>
<tr>
<td>Humboldt</td>
<td>2.18</td>
<td>0.20</td>
</tr>
<tr>
<td>Canary</td>
<td>1.71</td>
<td>0.33</td>
</tr>
<tr>
<td>Cariaco</td>
<td>1.35</td>
<td>0.024</td>
</tr>
<tr>
<td>California</td>
<td>0.99</td>
<td>0.05</td>
</tr>
</tbody>
</table>

2. Ocean–shelf oxygen flux model

We propose a conceptual model as a basis to understand the incidence and variability of natural shelf hypoxia. In this model, variability in hypoxia in shelf sub-thermocline waters is driven by the interaction of ventilation fluxes of oxygen (electron acceptor) derived from the ocean–shelf boundary and of shelf-based biogeochemical supply of electron donors (POC and reduced metabolites from anaerobic respiration). Generically, oxygen flux variability in sub-thermocline waters ($H \frac{\partial O_2}{\partial t}$) (dimensions: ML$^{-2}$ T$^{-1}$ e.g. : mol O$_2$ m$^{-2}$ y$^{-1}$) can be expressed as:

$$H \frac{\partial O_2}{\partial t} = FO_{2\text{Adv}} - FO_{2\text{Bgc}}.$$  

Here $FO_{2\text{Adv}}$ is the sub-thermocline ventilation flux produced by the ocean–shelf boundary condition, $FO_{2\text{Bgc}}$ is the biogeochemical oxygen uptake on the shelf, and $H$ is the mean
Figure 2. (a)–(c) Shows the conceptual model fluxes (carbon in green and oxygen in blue) for the wide shelf (a), narrow shelf (b) and marginal basins (c). It indicates the key fluxes that modulate the characteristics of shelf hypoxia: the ocean–shelf ventilation (FO2adv) and carbon export (FCexp−OS) fluxes as well as the shelf-based sediment and water column carbon and oxygen fluxes. The orange dotted line in (c) refers to the adjustment in the depth of the sub-oxic layer (Zsub−Ox) in response to the periodic ventilation of the basin.

depth range over which low-oxygen sub-thermocline waters impinge on the shelf. Seasonal hypoxia will develop or be sustained if the temporally integrated net flux in equation (1) is negative. An important assumption in this model is that it applies over the whole shelf-scale where the water column depth is greater than the maximum depth of the summer mixed layer. Under these stratified conditions, the contribution from vertical mixing of aerated surface water towards the ventilation of sub-thermocline waters is small. This assumption is likely to hold over the spring–summer period in upwelling systems, where stratification is driven by buoyancy fluxes from solar warming and/or from cold upwelled thermocline waters. In tropical and to some extent in sub-tropical shelf-upwelling systems, the role of basin-scale thermocline adjustments, Kelvin waves and eddies also need to be taken into account (deYoung et al 2004, Gruber et al 2006, Dewitte et al 2008a, 2008b, Chaigneau et al 2009). In winter, in sub-tropical and temperate upwelling systems, an additional vertical turbulent mixing term needs to be included as this can become the dominant scale of ventilation fluxes.

The individual fluxes that make up the physical ventilation and biogeochemical oxygen uptake are summarized in two conceptual models for wide- and narrow-shelf upwelling (figures 2(a) and (b)) and a marginal basin ‘Cariaco type of system’ (figure 2(c)) where ventilation is restricted by exchange dynamics between waters over a marginal basin on the shelf and the open sea.

The shelf upwelling models are spatially integrated along the shelf axis (figures 2(a) and (b)) and contrast the fluxes between wide-shelf and narrow-shelf systems. They include the primary biogeochemical aerobic (FO2aer) and anaerobic (FO2anr) fluxes that characterize the biogeochemical oxygen sink (FO2bgc) on the shelf (equation (2)), and the oxygen ventilation flux from the shelf boundary (FO2adv).

\[ \text{FO2bgc} = \text{FO2wc} + \text{FO2sed} \]

where

\[ \text{FO2sed} = \text{FO2aer} + \text{FO2anr}. \]

The biogeochemical oxygen sink comprises the water column (FO2wc) and sediment (FO2sed) oxygen sinks (equation (2)) where the latter is itself made up of two terms: aerobic (FO2aer) and anaerobic (FO2anr) fluxes. An important contrast between the two shelf modes is the proportion of the surface production carbon flux (FCexp) that is exported across the ocean–shelf boundary (FCexp−OS) before it can be metabolized on the shelf (figures 2(a) and (b)). In the Namibian wide-shelf system, the inner shelf acts as a trap for the carbon flux out of the euphotic zone, which leads to the formation of the anoxic mud belt (Monteiro et al 2005). This model proposes that wide-shelf systems such as Namibia, central/northern Peru and marginal basins are characterized by water column physics that enhance the retention of POC (FCexp−OS is small) on the shelf, and increase the magnitude of the benthic boundary layer oxygen sink through aerobic and anaerobic oxidation of carbon (FO2aer and FO2anr). The latter contributes to the persistence of hypoxic and anoxic conditions by increasing the magnitude of the FO2bgc term in equation (1).

In contrast, narrow-shelf systems such as those found in the Humboldt (northern Chile) and in the northern Benguela
(Angola) and those with eddy-enhanced cross-shelf export, especially anticyclonic, into the ocean domain such as the California system (Gruber et al. 2006), may have a relatively greater loss of carbon to the open ocean across the shelf boundary and thus may reduce the forcing of natural shelf hypoxia by the biogeochemical fluxes. In these latter systems FC_{exp–os} is large while, FO_{2,bgc} is small, and therefore reflect changes in the magnitude of ocean–shelf ventilation fluxes in a more direct way.

