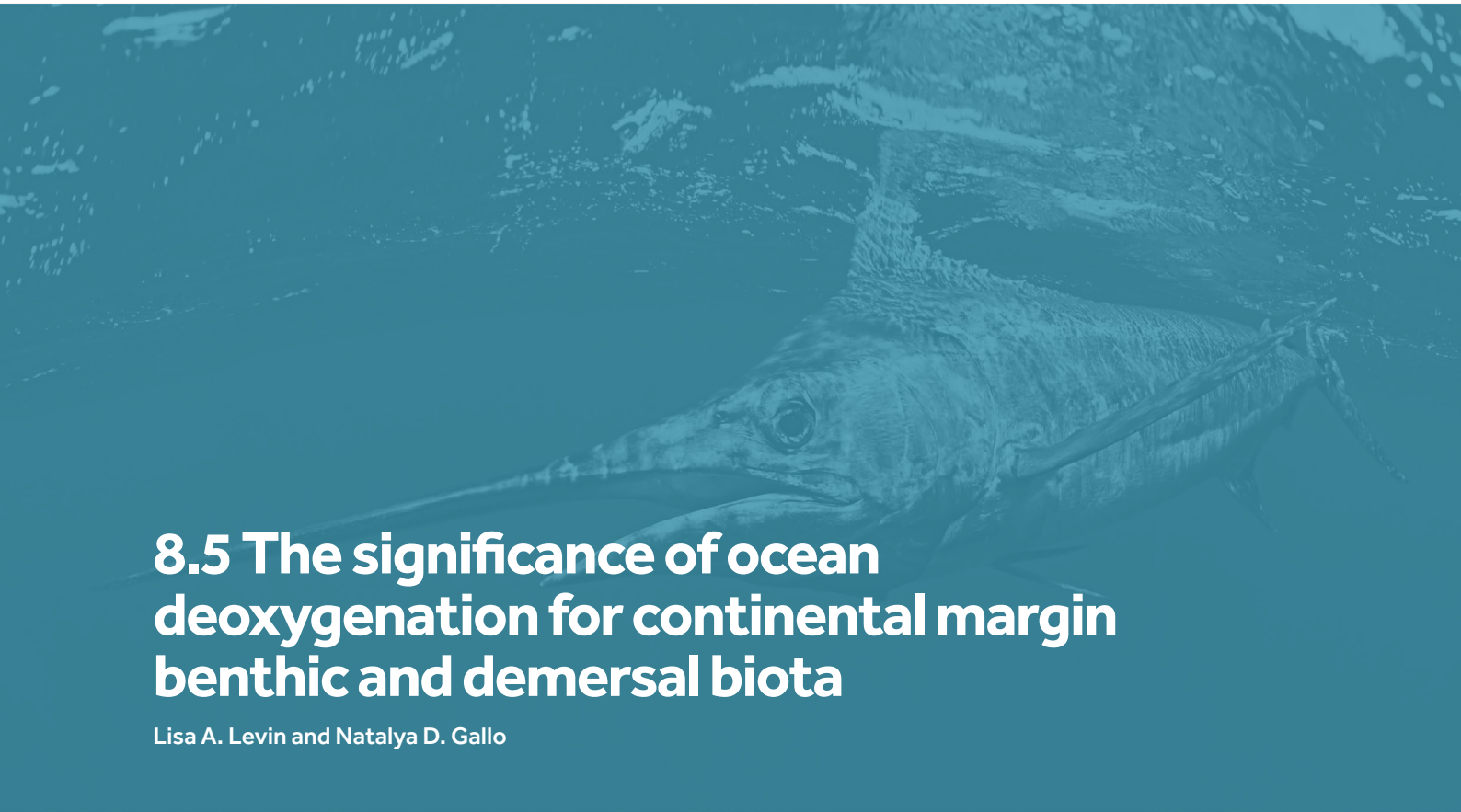




Ocean deoxygenation: Everyone's problem

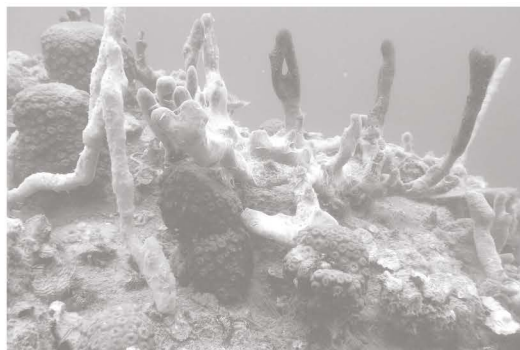
Causes, impacts, consequences and solutions

Edited by D. Laffoley and J.M. Baxter



8.5 The significance of ocean deoxygenation for continental margin benthic and demersal biota

Lisa A. Levin and Natalya D. Gallo



IUCN GLOBAL MARINE AND POLAR PROGRAMME



8.5 The significance of ocean deoxygenation for continental margin benthic and demersal biota

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Summary

- Continental margins in upwelling areas are exposed to naturally occurring hypoxia over an area of 1.1 million km²; the resulting oxygen gradients provide excellent natural laboratories for understanding adaptations, tolerances, thresholds and ecosystem responses to ocean deoxygenation.
- Expanding oxygen minimum zones will change the structure and function of benthic communities on continental margins through alteration of the taxonomic composition, body size, food-web structure, bioturbation and carbon cycling.
- Community diversity is especially sensitive to hypoxia, with decreases in diversity consistently observed under hypoxic conditions across all size classes of animals (from meiofauna to demersal fish). Loss of diversity can lead to reduced adaptive capacity and less resilience to various perturbations.
- Deoxygenation on continental margins is causing habitat compression for hypoxia-intolerant demersal and benthic species, and habitat expansion for hypoxia-tolerant species, leading to altered species interactions, including those with humans.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen concentrations and expansion of oxygen minimum zones on continental margins will lead to loss of invertebrate and fish biodiversity.	<ul style="list-style-type: none"> • Shift from complex organisms with high mobility to simple, soft bodied taxa. • Reduces the types and value of demersal fisheries species. • Loss of ecosystem adaptive capacity and resilience.
Deoxygenation on continental margins is causing habitat compression for hypoxia-intolerant demersal and benthic species and habitat expansion for hypoxia-tolerant species.	<ul style="list-style-type: none"> • Animals effectively experience habitat loss. • Altered species interactions including predation and competition for resources. • Forms high-density aggregations with increased susceptibility to overfishing. • Expanded ranges of some species have potential to alter community structure and fisheries resources.
In upwelling regions oxygen minima create strong oxygen gradients across continental margins; deoxygenation causes expansion of oxygen minima.	<ul style="list-style-type: none"> • Causes dramatic zonation of benthic fauna • Reveals oxygen tolerance thresholds that vary among size and taxonomic groups, providing clues about vulnerabilities to ocean deoxygenation • Bioturbation and carbon cycling decline with oxygen loss and exhibit distinct tipping points
Oxygen declines can shift trophic pathways (towards bacteria, protozoans and shorter food chains).	<ul style="list-style-type: none"> • Carbon reaching the sea floor, normally processed by metazoans is consumed by protozoans at very low oxygen levels, with potential for reduced trophic transfer. • Demersal fish shift from feeding in the water column (pelagic diets) to feeding on benthos under hypoxia, reducing benthic – pelagic coupling, increasing the length of the food chain, and reducing trophic transfer efficiency to top predators. • Chemosynthesis and the role of chemosynthetic symbionts can increase in importance.

8.5.1 Introduction

Continental margins, including subtidal shelf, slope and rise habitats (to about 3000 m) often exhibit very strong oxygen gradients with depth, and sometimes with distance from shore (Paulmier et al., 2011). On eastern boundary margins and in other areas, where upwelling enhances productivity, oxygen levels reach low values creating oxygen minimum zones, and such areas are expanding as a result of ocean deoxygenation (Levin, 2018; Stramma et al., 2008). Animals living in these low-oxygen zones are also subject to hypercapnic conditions, as oxygen minimum zone environments are also carbon maximum zones (Paulmier et al., 2011) and are characterized by carbonate undersaturation, and low pH conditions (Feely et al., 2008). On many upwelling shelves, for example off Oregon (Chan et al., 2008), southern California (Nam et al., 2015), Peru

(Graco et al., 2017), Namibia (Hamukuaya et al., 2001), Pakistan (Woulds et al., 2007) and India (Naqvi et al., 2006), there is pronounced oxygen seasonality, linked to winds and upwelling or in some cases fluctuating undercurrent strength. There are also oxygen variations associated with climate cycles such as El Niño-Southern Oscillation ENSO (Nam et al., 2011). People rely heavily on the ocean's continental margins, for food (fishing and aquaculture), energy, sand and minerals, shipping, recreation, and tourism (Levin & Sibuet, 2012). Human activities also modify the physical and biogeochemical environment through trawling, drilling, spills, and dumping, through river-borne nutrient inputs from watersheds, and through land-derived atmospheric inputs (Levin et al., 2015).

Eutrophication and associated algal blooms have created large, low-oxygen 'dead zones' on the sea

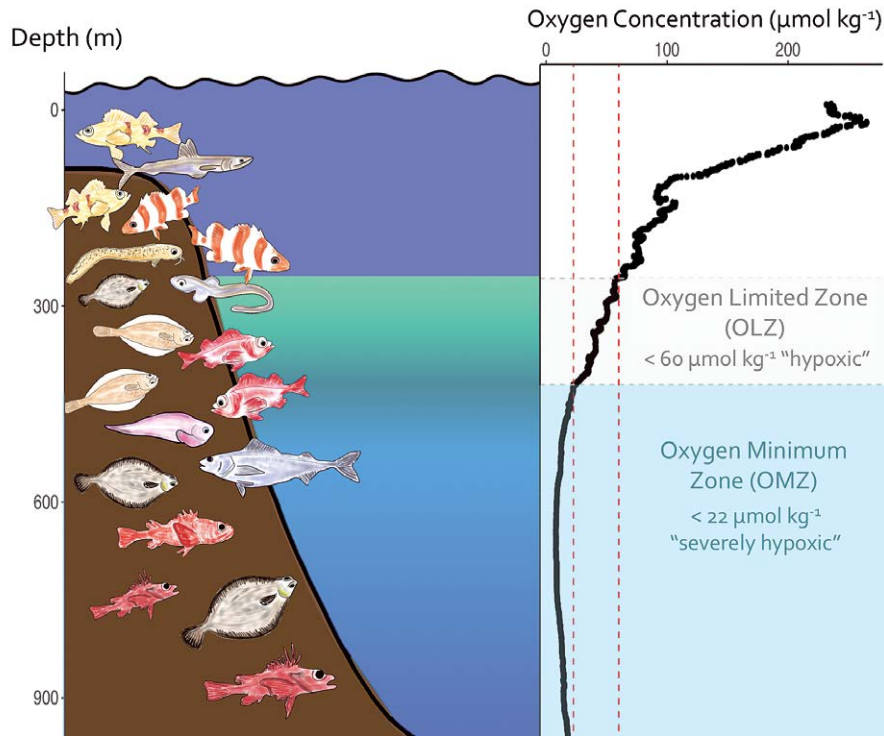


Figure 8.5.1 A conceptual diagram for the Southern California Bight on the US West Coast, showing how the depth distribution of the continental margin demersal fish community changes with depth and different oxygen conditions termed the oxygen-limited zone (OLZ) and the oxygen minimum zone (OMZ) (shown on the right). Community composition, density, diversity, and trophic interactions are all ecological metrics that can be sensitive to hypoxia, but changes occur under different oxygen thresholds in different regions. Note: drawing is not to scale.

floor of the Gulf of Mexico, Chesapeake Bay, the Baltic Sea, and many other areas (Diaz & Rosenberg, 2008) but this is distinct from the natural formation of hypoxic benthos on continental margins where oxygen minimum zones (OMZs $< 22 \mu\text{mol O}_2 \text{ kg}^{-1}$, Helly & Levin, 2004; Paulmier & Ruiz-Pino, 2008) and oxygen limited zones (OLZ = $22\text{--}60 \mu\text{mol O}_2 \text{ kg}^{-1}$, Gilly et al., 2013) impinge on the continental margin beneath upwelling sites. The oxygen concentrations cited above for the OMZ and OLZ are most often invoked for the Pacific and Indian Oceans and higher limits (45 and $90 \mu\text{mol O}_2 \text{ kg}^{-1}$, respectively) are sometimes applied to the Atlantic Ocean (Gilly et al., 2013). Conservatively, OMZs cover over $1.1 \times 10^6 \text{ km}^2$ of sea floor, primarily in the eastern Pacific, Northern Indian Ocean and off West Africa (Helly & Levin, 2004). The OMZ typically intercepts the sea floor between 100 and 1000 m , but the depth and thickness of hypoxia exposure varies regionally (affected by mixing, isolation and currents) (Helly & Levin, 2004) and seasonally (Paulmier & Ruiz-Pino, 2008) and these areas are expanding (Stramma et al., 2008). Records from the past 50 years reveal oxygen loss beyond oxygen minimum zones, in many other regions of the open ocean (Schmidtko et al., 2017). Regional differences and variability of oxygen minimum zone conditions, with a focus on continental

margins (hereafter margins), are reviewed in Gallo and Levin (2016). Strong temporal and vertical gradients in temperature, oxygen and carbon dioxide at the upper and lower boundaries of OMZs (Paulmier et al., 2011), make upwelling margins excellent natural laboratories for evaluating the influence of climate variables, including declining oxygen, on marine life (Sperling et al., 2016). However, ocean deoxygenation may also be manifested on other types of margins where eutrophication or water mass changes reduce oxygen availability (Breitburg et al., 2018). Because oxygen is required to sustain the majority of organisms (anaerobic microbes are an exception), the ocean deoxygenation-induced expansion of hypoxia on margins will have major consequences for organisms and communities on or near the sea floor.

8.5.2 Margin fauna

Here we consider the continental margin floor (primarily $> 200 \text{ m}$), and the benthic and demersal protozoans, invertebrates and fishes that live there. Most of the sea bed is covered with sediments, inhabited by meiofaunal- ($> 0.042 \text{ mm}$), macrofaunal- ($> 0.3 \text{ mm}$) and megafaunal-sized ($> 1 \text{ cm}$) protozoans and invertebrates that live in or on the substrate, and by benthic and demersal fishes

that may live on or interact with the sediment (Figure 8.5.1). There are also hard substrates in these settings – such as carbonates (which are a product of methane seepage), lithified continental sediment, or biotic substrates formed through accumulation of animal skeletons. These also host a wealth of biodiversity. Both single-celled organisms (Protozoa), and multi-celled animals (Metazoa) thrive on margins. Although this section focuses on the benthic and demersal communities, it is worthwhile to note that ecological processes mediated through the food web (i.e. benthopelagic coupling), ensure that impacts on pelagic and benthic communities do not occur in isolation, but are related and may be magnified through the ecological interactions of these scientifically defined zones.