Carbon in the form of POC is the primary electron donor; so it is useful to initially define the biogeochemical carbon fluxes characterized in figures 2(a)–(c). The balance between the carbon remineralization fluxes in the water column (FC_{WC}) and the sediment (FC_{Sed}), and the input (FC_{exp}) and export of POC across the shelf boundary (FC_{exp–os}), is given in equation (3)

$$\text{FC}_{\text{WC}} + \text{FC}_{\text{Sed}} = \text{FC}_{\text{exp}} - \text{FC}_{\text{exp–os}}. \tag{3}$$

The carbon flux balance shows how the magnitude of shelf metabolism, which governs the magnitude of the oxygen sink (left-hand side), depends on the relative magnitudes of the phytoplankton carbon export flux (FC_{exp}) across the thermocline and that which is exported off the shelf across the ocean–shelf boundary (FC_{exp–os}), typically in a nepheloid layer (Inthorn et al. 2006, Waldron et al. 2009), before it can contribute to shelf metabolism. The importance of this balance is that it allows the shelf bathymetry to be implicit in the model, as described in the conceptual shelf geometry diagrams (figures 2(a) and (b)). In the case of the wide-shelf system, increased internal shelf metabolism can play a key role in amplifying the variability of the ocean boundary conditions. Such a process is likely to be at work in the tropical shadow zones where the shelf–ocean transport is enhanced by the westward–downward propagation of Rossby waves (Dewitte et al. 2008b, Ramos et al. 2006, 2008, Paulmier and Ruiz-Pino 2009).

The biogeochemical oxygen uptake flux (FO_{2,bgc}) is then linked to carbon through a stoichiometric ratio:

$$\text{FO}_{2,\text{bgc}} = \text{FC}_{\text{WC}} \times \alpha + \text{FC}_{\text{Sed}} \times \beta, \tag{4}$$

where $\alpha$ and $\beta$ are the C:O stoichiometric ratios for water column and sediment remineralization of carbon and associated oxygen uptake over the temporal scale of integration. In both cases, these ratios would be reasonably predictable if dominated by aerobic respiration but in conditions when anaerobic pathways dominate the oxidation of POC, these ratios represent the magnitude of the sediment flux of reduced metabolites and their impact on the oxygen uptake in the benthic boundary layer. The flux of reduced metabolites from the sediment, and benthic boundary layer anaerobic activity, have to be made explicit on a sub-seasonal scale because typically their influence can vary over a part of the seasonal cycle (Monteiro et al. 2006). The sediment flux of anaerobic metabolites [$\text{HS}^-$, $\text{NH}_4^+$, $\text{CH}_4$] can be reduced by the presence of sulfide-oxidising Beggiatoa bacterial mats, and increased by CH$_4$ ebullition, which enhances mass transfer rates of other electron donors (Di Toro 2004, Brüchert et al. 2009). This gives methane a dual role as an oxygen sink term, in the case of dissolved CH$_4$, as well as a parameter which can enhance physical transport (when its production exceeds its solubility in pore waters so bubbles form and rise). The sediment oxygen sink flux includes the benthic boundary layer if uptake of oxygen is in the water column but driven by sediment fluxes. Thus it comprises both aerobic (FO$_{2,\text{aer}}$) and anaerobic metabolism (FO$_{2,\text{anr}}$) (equation (5))

$$\text{FO}_{2,\text{Sed}} = \text{FO}_{2,\text{aer}} + \text{FO}_{2,\text{anr}}[\text{HS}^-, \text{CH}_4, \text{NH}_4^+]. \tag{5}$$

In the case of the methane flux exceeding its local solubility, the magnitude of the oxygen sink should be adjusted to account for the enhanced transport of reduced species from pore waters, caused either by the presence of bubble tubes or by sediment mixing due to rising bubbles.

A model suitable for a situation like the Cariaco basin or Santa Barbara basin, where a productive coastal area overlies a basin or other environment with restricted circulation with the open ocean is depicted in figure 2(c). These systems are also driven by the interaction of the ventilation by intrusions of sub-thermocline ocean water from outside the basin with the flux of reductants from below sill depth in the basin caused by decomposition of phytoplankton carbon export flux derived from the coastal upwelling system (figure 2(c); equation (1)) (Scranton et al. 2001, 2006). The main differences with the open-shelf situation are that the extent of lateral advection is reduced dramatically by the bathymetry, meaning that ventilation (FO$_{2,\text{adv}}$) is driven by an overflow of denser water from outside the basin, which can sink into the basin to a depth controlled by the density of the intrusion and of the bottom waters (figure 2(c)). The combined physics and biogeochemical dynamics within this geometry create a system that is layered in a biogeochemical sense with well-defined but temporally variable oxic, sub-oxic and possibly anoxic boundaries (Scranton et al. 2001, 2006). The system adjusts to changing ventilation fluxes with changes in the depths of the disappearance of oxygen, the thickness of the sub-oxic layer (where oxygen and sulfide concentrations are both below 1–2 μmol L$^{-1}$), microbial ecology and the depth of the first appearance of sulfide (Scranton et al. 2006).

### 3. Comparative basin-scale characteristics

If shelf hypoxia variability in upwelling systems were coupled to carbon export production (C$_{EX}$), the expected seasonal cycle would be closely coupled to the wind stress seasonal cycle. The characteristics of the seasonal cycle of equatorward wind stress for the Humboldt and Benguela upwelling systems are depicted in figures 3(a) and (b). They confirm that the tropical–sub-tropical zones are characterized by winter–early spring upwelling-favourable wind in contrast to the temperate–sub-tropical zones, characterized by spring–summer equatorward wind stress.
Both indicate that the mid-latitude winter cyclones modulate the seasonal cycle up to about 32°S and 28°S in the Humboldt and Benguela upwelling systems respectively. This is the expected boundary between shelf hypoxia regimes that undergo seasonal winter ventilation reset and those where ventilation is modulated by equatorial waveguide dynamics. However, significant differences can be seen in the tropical wind stress, which show a low magnitude throughout the year in the SE Atlantic as a result of a strong asymmetry in its monsoonal character (figure 3 (right)) compared to the equivalent zone in the Pacific ocean (figure 3 (left)). This reflects the asymmetry in the strength of the seasonal tropical easterly wind stress when the enhanced heating of NW Africa in the northern hemisphere summer strengthens the pressure gradients driving equatorial upwelling (Chang et al. 2006). This seasonal asymmetry results in a comparable response of the seasonal Kelvin wave that links the tropics to the boundary conditions of both Angola and Namibia. The eastern tropical Pacific wind regime is more symmetrically monsoonal in character.