8.5.3 Trends and impacts

There are relatively few modern studies that have documented directly the effects of changes in oxygen over time on the benthic and demersal biota of margins. Important exceptions involve temporal effects of ENSO cycles and seasonality on the Peru, Chile, and California margin faunas (Arntz et al., 2006; Sato et al., 2017). A greater body of knowledge exists about the effects of oxygen loss based on changes observed along cross-margin spatial gradients. The eastern Pacific and Arabian Sea margins in particular have yielded cross-margin studies of different animal size classes. These are often used to make predictions about the influence of deoxygenation in a ‘space for time’ translation, and to predict vulnerability of specific areas to changing conditions (e.g. Sperling et al., 2016). The results of these studies are discussed in the sections below.

8.5.3.1 Density

Oxygen effects on density over the full range of oxygen exposures are often not discernable in part because surface productivity or biological interactions appear to be more important drivers of density than oxygen. For small organisms (microbes, foraminifera, metazoan meiofauna) densities may peak at the lowest oxygen levels in OMZs due to an abundance of detrital food combined with an absence of predators (e.g. Levin et al., 1991; Neira et al., 2001, 2018). The density of larger taxa is generally reduced within OMZ core areas and increases downslope as oxygen levels rise. However, animal densities sometime exhibit a large maximum within or at the edge of the OMZ, at oxygen concentrations just above physiological thresholds

(Gallo et al., 2019; Gooday et al., 2010; Levin, 2003; Wishner et al., 1990). This has been termed an edge effect (Levin, 2003; Mullins et al., 1985). However, these density maxima sometimes occur at very low oxygen levels and give rise to density trends that appear to decrease as oxygen conditions continue to increase; other influences (e.g. food or predators) take precedence over dissolved oxygen conditions in determining faunal densities at higher oxygen levels. Off Peru, a study of benthic biomass changes across oxygen and depth gradients found that macrobenthic biomass peaked at $\sim 26.3 \mu\text{mol O}_2 \text{ kg}^{-1}$ and then declined as oxygen levels decreased (Rosenberg et al., 1983). In this study, demersal fish catches were positively correlated to high macrobenthic biomass, but negatively correlated to the occurrence of filamentous bacteria that occur in severely hypoxic environments (Rosenberg et al., 1983).

Dramatic changes in density can also occur with very minor changes in oxygen, where these gradients cross threshold levels. For example, in the eastern tropical Pacific, the Volcano 7 seamount rises into the oxygen minimum zone, resulting in steep gradients in oxygen availability for the benthic community. Here, the lowest density megafauna communities were observed at the lowest oxygen concentrations ($\sim 3.5\text{--}4 \mu\text{mol O}_2 \text{ kg}^{-1}$), while high-density communities were encountered 50 to 100 m deeper, where oxygen concentrations were only slightly higher ($\sim 5\text{--}7 \mu\text{mol O}_2 \text{ kg}^{-1}$) (Levin et al., 1991; Wishner et al., 1995). At oxygen levels higher than this, megafauna densities decreased again, showing a non-linear relationship between oxygen availability and density, and likely reflecting the influence of other factors. In coastal systems with eutrophication-driven hypoxia, the complicated nature of hypoxia occurrence and fisheries landings (arising from enhanced food availability and habitat compression) has also been documented (Breitburg, 2002; Breitburg et al., 2009; Craig et al., 2012). Changes in fisheries landings across oxygen gradients are further discussed in this report in Chapter 10.

Species tolerant of severe hypoxia can attain unexpectedly high densities under low oxygen conditions. Examples include crustaceans such as tuna crabs (*Pleuroncodes planipes*) off Panama (78 ind m^{-2} ; Pineda et al., 2014) or spider crabs (*Encephaloides armstrongii*) off Oman (47 ind m^{-2} ; Smallwood et al., 1999) (Figure 8.5.2), which can occur at oxygen concentrations of $2 \mu\text{mol O}_2 \text{ kg}^{-1}$ and $9\text{--}13 \mu\text{mol O}_2 \text{ kg}^{-1}$, respectively. Some demersal fish species also exhibit

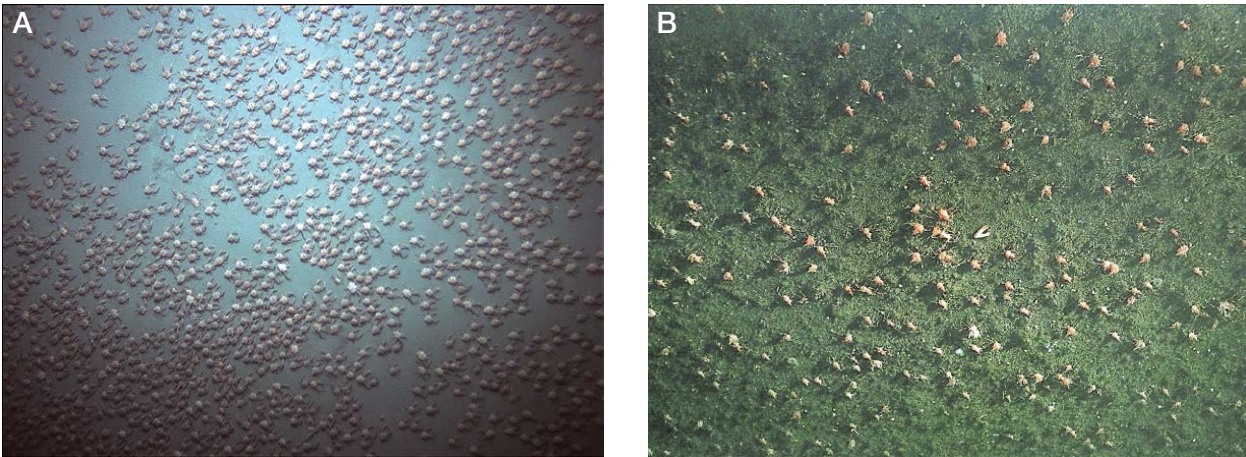


Figure 8.5.2 Examples of high-density crab aggregations within oxygen minimum zones. (A) Tuna crabs (*Pleuroncodes planipes*) off Panama (from Pineda et al. 2014) and (B): *Encephaloides armstrongii* off Oman. © Dr Brian J. Bett, National Oceanography Centre, UK.

remarkably high tolerance to hypoxia and can occur at very high densities. This has been observed in the Gulf of California for the cusk-eel, *Cherublemma emmelas* (3.5 fish m^{-2} at $1.6 \mu\text{mol O}_2 \text{ kg}^{-1}$) (Figure 8.5.3) (Gallo et al., 2019) and on the Volcano 7 seamount summit for the grenadier, *Nezumia liolepis* (at $<4 \mu\text{mol O}_2 \text{ kg}^{-1}$) (Levin et al., 1991; Wishner et al., 1990). While the occurrence of high-density communities of highly adapted species under low oxygen conditions are biologically and ecologically intriguing, most species are *not* able to thrive under oxygen-depleted conditions. A global review for benthic and demersal marine organisms found that the sub-lethal oxygen limit for demersal fish species ranges from $62\text{--}186 \mu\text{mol O}_2 \text{ kg}^{-1}$, while the sub-lethal limit for benthic invertebrates (including crabs, worms, and oysters) ranges from $15\text{--}124 \mu\text{mol O}_2 \text{ kg}^{-1}$ (Vaquer-Sunyer & Duarte, 2008). Most of these data were derived from studies carried out on Atlantic species with potentially limited adaptation to hypoxia; thresholds are much lower for species on upwelling margins that have evolved and adapted to hypoxia (Chu & Tunnicliffe, 2015).