Most eastern boundary coastal upwelling systems extend from the tropics to the mid-latitudes and are exposed to a meridional gradient of ocean ventilation that interacts with variable shelf geometry and a shelf oxygen sink. However, while meridional gradients in the oxygen boundary conditions define to some extent the spatial characteristics of variability, it is the ocean basin thermocline adjustment scales in the tropical regions that define the temporal scales of variability (Jansen et al. 2009). Through the connexion between equatorial Kelvin waves and coastal-trapped and extra-tropical Rossby waves (Vega et al. 2003, Ramos et al. 2006, 2008) for the Humboldt system and Rouault et al. (2007) for the Angola system, these factors may influence the temporal variability of hypoxia through advection and mixing processes which modulate the ventilation rate (see Gutierrez et al. (2008) for the Humboldt system). In the context of planetary waves, basin (Pacific versus Atlantic) length-scales influence the temporal characteristics of their propagation, which then define the adjustment timescales of the thermocline in those basins. Thus, while hypoxia variability is characterized by a strong seasonal modulation in the Atlantic (figure 4(a)), the variability in the Pacific is characterized by a weak seasonal signal but a strong interannual–semi-decadal ENSO-scale (figure 4(b)) and the signal has a strong interannual character in the Cariaco system (figure 4(c)).

The conceptual shelf hypoxia model has shelf width as a key parameterization of POC retention on the shelf (figures 2(a) and (b)). Regional differences in shelf geometry are evident between the Humboldt and Benguela systems (figures 5(a) and (b)), which are expected to result in important differences in the amplitude or sensitivity in the response of shelf hypoxia to ocean boundary forcing. Whereas the Humboldt is largely a narrow-shelf system with limited wide-shelf sectors (6°S–15°S and 32°S–36°S), the Benguela is a wide-shelf system with a limited narrow northern sector 6°S–16°S (figures 5(a) and (b)).

In summary, variability of natural shelf hypoxia needs to be analysed in terms of the following factors.

Ocean boundary ventilation:
- distance from the tropical oxygen minimum zone (OMZ);
- ocean basin-scale characteristics: thermocline adjustment scales;
- rates of ocean–shelf exchange;
- decadal-scale changes in oxygen and nutrient concentrations in the ocean interior.
Figure 4. (a)–(c) Plots showing the contrasting seasonal and interannual characteristics of hypoxia in the three upwelling systems 23°S in the Benguela (a) (ml L$^{-1}$), at 18°S and 23°S in the Humboldt (b) and in the Cariaco basin (c) (μmol kg$^{-1}$). They highlight the differences between the strong seasonality of wind stress (figure 3) and temporal scales of the hypoxia response. It contrasts the seasonal scales of variability in the Benguela with the ENSO linked interannual mode in the Humboldt and an interannual mode in the Cariaco basin linked to episodic inflows of aerated mode waters and terrigenous Fe. Part (a) reproduced from Monteiro et al 2006 Geophys. Res. Lett. 33 L16614. Part (b) reprinted from Escribano et al 2004 Deep-Sea Res. II 51 2389–411, copyright (2004), with permission from Elsevier. Part (c) supplied in a personal communication from Taylor (2010).

Figure 5. (a), (b) The contrasting bathymetry characteristics between the Humboldt (a) and the Benguela (b) upwelling systems highlighting the mostly narrow-shelf character of the former and wide-shelf of the latter. Within each system there are significant contrasts in the wider shelf of the central Peru (6°S–15°S) and the narrow shelf off Angola (10°S–15°S). Differences in shelf bathymetry play an important role in the modulation of seasonal and interannual hypoxia.
Figure 6. (a)–(c) The regional scale characteristics of the dissolved oxygen in the SE Atlantic ocean. It shows that the Benguela system has two main sub-thermocline boundary conditions separated at the shelf edge at approximately 26°S: equatorial OMZ $O_2 < 1.4 \text{ ml L}^{-1}$ (4°S–26°S) and the well-ventilated Cape basin South Atlantic central water $O_2 > 4 \text{ ml L}^{-1}$ south of 26°S (c). The preferential upwelling of these two boundary conditions at 17°S and 26°S can be seen in the temperature section (b). Reprinted from Monteiro et al 2008 Deep-Sea Res. I 55 435–50, copyright (2008), with permission from Elsevier.

Shelf POC flux dynamics that govern the magnitude of the oxygen sink:
- shelf-width scales (figures 5(a) and (b));
- seasonal wind stress variability.

4. Benguela upwelling system

The Benguela upwelling system (BUS), located in the South-East Atlantic ocean (4°S–35°S), comprises three main sectors: the northern Congo–Angola sector (4°S–16°S), central Namibia (16°S–26°S) and southern South Africa (26°S–35°S) sectors, with sharply contrasting seasonal and interannual hypoxia variability characteristics (Monteiro and van der Plas 2006). The conceptual hypoxia shelf model is used here to explain the contrasting seasonal phasing and sensitivities of shelf hypoxia as a response to the interaction of open ocean oxygen boundary conditions and shelf bathymetry.

4.1. Ocean oxygen boundary conditions

The large-scale circulation systems that define the oxygen boundary conditions of the Benguela comprise the cyclonic tropical gyre in the eastern tropical Atlantic and the eastern boundary of the anticyclonic sub-tropical gyre (Shannon and Nelson 1996, Lass and Mohrholz 2008, Karstensen et al 2008, Stramma et al 2008). The eastern tropical cyclonic gyre that defines the spatial boundaries of the south Atlantic OMZ, sometimes also referred to as the Angola gyre, is similar to the Humboldt system, and is largely confined to the ‘shadow’ zone north-east of the South Atlantic gyre (Lass and Mohrholz 2008). The eastern tropical Atlantic OMZ core is located 4°S–15°S but extends poleward to 26°S as a narrow semi-annual slope flow along the Namibian shelf. This poleward extension results from the asymmetric, semi-annual relaxation of equatorial easterly wind stress. This relaxation, which is stronger in the spring, propagates a Kelvin wave poleward along the coastal waveguide (Rouault et al 2007). The boundary between the hypoxic tropical OMZ system and the well-ventilated Cape basin mode waters lies on the slope in 26°S–27°S (figure 6) and forms the boundary between the Namibian and South African sub-tropical and temperate upwelling sub-systems (Duncombe Rae 2005, Monteiro and van der Plas 2006).