An additional difficulty of interpreting the influence of oxygen conditions on density trends is that low-oxygen events can give rise to immediate habitat compression of sensitive species. This can result in temporary high-density aggregations that can increase susceptibility to overfishing. For example, in the Gulf of Mexico, aggregations of brown shrimp and demersal fishes occur along the edges of hypoxic areas (Craig, 2012). In the Sea of Oman, seasonal oxycline shoaling during the summer and autumn has also resulted in habitat compression for artisanal fisheries species, resulting in increased fisheries landings (Piontkovski & Al-Oufi, 2014).

Unfortunately, there is no simple, easily generalized relationship between oxygen conditions and density that can be used to predict the influence of deoxygenation on general community density patterns. However, regionally, some informative trends do exist. For example, the catch per unit effort (CPUE) for selected demersal fish species along the US West Coast is positively related to near-bottom oxygen concentrations, with CPUE decreasing more significantly as oxygen concentrations decrease (Keller et al., 2015). It should be noted that CPUE reflects the biomass as well as numbers of animals caught, and cannot be directly related to trends in density, as different species differ significantly in size. CPUE and density could show different relationships across oxygen gradients if larger-bodied species are replaced by numerous smaller-bodied species as oxygen conditions decline. Considering the different relationships between oxygen and density versus CPUE

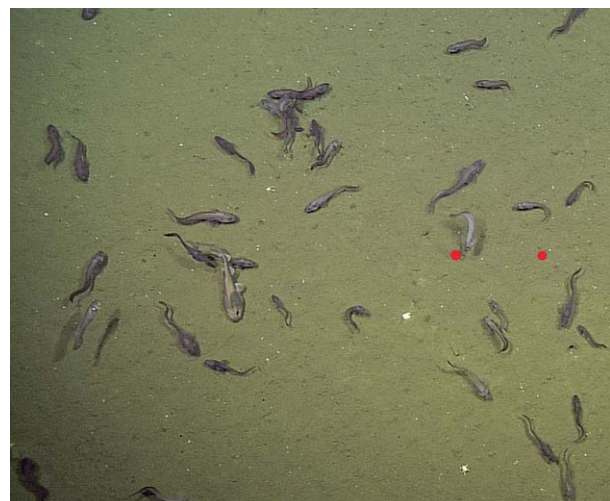


Figure 8.5.3 High density fish aggregations of cusk eel *Cherublemma emmelas* were observed in the Gulf of California at very low oxygen concentrations ($1.61 \mu\text{mol kg}^{-1}$) (from Gallo et al. 2019). Image from MBARI's ROV Doc Ricketts, red lasers are 29 cm apart.

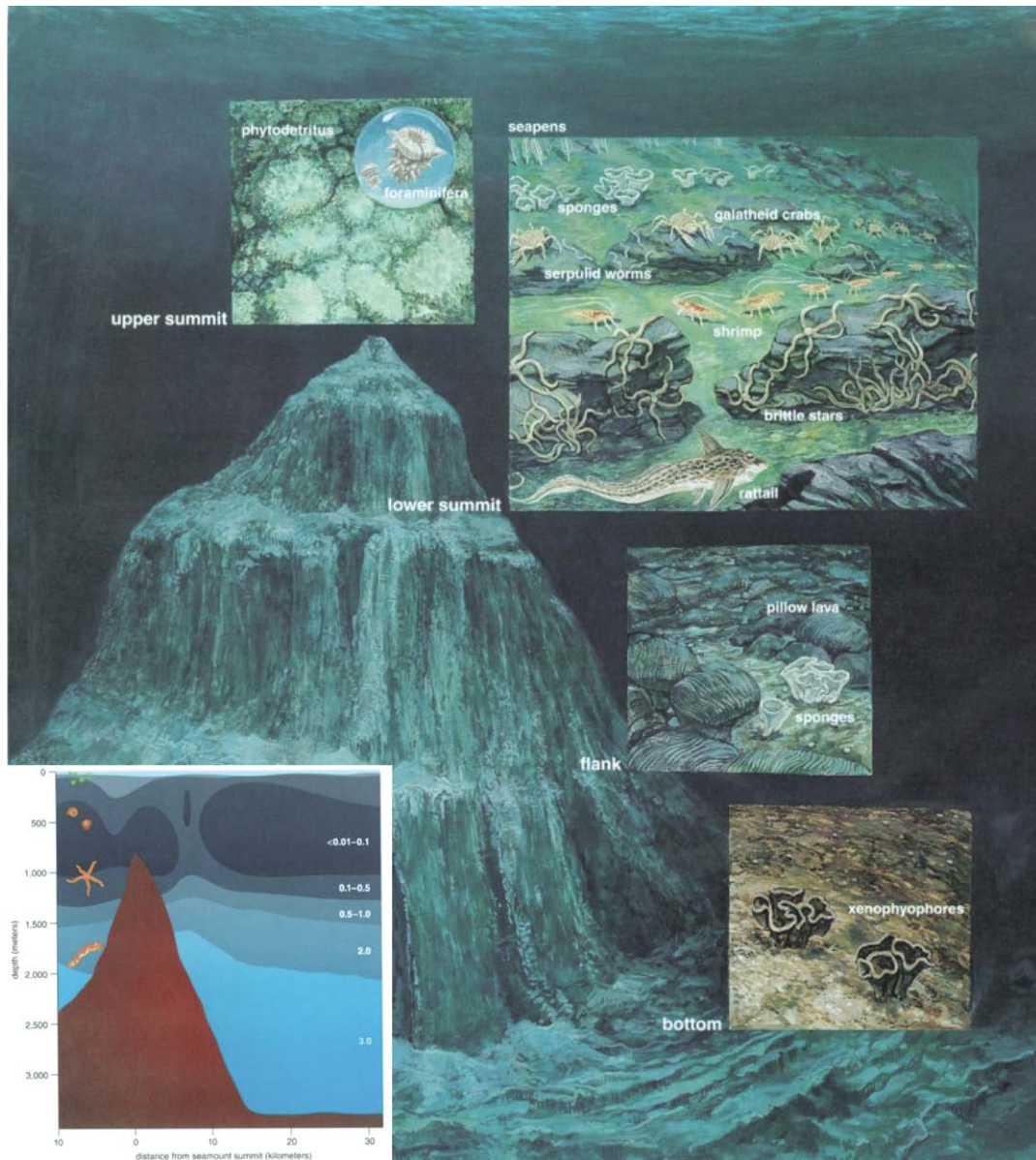


Figure 8.5.4 Strong faunal zonation occurs on Volcano 7 in the East Pacific west of Acapulco, Mexico in response to oxygen gradients. The upper and lower summit of this seamount protrude into the oxygen minimum zone (from Levin 1992).

or biomass, may be important from the perspective of food web interactions as well as fisheries efforts.

8.5.3.2 Depth distribution and zonation

Sharp faunal zonation across oxygen gradients on continental margins indicates the existence of strong tolerance thresholds for benthic biota. Such zonation was first noted for invertebrates and fish on the California continental margin (Thompson et al., 1985) and the flanks of the Volcano 7 seamount off Mexico (Levin et al., 1991; Wishner et al., 1990, 1995) (Figure 8.5.4), but has since been documented for macrofauna on the margins of Chile (Gallardo et al., 1995, 2004), Peru

(Levin et al., 2003), Oman (Levin et al., 2000), Pakistan (Hughes et al., 2009; Levin et al., 2009), India (Hunter et al., 2012; Raman et al., 2015) and for megafauna and demersal fish on the margins of Chile (Quiroga et al., 2009; Sellanes et al., 2010), Mexico (Papiol et al., 2017), India (Hunter et al., 2011), Pakistan (Murty et al., 2009), Central America (Bianchi, 1991; Stromme & Saetersdal, 1988), Namibia (Hamukuaya et al., 2001; Mas-Reira et al., 1990), and Oman (Piontkovski & Al-Oufi, 2014; Piontkovski et al., 2012), in submarine canyons off Hawaii (De Leo et al., 2012), and in a Canadian seasonally hypoxic inlet (Chu & Tunnicliffe, 2015). These gradients are maintained by species-specific oxygen tolerances but potentially also by the absence of larger predators at

each oxygen level (Levin, 2003). Dramatic differences in macrofaunal colonization potential, potentially reflecting larval availability and tolerances, were observed in short-term experiments conducted across oxygen gradients on the Indian continental margin (Levin et al., 2013). If hypoxia lengthens recovery time or reduces recolonization potential following disturbance, then ocean deoxygenation is likely to reduce ecosystem resilience.