Currently, it is not clear what constrains the location of this boundary. Wind stress characteristics are monsoonal north of 20°S with peaks in the austral (stronger) winter and (weaker)
summer and relaxation in the spring and autumn equinox. South of this boundary the seasonal cycle of equatorward wind stress is annually driven by the migration and intensification of the South Atlantic High pressure cell and the sub-seasonal modulation of the pressure gradients by the mid-latitude cyclones (Shannon and Nelson 1996, Shillington et al 2006). On a basin-scale, the south Atlantic thermocline dynamics do not show the same interannual (4–5 year) ENSO locked variability as the eastern Pacific ocean but are dominated by a stronger seasonal mode of variability and an interannual variability that seems to be related to the low frequency modulation of the seasonal cycle (Chang et al 2006, Li and Philander 1997). This is an important dynamical factor that separates the temporal variability characteristics of the eastern Pacific (mainly interannual mode) and the Atlantic (mainly seasonal mode). The conceptual model is examined in the context of the tropical, sub-tropical and temperate sectors of the Benguela upwelling system but the latter can be found in the supplementary information (available at stacks.iop.org/ERL/6/025002/mmedia).

4.2. Northern Benguela (Congo–Angola) tropical system

The northern-most sector of the Benguela upwelling system, largely off the coast of Angola (3°S–16°S), is characterized by a narrow shelf, similar to the southern Peru–Chile (figures 5(a) and (b)), which is influenced by the seasonal modulation of ocean thermocline depth through an asymmetric monsoonal easterly wind stress and Kelvin wave response (Rouault et al 2007). In terms of the conceptual hypoxia model proposed in this study the narrow shelf predicts the export of most of the shelf carbon production into the OMZ either in the surface layer through Ekman transport and/or advection by mesoscale eddies or filaments or as a benthic nepheloid layer (Inthorn et al 2006). The loss of a large part of the seasonal shelf productivity across the ocean–shelf boundary ($C_{exp}$–$OS$) reduces the shelf oxygen sink and strengthens the hypoxia of the ocean boundary condition.

The seasonal oxygen climatology in the northern BUS is characterized, as predicted, by an asymmetric monsoonal semi-annual oxygen minimum in the winter–spring with a weaker hypoxia in mid-summer (figures 7(a) and (b)) (Monteiro and van der Plas 2006). This seasonal climatology is derived from the northern shelf off Congo based on a quasi-twice-weekly time series of temperature, salinity and oxygen in 18–20 m off Pointe Noire collected in 1969–80 (NODC: www.nodc.noaa.gov). The two seasonal oxygen minima seen on the shelf are separated by strong ventilation periods during the two equinox periods when the relaxation of the easterly winds sets up a Kelvin wave that propagates eastwards along the equatorial waveguide and poleward along the coast. Unexpectedly, however, the monsoonal seasonal cycle of hypoxia is inversely correlated to salinity. We believe the reason for the inverse relationship is that this time series was sampled in close proximity to the region of freshwater influence (ROFI) at the mouth of the Congo river, and thus that the salinity is modulated by the monsoonal river runoff which peaks in the equinoxes (figure 7(a)). This is in contrast to shelf hypoxia away from the ROFI which is, as expected, positively correlated to the salinity (figure 7(b)). Local intensification of stratification-driven hypoxia due to enhanced freshwater fluxes, such as seen in the Gulf of Mexico, is not a factor in the seasonal cycle as the aeration response is opposite to the one expected. In this system, hypoxia variability is driven completely by ocean boundary forcing.

Although this sector of the Benguela system is similar to the southern Peru–Chile Humboldt system in terms of bathymetry and of OMZ-geography, the characteristics of temporal variability are quite different because of the contrasting basin-scale thermocline adjustment scales (Li and Philander 1997, Chang et al 2006, Jansen et al 2009). Off Congo–Angola, the main mode of variability is dominated by the monsoonal equatorial Atlantic seasonal cycle, whereas in the Pacific the dominant mode is the interannual ENSO-scale (Illig and Dewitte 2006). However, because of the narrow shelf and direct forcing from the adjacent ocean thermocline and associated OMZ, both experience increased aeration during El Niño or equivalent Benguela Niño periods. In both cases, the net effect of the Niño is the deepening of the eastern basin thermocline, and aeration of the shelf water column with well-ventilated tropical surface waters.

Figure 7. (a), (b) Decadal climatology (1969–80) of monthly dissolved oxygen and salinity observations off Pointe Noire (4°S) showing the asymmetry of the seasonal cycle with a strong amplitude in the austral winter and a weak one in the austral summer (a). It shows that the oxygen reflects the direct seasonal response of the OMZ. The salinity minima reflect the seasonal equinox runoff peaks of the Congo river but play no role in the oxygen seasonal cycle as they coincide with a period when ventilation is at a maximum. The OMZ oxygen–salinity relationship at 12°S shows the expected positive correlation. The variance of this bi-annual sampling reflects the seasonal and positional differences of the sampling vessel.

Figure 8. (a), (b) The seasonal cycle of oxygen and temperature for a period of 10 years at 23°S off the central Benguela. It shows that the seasonal cycle is the strongest mode and that the interannual variability reflects modulation of the amplitude of the seasonal cycle. This is in sharp contrast to the Humboldt system where the strongest mode is the ENSO interannual timescale. The ventilation mechanism that drives this seasonal variability is graphically depicted in supplementary figures A3(a) and (b) (available at stacks.iop.org/ERL/6/025002/mmedia). Reprinted from Monteiro et al 2008 Deep-Sea Res. I 55 435–50, copyright (2008), with permission from Elsevier.

4.3. Central Benguela (Namibia) sub-tropical system hypoxia

The central BUS is a wide-shelf system with significant narrowing at the northern (Cape Frio 17°S) and southern boundaries (figure 5(b)) (Luderitz 27°S) (Rogers and Bremner 1991). Preferential exchange between the slope and the shelf is restricted largely to the Cape Frio and Luderitz upwelling centres which are also regions of maximum wind stress curl (Monteiro et al 2006, Lass and Mohrholz 2008). This system behaves like the conceptual wide-shelf system with strong retention of the upwelling-driven POC flux, which gives it large and annually persistent sediment—benthic boundary layer oxygen sink. The seasonal cycle of hypoxia/anoxia, the strongest mode of variability, is characterized by late winter–spring ventilation and late summer–autumn hypoxia/anoxia (figures 8(a) and (b)). The interannual variability reflects changes in the intensity of the seasonal cycle drivers of ventilation, one of the most complex dynamics in this upwelling system (Monteiro et al 2008).

The shelf boundaries span two extremes of regional ocean oxygen distribution. Firstly, the hypoxic and saline OMZ waters, which advect onto the shelf preferentially at the northern boundary (Cape Frio). Secondly, the fresher and aerated Cape basin South Atlantic central water (SACW) derived from Modal waters, which advect onto the shelf preferentially at Luderitz upwelling centre (Monteiro et al 2006). Shelf hypoxia develops a temporal dynamic defined by the seasonal phasing of the meridional shelf ventilation flows of the two ocean boundary water types once on the shelf (see supplementary figures A3(a) and (b) available at stacks.iop.org/ERL/6/025002/mmedia) (Monteiro et al 2006, 2008, Lass and Mohrholz 2008).

The retention of upwelling-driven shelf production (POC) and the resulting elevated biogeochemical oxygen sink is largely controlled by the physical characteristics of the inshore organic-rich diatomaceous mud belt (50–150 m water depth), the depositional characteristics of which are defined by the interaction between the internal tides and the bathymetry (Monteiro et al 2005, van der Plas et al 2007). Seasonal production and POC deposition peaks in the spring to early summer period, while the seasonal hypoxia–anoxia intensifies in late summer at a time when the POC flux is almost at a minimum (figures 9(a) and (b)). This shows that the hypoxia seasonal cycle is not sensitive to the temporal characteristics of the POC flux directly, but rather it responds to changes in the physics that govern the ventilation of the shelf. This is shown in the anti-correlated relationship between salinity—a proxy for the contribution of the two oxygen boundary conditions to the shelf, and the seasonal climatology of oxygen. We suggest that in Namibia, as in other comparable systems, the role of the POC flux is only to regulate the magnitude of the mean annual oxygen demand, which determines the threshold of ventilation required to keep the system aerated, but plays no role in the hypoxia seasonal cycle.

The interannual variability in this system is the result of changes in the seasonal mode owing to the adjustments of
the relative strengths of the ventilation fluxes from the OMZ and the Cape basin waters from the Cape Frio and Luderitz upwelling cells, respectively. If this ventilation flux weakens or fails (Benguela Niño 1985), the seasonal hypoxia strengthens due to the seasonal dominance of the reduced ventilation from hypoxic OMZ water. The ecosystem consequences in general, and the impact on demersal fisheries specifically, are well documented for the Benguela and globally (Monteiro et al. 2008, Ekau et al. 2010). Moreover, the occurrence and intensity of methane-driven sulfide emissions on the Namibian shelf are also linked to the interannual cycles of decreased ventilation in contrast to alternative models such as the seasonal cycle of shelf primary productivity-linked POC (Weeks et al. 2004) or remote forcing mechanisms (Emeis et al. 2004). This view is supported by a similar response of seasonal anoxia in the Canary upwelling system (Kock et al. 2008). These data show that methane saturation intensifies when the shelf is being ventilated by hypoxic SACW and weakens when the shelf is ventilated by the more aerated NACW.

This complex interaction between oxygen boundary conditions and shelf dynamics reflects an important difference between the Namibian and Angolan upwelling systems, which gives rise to opposing responses to the Benguela Niño. These periods are characterized by an intensification of the equatorial waveguide signal and increased advection of the warm tropical water poleward onto the Namibian shelf (Rouault et al. 2007). This strengthens surface layer stratification and intensifies the impact of the hypoxic OMZ boundary forcing. During this time, wind stress at Luderitz is typically also weaker than the seasonal mean state (Monteiro et al. 2008). Under these Benguela Niño conditions, the northern Benguela shelf in Angola becomes better oxygenated like the Humboldt upwelling system (HUS), whereas off Namibia the extent of hypoxia and anoxia intensifies (Monteiro et al. 2008).

5. Hypoxia variability in the Humboldt upwelling system (HUS)

5.1. Regional context

In terms of the model combining the ocean boundary forcing and shelf geometry that is proposed in this study, hypoxia variability in the HUS is characterized by three shelf bathymetry regimes: a wide shelf 6°S–15°S off Peru, a narrow shelf between 15°S–35°S and a wider shelf south of 35°S–40°S (figure 5(a)). There are two ocean boundary forcing regimes defined by the large-scale oceanography of the eastern south Pacific (ESP) ocean: the tropical and sub-tropical Peru and northern Chile regime (5°S–30°S) and a temperate region south of 30°S (figures 10(a) and (b)). The ocean boundary condition for oxygen in these shelf regions are the tropical OMZ, its poleward extension along the slope, and the relatively better ventilated ESPIW (eastern south Pacific intermediate water). The main boundary between these regimes appears to be the westward flow of well-aerated ESPIW that reaches the coast at approximately 32°S–34°S (figure 10(a)).

The OMZ of the ESP is embedded in the complex Humboldt current system (figures 10(a) and (b)). The eastern tropical Pacific is a well-defined ‘shadow zone’ with a weak thermocline ventilation rate (Luyten et al. 1983). The ‘shadow zone’ of the ESP, the minimal meridional and lateral replenishment of surface waters (Reid 1965), unvegetated by basin-scale wind-driven circulation, may explain why biogeochemical processes associated with O₂ consumption are so effective in maintaining such an extended OMZ.
In the ESP, minimum oxygen values are reached at 200–500 m depth (Paulmier and Ruiz-Pino 2009, Fuenzalida et al. 2009). In the eastern Pacific, waters become sub-oxic ($O_2 < 20 \mu mol kg^{-1}$) with dissolved oxygen concentration of less than $1 \mu mol kg^{-1}$ (see for instance the figure 5 of Tsuchiya and Talley (1998), which shows particularly low oxygen content between $3^\circ S$ and $17^\circ S$ along the $88^\circ W$ section). Near the coast, $O_2$ concentrations tend to be even lower ($<2$ nmol kg$^{-1}$, cf figures 5 and 6 in Revsbesch et al. 2009) and the OMZ core slopes downward in the seaward direction, reflecting the upwelling (cf Paulmier et al. 2006) for northern and central Chile). The OMZ appears to be maintained locally by the biological oxidation activity associated with the upper sub-oxic layer which offsets the turbulent diffusive flux of oxygen that continually ventilates the OMZ (Paulmier et al. 2006). The westward extent of the OMZ may be interpreted as resulting from the offshore advection of low-oxygen waters by the seasonal Rossby waves (figures 11(a) and (b)).