Most of these studies reflect faunal response to oxygen gradients at a single point in time, and there are relatively few very long time series that document responses to changes in oxygenation. Several studies document a) changes in continental margin faunal composition and activity in response to seasonal changes in oxygenation (Gutierrez et al., 2008; Macpherson & Gordo, 1992; Sellanes & Neira, 2006; Woulds et al., 2007); b) responses to ENSO-related or episodic changes in oxygenation (Gutierrez et al., 2008; Hamukuaya et al., 2001; Levin et al., 2002); and c) long-term changes in species distribution on margins known to experience shoaling oxygen minimum zones (Sato et al., 2017). Studies on the Peru shelf (94 m) during oxygenation events associated with El Niño reveal successional

stages that range from nematode dominance under extreme oxygen deficiency, to *Thioploca* (bacterial) dominance at 10–20 $\mu\text{mol O}_2 \text{ kg}^{-1}$, to macrofaunal dominance at $> 40 \mu\text{mol O}_2 \text{ kg}^{-1}$ (Gutierrez et al., 2008) (Figure 8.5.5). Off central Chile, meiofaunal abundance was positively correlated with chlorophyll *a* and oxygen content over 1997–1998 during a major El Niño. On the Namibian shelf and margin, four clear demersal fish assemblages were identified that correlated with environmental variables, including oxygen (Hamukuaya et al., 2001; Mas-Reira et al., 1990). During the upwelling season when hypoxic conditions were more prevalent, the northern shelf assemblage expanded its distribution into deeper water (Mas-Reira et al., 1990); the northern and central shelf assemblages expanded into deeper water during the 1993 and 1995 Benguela Niño as well (Hamukuaya et al., 2001). These responses to changes in oxygenation indicate that these communities are sensitive to oxygen regimes, both on short and long timescales.

Across seasonal timescales, benthic communities also exhibit faunal composition changes in response to changes in oxygenation. The Saanich Inlet is a relatively shallow (230 m) fjord system in the Canadian N. Pacific

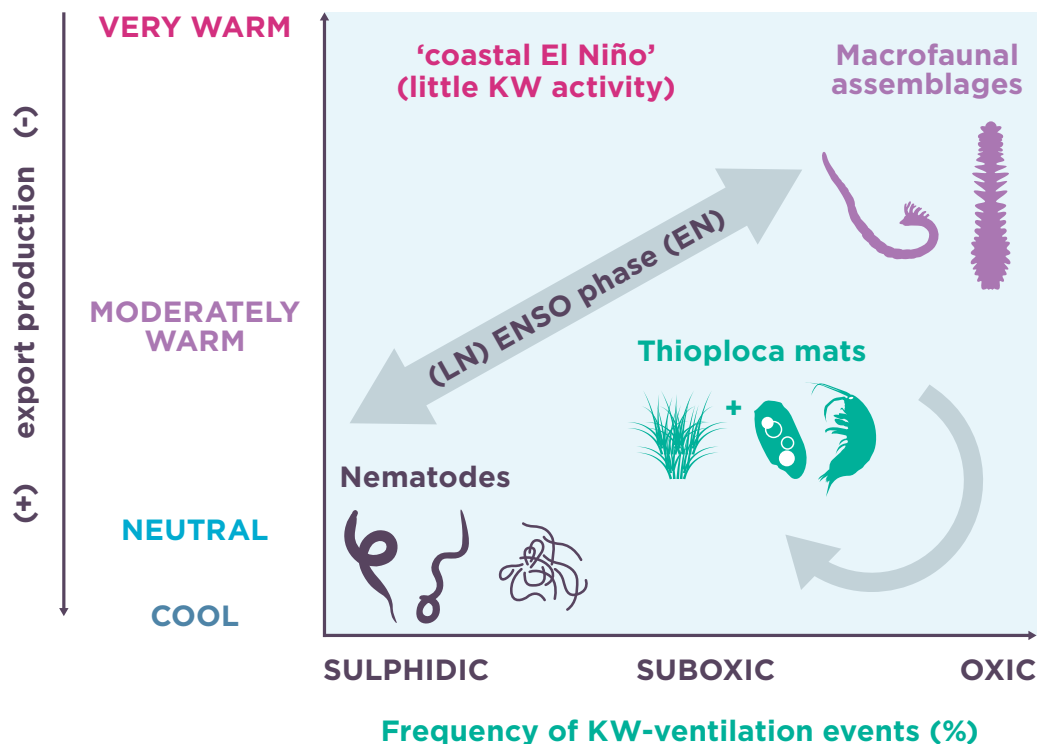
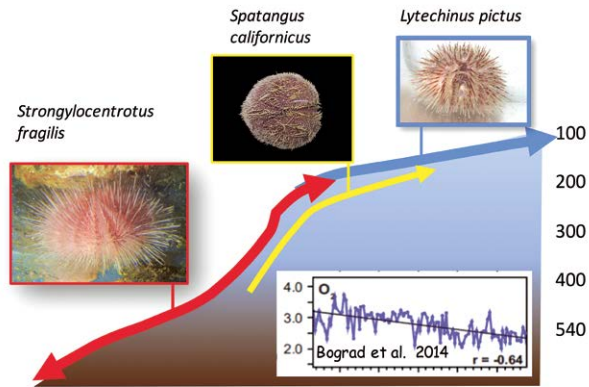


Figure 8.5.5 Shifts in benthic community dominance off Callao, Peru (93 m) as a function of oxygenation and export production. Macrofauna dominate under oxygenated conditions ($> 40 \mu\text{mol O}_2 \text{ kg}^{-1}$); Filamentous sulphide oxidizing bacteria dominate during weak El Niño ($20\text{--}40 \mu\text{mol O}_2 \text{ kg}^{-1}$); Nematodes dominate under lowest oxygen conditions ($< 20 \mu\text{mol O}_2 \text{ kg}^{-1}$). KW = Kelvin Wave; LN = La Niña, EN = El Niño. Based on Gutierrez et al. 2008; Figure courtesy of D. Gutierrez.

that goes seasonally hypoxic during the summer and is reoxygenated during the autumn and winter. Benthic communities exhibited consistent responses to changes in oxygenation across an eight-year study, with increases in the abundance of spot prawn, pink

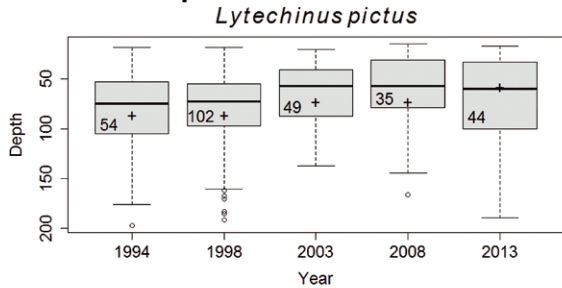
shrimp, and sea whips under high-oxygen conditions, and increases in the abundance of slender sole and squat lobsters observed under low-oxygen conditions (Chu & Tunnicliffe, 2015). Community responses to seasonal and interannual changes in oxygenation can inform our understanding of species-specific tolerance limits to hypoxia.

Compression and expansion of sea urchins on the southern California Bight



Pronounced shoaling of the OMZ (which also has low pH waters) has occurred in the southern California Bight over the past 25 years (Bograd et al., 2008, 2015). Among echinoids, two burrowing, irregular urchins (*Brissopsis pacifica* and *Spatangus californicus*) common within the oxygen minimum zone (OMZ), have expanded their depth distributions from 2003-2013. The pink urchin, *Strongylocentrotus fragilis*, expanded upslope and increased in density, while the painted urchin *Lytechinus pictus* experienced habitat compression to shallower

Depth Distribution



Density

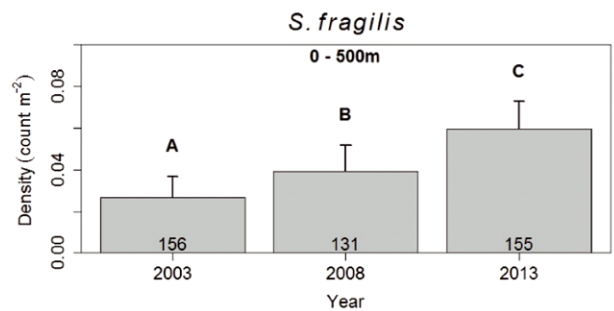
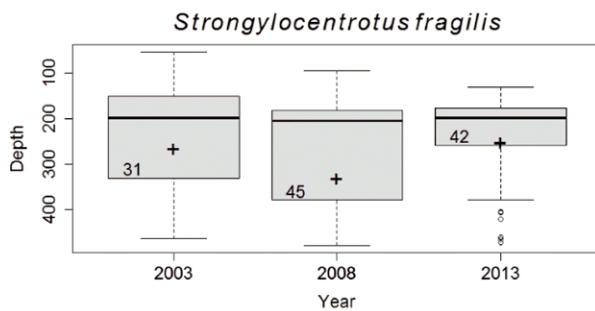
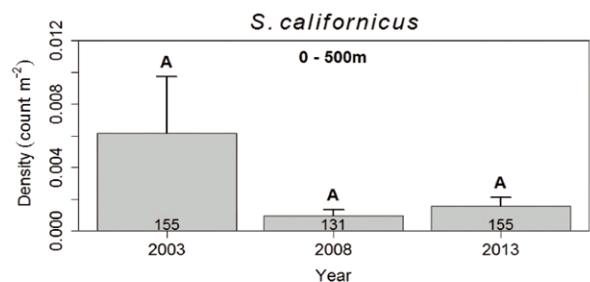
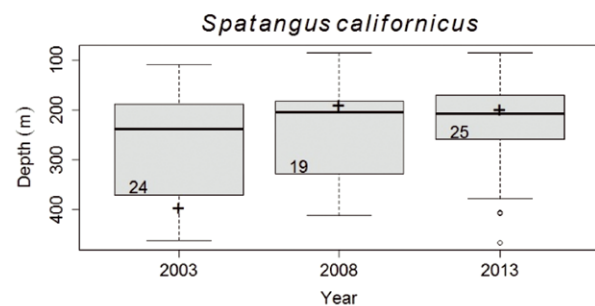
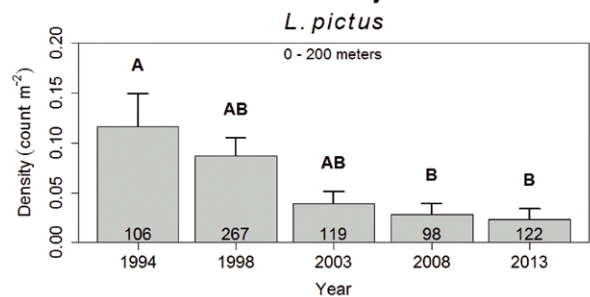


Figure 8.5.6 Changes in sea urchin distribution along the southern California Bight shelf and slope over the past 15-25 years as reported in Sato et al. (2017), based on data from the Southern California Coastal Water Research Project trawl surveys. Oxygen has declined by 20-30% at depths of 200-300 m (Bograd et al., 2014).

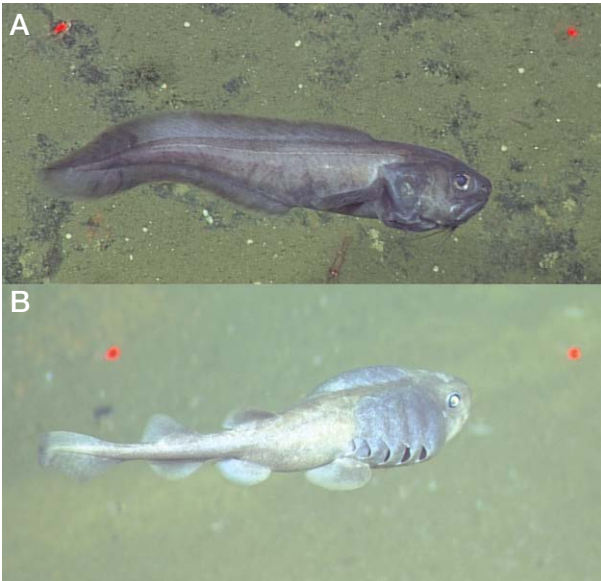


Figure 8.5.7 (A) The cusk eel, *Cherublemma emmelas*, and (B) the catshark, *Cephalurus cephalus*, represent some of the most hypoxia-tolerant fish species known. They live under suboxic and nearly anoxic conditions in the Gulf of California and their distribution extends throughout the eastern tropical Pacific (Gallo et al., 2019). Images from MBARI's ROV *Doc Ricketts*, red lasers are 29 cm apart.

depths and exhibited lower densities from 1994–2013 (Sato et al., 2017) (Figure 8.5.6). These species also appear influenced by ENSO, with stronger El Niño (associated with increased oxygenation) favouring *L. pictus* and negatively affecting *S. fragilis* and *B. pacifica* (Sato et al., 2017).

8.5.3.3 Taxonomic composition

Low oxygen availability on margins selects for a suite of hypoxia-tolerant, soft-bodied taxa such as nematodes, polychaetes, and some calcareous foraminifera. Most calcifying invertebrates tend to disappear in suboxic settings ($< 5 \mu\text{mol O}_2 \text{ kg}^{-1}$). There are, however, some notable exceptions such as the snail *Alia permodesta* and the mussel *Amygdallum politum*; these taxa tend to have very thin shells in suboxic or anoxic sediments (Levin, 2003; Moffitt et al., 2015b). *Bathybembix bairdii*, a deepwater sea snail, is a common inhabitant of the oxygen minimum zone core in the Southern California Bight and does not appear to have thin shells, although oxygen conditions do not reach suboxic conditions in this region (personal observation N. Gallo). The “core” of the OMZ refers to the depths with the lowest oxygen conditions observed within the water column, and oxygen levels increase both shallower and deeper than this core region. The most hypoxia-tolerant species can be found in the OMZ core. Among metazoan meiofauna

in OMZs, nematodes dominate in the lowest oxygen conditions and the ratio of nematodes to copepods steadily decreases with increasing oxygenation (Levin et al., 1991; Neira et al., 2001, 2018). Surprisingly, some fish can tolerate even lower oxygen concentrations than macro-invertebrates. The cusk eel, *Cherublemma emmelas* and the catshark, *Cephalurus cephalus* (Figure 8.5.7) live under suboxic ($[\text{O}_2] < 5 \mu\text{mol kg}^{-1}$) and nearly anoxic ($[\text{O}_2] < 2 \mu\text{mol kg}^{-1}$) conditions in the Gulf of California and their distribution extends throughout the eastern tropical Pacific (Gallo et al., 2019).