An important feedback from the losses of shelf carbon to the open ocean is that this flux maintains and enhances the OMZ (Paulmier et al. 2006) and, in turn, its impact on the OMZ is defined by the Rossby wave propagation timescales (figures 11(a) and (b)) and/or horizontal eddy advection. This feedback is not well understood and may be an important part of understanding long-term trends in the OMZ. From the south, large-scale intermediate water masses (antarctic intermediate water (AAIW) and eastern south Pacific intermediate water (ESPIW)) penetrate into the ESP (Karstensen and Quadfasel 2002, Karstensen 2004, Schneider et al. 2005). The ESPIW deepens westward and northward from its outcrop region (around $32^\circ S$) reaching 150 m depth.

The conceptual model is now examined in the context of the tropical, sub-tropical and temperate sectors of the Humboldt upwelling system but the latter can be found in the supplementary information (available at stacks.iop.org/ERL/6/ 025002/mmedia).

### 5.2. Temporal variability of hypoxia in the tropical and sub-tropical zone

Temporal variability of hypoxia in the northern Peru–central Chile sector ($5^\circ S–30^\circ S$) is characterized by a strong interannual variability linked to the semi-decadal ENSO and much weaker monsoonal cycle, as well as sub-seasonal modulation from coastal-trapped waves (Morales et al. 1999, Escribano et al. 2004); see figure 4(b). This is clearly depicted in the 5-year time series from Arica ($18^\circ S$) in northern Chile that contrasts the temperature and oxygen concentration in the upper 50 m of the shelf water column between the warmer and ventilated 1997–8 ENSO period and the more persistently cold and hypoxic subsequent non-ENSO period 1998–2002 (figure 4(b)).

A narrow shelf couples the near-shore more directly to the eastern Pacific ocean OMZ thermocline, which is modulated by semi-decadal and sub-seasonal Kelvin waves (Dewitte et al...
et al (Karstensen related to the existence of sub-oxic conditions in the SEP OMZ outcrop regions of the SEP (Yeager and Large 2004) is directly

Peru–Chile coast can indeed be considered as an extension of the equatorial waveguide at a variety of timescales, from intraseasonal to decadal (Hormazabal et al 2001, Pizarro et al 2001, 2002, Ramos et al 2006, Pizarro and Montecinos 2004).

The associated coastal-trapped Kelvin wave variability can drastically modify the vertical temperature (cf Blanco et al (2002) at 21°S for instance) and especially O2 (cf Morales et al (1999) who analysed the structure variability of the 1 ml L−1 (~40 μM) isoline between 18° and 24°S along the coast).

The coastal-trapped Kelvin wave can influence the biogeochemical processes, namely the bacterial aerobic remineralization or zooplankton respiration (Paulmier et al 2006, Escribano et al 2009, for instance, assuming that low frequency large-scale tropical circulation variability reflects the change in the mean ventilation, one may qualitatively measure the influence of the mean ventilation on the OMZ structure. Thus, Helly and Levin (2004) report 60% reduction in the sea floor area influenced by the eastern south Pacific OMZ (<20 μmol kg−1) off Peru and northern Chile during El Niño years. Oceanic reanalysis products combined with existing O2 data also indicate that reduced ventilation in the outcrop regions of the SEP (Yeager and Large 2004) is directly related to the existence of sub-oxic conditions in the SEP OMZ (Karstensen et al 2008).

Given the coherence of equatorial planetary wave forcing from 5°S–30°S, shelf-width geometry is the next key factor in understanding the differences in shelf hypoxia response between the wide shelf in northern–central Peru (6°S–15°S) and the narrow shelf in central–southern Peru–central Chile (15°S–35°S). The narrow-shelf model, with greater losses of primary production carbon fluxes, predicts that hypoxia variability in the latter area will reflect the south eastern Pacific thermocline—OMZ variability in both phasing and magnitude. The corollary to this is that the greater export flux of POC from the narrow-shelf domain into the OMZ will make a greater contribution to sustaining or even strengthening the hypoxia in the OMZ (Paulmier et al 2006). In contrast, in wide-shelf zones such as northern Peru, greater POC retention builds up in the organic-rich sediment and leads to a higher mean annual oxygen sink on the shelf but minimal impact on the seasonal cycle of hypoxia/anoxia. The reason is that the seasonal POC flux generated in response to the upwelling cycle is adding to a large stock of sediment POC which damps the seasonal cycle of resulting shelf oxygen sink. The elevated wide-shelf oxygen sink requires a higher oxygen ventilation flux to sustain non-anoxic conditions and in the case of northern–central Peru, this occurs on a sustained basis only during significant ENSO conditions (Escribano et al 2004, Gutierrez et al 2008). The much smaller amplitude of seasonal ventilation and the short period of intraseasonal Kelvin waves mean that thermocline variability does not provide adequate ventilation, and explains why these sediments exhibit the biogeochemical and ecological characteristics of sustained anoxia (Gutierrez et al 2008).

The human and ecological consequences of the combined effects of the wide-shelf POC trapping and OMZ ventilation in central Peru are reflected by what the fishers term the ‘aguajes’ reports associated with H2S emissions and mass fish mortalities between 12°S–14°S (Dugdale et al 1977).

The poleward extent of the effects of the equatorial waveguide are shown in the temperature anomaly time series from a number of locations (18°S–36°S) (cf figure 3 in Escribano et al (2004)), which shows that the equatorial anomaly signal weakens at about 30°S (Coquimbo) and is absent south of this latitude. Beyond this latitude, the seasonal cycle of hypoxia shifts rapidly towards a summer peak linked to the local wind stress seasonal cycle in the so-called Coastal Jet region off Central Chile (Renault et al 2009). This marks the boundary where the shelf shifts to being better ventilated by the aerated ESPIW. In this temperate region the seasonal cycle of hypoxia is closely linked to wind forcing that peaks in the summer (Ahumada et al 1983, Cornejo et al 2006; cf figure 3).