8.5.3.4 Diversity

Hypoxia associated with oxygen minimum zones or anoxic basins is known to reduce diversity of most animal groups ranging from foraminifera and metazoan meiofauna to invertebrate macrofauna and megafauna, as well as fishes (Levin, 2003; Rex & Etter, 2010). Reductions in species richness and elevated dominance occur at different oxygen thresholds, depending on animal size class; small taxa are generally more tolerant than large ones. But there are within-group differences. For example, among deep-sea metazoan meiofauna, nematodes are more tolerant of hypoxia than copepods (Levin, 2003). But even small forms like nematodes and foraminifera exhibit declines in diversity when oxygen availability is very low. Dramatic shifts in diversity can occur among macrofauna across small oxygen gradients. For example, on the Pakistan continental margin, where oxygen increases from 5 to 10 $\mu\text{mol O}_2 \text{ kg}^{-1}$ between 700 and 1100 m, the ecosystem moves from a single species assemblage with no bioturbation to a multi-species, highly bioturbated system (Levin et al., 2009) (Figure 8.5.8). Notably, the epibenthic community in a British Columbia fjord maintains high diversity despite annual exposure to $< 44 \mu\text{mol O}_2 \text{ kg}^{-1}$. This is potentially attributable to behavioural and physiological adaptations, periodic anoxia limitation of competitive dominants, and community evolution during low-oxygen periods of the Paleozoic (Chu et al., 2018; Tunnicliffe, 1981).

Diversity trends for the demersal fish community are also closely tied to bottom-water oxygen conditions, with diversity decreasing in a non-linear fashion with oxygen. This pattern holds true across different regions along continental margins in upwelling areas (Gallo & Levin, 2016). Off Oregon (Keller et al., 2010) and along the entire US West Coast (Keller et al., 2015) demersal fish and megafauna species richness is positively correlated

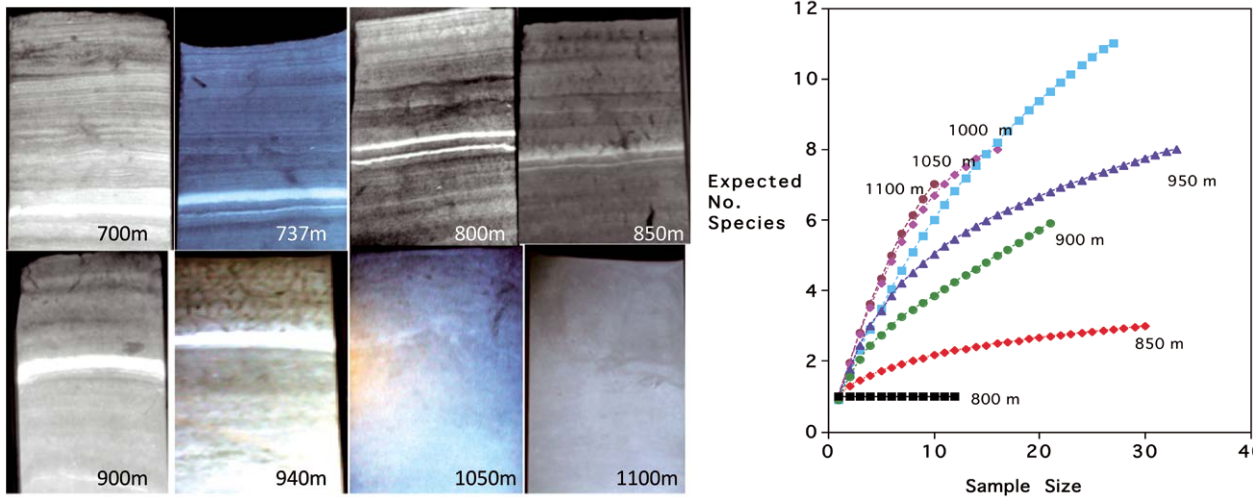


Figure 8.5.8 Abrupt changes in bioturbation as revealed by sediment x-radiographs (left) accompany increases in macrofaunal density (right) across the Pakistan margin. Bottom-water oxygen concentration increases with water depth from about $5 \mu\text{mol kg}^{-1}$ at 700 m to $10 \mu\text{mol kg}^{-1}$ at 1100 m (from Levin et al., 2009).

with near-bottom oxygen concentrations. In a Canadian seasonally hypoxic inlet, high single-species dominance (Matabos et al., 2014), increased homogenization and decreased species richness (Chu & Tunnicliffe, 2015) characterized the megafauna community during severely hypoxic periods. Off Namibia, the demersal fish assemblage that lived in the most hypoxic conditions on the central shelf, was characterized by lower diversity and higher dominance than other identified demersal fish assemblages in nearby areas (Hamukuaya et al., 2001). A demersal fish assemblage immediately adjacent to the Namibian low-oxygen shelf assemblage was found to have 2.5 times higher diversity than the low-oxygen assemblage (Mas-Reira et al., 1990), indicating the strong influence of oxygen on community diversity trends.

8.5.3.5 Body size

Smaller metazoans are more tolerant of low-oxygen conditions, in part because they have a larger surface area to volume ratio, facilitating oxygen diffusion. Thus, it is not surprising that larger animals (macrofauna and megafauna) are more vulnerable to deoxygenation than smaller fauna (metazoan meiofauna), and that small taxa dominate at the lowest oxygen levels (Gooday et al., 2009; Quiroga et al., 2005). However, among meiofaunal taxa, those species that are resilient to hypoxic conditions may attain relatively larger body size, presumably due to high food availability (Neira et al., 2001). In organisms that have specialized respiratory organs, higher respiratory surface area is needed under hypoxic conditions. This selective pressure on respiratory surface area is apparent in a number of highly adapted

oxygen minimum zone species that exhibit extensive gill surface areas (see examples in Levin (2003) and Gallo & Levin (2016)).

Foraminifera also become smaller under oxygen depleted conditions (Bernhard & Sen Gupta, 1999). However, their extreme hypoxia tolerance is likely linked to nitrate respiration and denitrification (Pino Ochoa et al., 2010).

Hypoxia is understood to reduce fish body size, but the underlying mechanism remains a scientifically contentious question and one that will require additional research. Pauly (2010) posits that given anatomical constraints related to respiratory surfaces, the growth and final size of fish is almost entirely determined by ambient oxygen concentration and temperature. This has led scientists to project that climate change will lead to a decrease in maximum fisheries catch potential, due to decreases in fish body size under lower oxygen conditions (Cheung et al., 2010, 2013). However, surface area to volume allometric relationships are typically described in terms of standard 3-dimensional shapes (spheres, cubes), whereas respiratory surfaces are folded surfaces that are not geometrically constrained in the same way (Wegner, 2011). As a result, physiologists have recently criticized this proposed relationship between fish size and environmental oxygen conditions as being based on erroneous assumptions (Lefevre et al., 2017), although some of these criticisms have been countered by Pauly and Cheung (2017). Deutsch et al. (2015) also found little relationship between body size and $\text{PO}_{2\text{crit}}$. Additional collaborations between fish physiologists, fisheries scientists and modelers are

needed to address this important question that may have critical implications for fisheries projections under future climate change.