6. Marginal basins

6.1. Regional context

On some upwelling system continental shelves, depressions or basins located on the shelf become oxygen depleted if renewal of waters within the basin is restricted. These systems may be considered a special case of the ‘wide-shelf’ model, where the carbon flux losses across ocean–shelf boundary are insignificant and remineralization is more likely to occur by anaerobic pathways in the water column due to the restricted circulation. Examples include the California borderland basins (Berelson 1991, Sholkovitz and Gieskes 1971), the Orca basin, and the Cariaco basin among others. Similar environments, which vary in detail largely due to the extent of isolation from the open ocean or other sources of dense oxygenated water, include the intermittently anoxic basins in the Baltic, fjords and some estuaries as well as the Black Sea (Oguz and Gilbert 2007).

Although not many time series exist in marginal basins, the CARIACO time series has resulted in a 15 year data set with monthly records of; among other things, oxygen and productivity (figure 12). In this system (Scranton et al 2006, Müller-Karger et al 2004), the seasonal POC flux derived from the high coastal productivity produced in this coastal upwelling system plays a minor role in explaining the interannual variability of the depth of the sub-oxic zone (the region where oxygen and sulfide are both at or below detection limits). The ‘classic’ picture of the oxygen supply to these systems is that, under normal conditions, oxygen is transported to the deep basin waters primarily by vertical eddy diffusion and is thus controlled primarily by the density
mid-depths of the basin (Astor to be strongly influenced by periodic injections of water into upwelling, passing eddies or storms, or advective transport be brought onto the shelf—for example, into the Baltic Sea—larger source of oxygen into deep waters. Dense water can relatively enriched in oxygen, may in fact represent a much transport of dense water from outside the basin, which is gradient. However, in addition to diffusive flux, advective transport of dense water from outside the basin, which is relatively enriched in oxygen, may in fact represent a much larger source of oxygen into deep waters. Dense water can be brought onto the shelf—for example, into the Baltic Sea—by upwelling, passing eddies or storms, or advective transport (Fonselius 1981, Astor et al 2003, Hagen and Feistel 2004). The conceptual model is examined in the context of both the Cariaco and California borderlands basins but the latter can be found in the supplementary information (available at stacks.iop.org/ERL/6/025002/mmedia).

6.2. The Cariaco basin

The Cariaco basin, which is a deep marginal basin on the Venezuelan continental shelf and is the largest truly marine anoxic basin, represents an extreme case of the situation demonstrated by the California borderland basins. It is very deep (1400 m) but isolated from the Caribbean by a shallow sill (maximum depths about 150 m) and underlies a region of strong seasonal upwelling and high primary productivity (Müller-Karger et al 2001). Bottom waters in this basin are permanently anoxic and sulfide concentrations are high (presently approximately 65 μM (Li et al 2008)). The density gradient in the basin is very weak so waters only slightly denser than those found at sill depth in the Caribbean can sink most or all of the way to the bottom. The depth of transition between oxic and sub-oxic (oxygen less than 5 μM; sulfide less than 2 μM) or anoxic (presence of sulfide) waters, however, seems to be strongly influenced by periodic injections of water into mid-depths of the basin (Astor et al 2003, Scranton et al 2001).

External factors like eddies (Andrade et al 2003, Astor et al 2003), the Caribbean Coastal Undercurrents (Andrade et al 2003) or changes in sea-level in the tropical Atlantic warm pool (Wang and Enfield 2003) or globally (Reuer et al 2003) can strongly influence the frequency or chemical characteristics of the intruding water. Unlike the California borderlands, the oxygen content of water dense enough to sink to the bottom of the Cariaco basin is quite high. However, oxygen levels would be subject to change as oxygen concentrations in the upper ocean change, possibly in association with climate change (Stramma et al 2008).

In a situation where a portion of the water column becomes sulphidic, intrusions of this nature also can alter the biogeochemical cycles in the water column. For example in the Cariaco basin, there is an intense microbial loop which is located at the transition zone between oxic and anoxic waters (Taylor et al 2001). While details of this loop are not fully known, it appears from simulation experiments that intermediate oxidation state sulfur species (sulfite, thiosulphate, elemental sulfur, polythionates) represent important oxidants and/or reductants for the microbes (Li et al 2008). Sulfur chemistry is also likely to be important in other situations (for example on the Namibian shelf where hydrogen sulfide is periodically emitted from sediments in large quantities (Brüchert et al 2009)).

In other environments, such as in the California borderlands or the Peru/Chile margin, nitrogen cycling (anammox, denitrification) in the water column can be very important, but rates and regional impact will fluctuate depending on external controls on oxygen supply (as well as supply of other chemical species) (Kuypers et al 2003, Paulmier and Ruiz-Pino 2009).

7. Synthesis

In this study, we have examined a conceptual model that helps explain why in most instances the phasing of shelf hypoxia is different from the seasonal cycle of POC production and sedimentation fluxes. The seasonal and interannual cycles of natural hypoxia variability in shelf upwelling systems, including marginal basins, can be explained on the basis of the interaction of shelf dynamics, which control POC retention, and remotely forced ocean boundary ventilation. The interaction of these two key factors regulates the sensitivity, the magnitude and phasing of the seasonal and/or interannual variability of shelf hypoxia. We propose a conceptual model typology based on shelf width to understand and predict the links between the magnitude of POC retention and the sensitivity to changing ocean basin oxygen fluxes. This model was examined using three contrasting upwelling systems (Benguela, Humboldt and marginal basin such as Cariaco) that provide a globally representative range of examples of ocean boundary–shelf dynamics configurations. A number of factors, summarized in table 2, contribute to a divergence in the POC and hypoxia seasonal cycles.

Firstly, while shelf POC production and retention is an essential component for the mean shelf oxygen demand climatology, it plays a minimal role in the seasonal cycle of hypoxia.
<table>
<thead>
<tr>
<th>Regions</th>
<th>Benguela upwelling system</th>
<th>Humboldt system</th>
<th>California borderland</th>
<th>Cariaco basin</th>
</tr>
</thead>
<tbody>
<tr>
<td>System type</td>
<td>Tropical</td>
<td>Sub-Tropical</td>
<td>Temperate</td>
<td>Tropical</td>
</tr>
<tr>
<td>Shelf Type</td>
<td>Narrow</td>
<td>Wide</td>
<td>Wide</td>
<td>Narrow</td>
</tr>
<tr>
<td>Oxygen Boundary conditions</td>
<td>Hypoxic OMZ</td>
<td>Hypoxic OMZ (N) Aerated modal (S)</td>
<td>Hypoxic-anoxic OMZ</td>
<td>Hypoxic-anoxic OMZ</td>
</tr>
<tr>
<td>Dominant Mode of Oxygen Variability</td>
<td>Seasonal</td>
<td>Seasonal</td>
<td>Seasonal (Interannual ENSO)</td>
<td>Seasonal (Interannual ENSO)</td>
</tr>
<tr>
<td>Mode of POC Flux</td>
<td>Seasonal</td>
<td>Seasonal</td>
<td>Seasonal (Interannual ENSO)</td>
<td>Seasonal (Interannual ENSO)</td>
</tr>
<tr>
<td>In phase with POC flux</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Physical boundary forcing:</td>
<td>Kelvin wave</td>
<td>Sub-tropical anticyclone; Kelvin wave; Rossby wave</td>
<td>Ventilation by modal waters and mixing associated to mid-latitudes depressions</td>
<td>Kelvin wave; Undercurrent; Rossby wave</td>
</tr>
</tbody>
</table>
The reason for this is that, in most instances, POC production and export fluxes either add to an existing reservoir of sediment POC that buffers the seasonality in the case of a wide-shelf, or are exported to the adjacent ocean in the case of narrow-shelf systems. In terms of the conceptual model this means that

$$\frac{\partial FO_{adv}}{\partial t} - c \left( H \frac{\partial O_2}{\partial t} \right) = 0$$

leading to $FO_{bgc}$

where $c$ is a constant according to the mean annual sink.

The important role for POC flux retention is to adjust the magnitude of the mean annual shelf oxygen sink. This not only determines the sensitivity of the system to changing ventilation but also sets the threshold for the minimum ventilation flux that initializes seasonal and/or interannual hypoxia/anoxia. The aerobic–anaerobic redox transition is important because sediment and water column anoxia increases the flux of reduced metabolites into the benthic boundary layer and enhances the biogeochemical consumption of oxygen. This implies that equation (1) is now simplified to link the seasonal hypoxia to the seasonal characteristics of physical advection of the ocean–shelf boundary oxygen concentrations onto the shelf:

$$H \frac{\partial O_2}{\partial t} = FO_{adv} - c.$$

We propose that the adjustments in the ventilation fluxes of sub-thermocline shelf waters by ocean oxygen boundary conditions drive the seasonal and/or interannual cycles of shelf hypoxia. While the range of mechanisms that drive this variability is wide, from planetary waves to wind-driven ocean–shelf exchanges and shelf advection, the net effect is that these forcing cycles are closely phased with observed shelf hypoxia. However, the remote ocean boundary conditions and shelf dynamics are coupled because the sensitivity of shelf hypoxia variability to remote boundary ventilation depends on the magnitude of the shelf oxygen sink. We suggest that wide-shelf systems are more sensitive to decreases in ocean ventilation flux because of their greater POC retention circulation dynamics, which increases the magnitude of the biogeochemical oxygen sink ($c$ in equation (6)). This may help to explain the particularly persistent anoxia off central Peru and Namibia and the appearance of hypoxia off Oregon on the Heceta Bank, a wider POC retention area (Grantham et al 2004).

This proposed understanding of the relationship between remote physical forcing and biogeochemical drivers has important implications for design of models that are used to understand the vulnerability of shelf ecosystems to climate change. It suggests that it is important to put greater effort on the physical ventilation dynamics, especially those that lead to preferential ocean–shelf exchange, which includes high resolution bathymetry. The biogeochemical drivers could, as a starting point, be simplified to a mean annual sediment oxygen sink with a change of state that reflects the enhanced role of reduced metabolites from anoxic sediments, without losing any significant sensitivity. This approach supports a shift towards reduced complexity in modelling to investigate coastal ocean water-column hypoxia variability which has traditionally emphasized an explicit treatment of the sediment biogeochemical fluxes (Middelburg and Levin 2009, Peña et al 2010). The detailed process approach will however remain necessary to understand the sensitivity of biogeochemical feedbacks that determine the range of states from aerated to deep anoxia as well as the micro- and macro-ecological responses.

This study also emphasizes how difficult it is to understand upwelling systems through comparative studies (Bakun and Weeks 2008) based on biogeochemical considerations alone. Understanding and predicting the response of upwelling systems to changes of wind stress requires the inclusion shelf characteristics and basin-scale adjustment scales considerations. This makes it difficult to compare not only systems such as HUB and BUS but also intra-system responses.

Overall, in order to understand shelf-based variability we need to understand the basin-scale mechanisms that link them and the scales that modulate them. Recent reviews suggest that not only is hypoxia deepening in tropical basins but oxygen concentrations are decreasing rapidly in the temperate and sub-polar North Pacific (Whitney et al 2007), North Atlantic (Gilbert et al 2005) and possibly the South Atlantic (Nondal 2010). This conceptual model emphasizes the need to understand and observe long-term changes to oxygen in the ocean interior. This applies especially to thermocline or mode waters as the primary drivers of long-term shelf hypoxia rather than the shelf oxygen respiration fluxes (Keeling et al 2010, Paulmier and Ruiz-Pino 2009).

Acknowledgments

This study is a contribution by the authors to the work of the SCOR WG128 on Global Shelf Hypoxia. PMSM was supported by funding from CSIR Parliamentary Grant facility, two Benguela Current LME grants and one from the Benefit Programme. MIS received support from the US National Science Foundation for participation in the CARIACO program, most recently under grant OCE0752014. Collaboration and support from colleagues in Venezuela, particularly Yrene Astor and Ramon Varela, have been critical to the success of the CARIACO program, together with Gordon Taylor for the CARIACO oxygen data and oxygen contour plot. Thanks to D Ruiz-Pino for inspiring discussions during the preparation of the CHOC project in 2002.

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