8.5.3.6 Behaviour

Some species of benthic vertebrates and invertebrates inhabiting OMZs rely on vision for predator avoidance and prey capture at the sea floor, while most have highly visual larval stages that develop in lit waters. However, vision is a metabolically expensive process and has high oxygen requirements. This has led researchers to suggest that hypoxia impairment to the visual system may mediate changes in the vertical distribution of species (McCormick & Levin, 2017). Visual impairment of marine larvae can occur at oxygen concentrations much higher than physiological tolerance limits (P_{crit}) (McCormick et al., 2019), suggesting that sub-lethal impacts could occur at higher than expected oxygen concentrations. Pelagic fish, crustaceans, and cephalopods, and some benthic fish and crustaceans, exhibit a decline in metabolic rate with depth that has been linked to reduced locomotory capacity, but also corresponds to reduced light and visual activity (Childress, 1995). Future studies may therefore consider the interaction of light and oxygen gradients on the distributions of species, and how these may change under ocean deoxygenation.

Other forms of behaviour, including benthic-pelagic migrations, hypoxia avoidance, natal homing, foraging, chemotactic prey detection, and mating may be influenced by hypoxia, and further research in these areas is needed. The tuna crab *Pleuroncodes planipes* is reported to shift from a benthic to pelagic habitat under anoxic conditions (Boyd, 1967), but observations of high densities at $<2 \mu\text{mol O}_2 \text{ kg}^{-1}$ at depths of 380–400 m off Costa Rica (Cordes et al., unpublished) and Panama (Fig. 8.5.2A) (Peneda et al., 2014), combined with tolerance studies (Seibel et al., 2018) suggest that oxygen alone may not explain this behaviour.

8.5.4 Ecosystem-level consequences of deoxygenation on margins

8.5.4.1 Trophic pathways

One characteristic of systems subject to oxygen loss that accompanies change in diversity is a simplification of the food web. Among macrofauna for example, carnivory is nearly absent at very low oxygen levels (Sperling et al.,

2013), possibly because both capture and digestion of prey are highly oxygen-intensive. Infaunal taxa that are normally carnivorous can become phytodetritus feeders under severe oxygen stress (e.g. Jeffreys et al., 2012). Mat forming, filamentous sulphur oxidizing bacteria may provide a significant part of the *in situ* production; these may or may not be consumed by grazers such as snails (e.g. *Alia permodesta*) (Moffitt et al., 2015b; Myhre et al., 2017). A number of oxygen minimum zone animals host symbiotic chemo-autotrophic bacteria including lucinid and solemyid clams, phalodrilinid oligochaetes, nematodes, and frenulate polychaetes (Levin, 2003). Thus chemosynthesis-based trophic pathways can become more prevalent under severe oxygen limitation.

Seasonal comparisons of carbon processing during pre-monsoon (well oxygenated) and post monsoon (poorly oxygenated) periods on the Pakistan shelf, and across the lower OMZ (700–1100 m) on the Pakistan continental margin reveal that bottom-water dissolved oxygen concentrations exert a strong control over metazoan macrofaunal organic matter processing. Above oxygen thresholds between 5 and 7 $\mu\text{mol O}_2 \text{ kg}^{-1}$ (0.11 to 0.16 $\text{ml O}_2 \text{ L}^{-1}$) metazoans were primary carbon processors; below these levels protozoans (foraminifera) performed this role (Woulds et al., 2007).

Benthic-pelagic coupling may also be reduced on upwelling margins, as seawater oxygen concentration has been found to be the single best predictor of migration depth for diel vertical migrators on the global scale (Bianchi et al., 2013) and demersal fish communities are often reliant on midwater organisms and benthic-pelagic feeding (Trueman et al., 2014). Gallo (2018) reports that a predominance of demersal fish species on the southern California margin feed on pelagic resources above the oxygen minimum zone ($< 450 \text{ m}$) but those in the OMZ core are benthic feeders (Figure 8.5.9). In estuarine systems, seasonal hypoxia is known to influence the trophic structure of the benthic community by diverting energy from consumers to microbes (Baird et al., 2004; Diaz & Rosenberg, 2008). Similar trends may be expected in continental margin settings where filamentous bacterial mats are dominant, such as off Peru, Chile, and Central America (Gallardo & Espinoza, 2007).

8.5.4.2 Bioturbation and carbon burial

Hypoxia-induced reductions in diversity and in body size generally contribute to diminished bioturbation

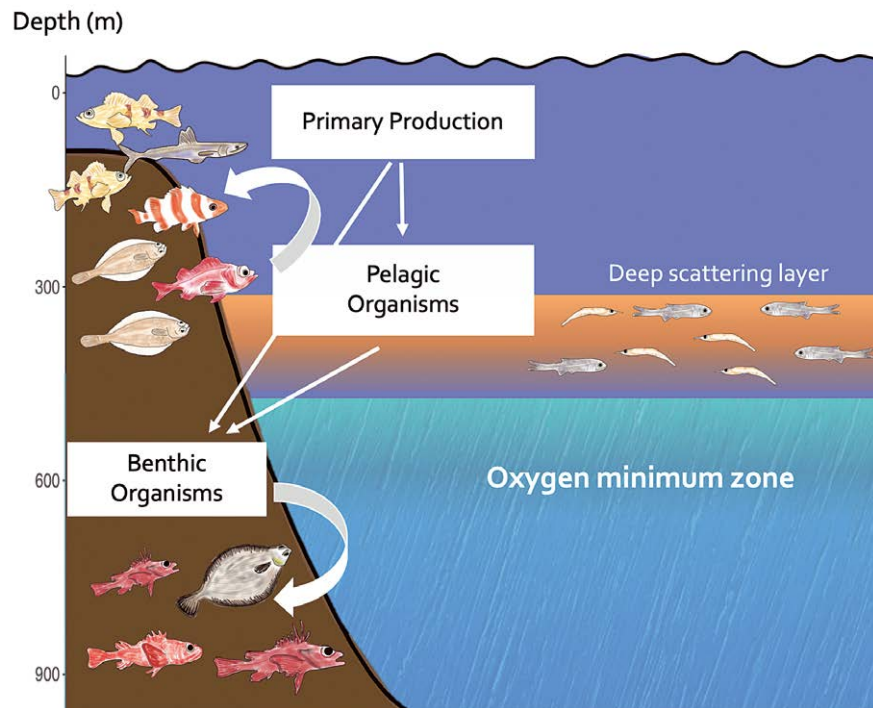


Figure 8.5.9 Conceptual diagram illustrating reduce benthic-pelagic coupling within the OMZ. Demersal fish above the oxygen minimum zone (OMZ) feed largely on pelagic prey whereas within the OMZ most demersal fish feed on benthic fauna (Gallo, 2018). Note: Drawing not to scale.

(particle mixing) and the generation of laminated or varved sediments (Calvert, 1964; Levin et al., 2009; Schimmelmann et al., 2016; Smith et al., 2000) (Figure 8.5.8), although gutless, symbiont-bearing taxa can carry out bioturbation (Levin et al., 2003). Bioturbation normally mixes organic matter and particles deep into the sediments and can contribute to burial of carbon. It is likely that ocean deoxygenation will expand the regions of the continental slope where mixing of sediments is limited. Dysoxic/anoxic laminated sediments generally contribute less to nutrient recycling (due to absence of animals) and bioturbators that contribute to carbon burial are largely absent (Aller, 1994). Thus, more labile organic material remains unused.

8.5.4.3 O_2 influence on chemosynthetic ecosystems

Continental margin communities are highly heterogeneous and often include methane seeps dominated by large structure-forming taxa such as bathymodiolid mussels, siboglinid tubeworms, and vesicomid clams which are supported by sulphide and methane oxidizing symbionts (Tunnicliffe et al., 2003). Among these foundation species, both mussels and tubeworms are notably absent within severe oxygen minimum zones on the East Pacific margin ($< 8 \mu\text{mol } O_2 \text{ kg}^{-1}$), despite their occurrence in the better oxygenated

waters beneath the OMZ (Levin, pers. observation). Their absence is possibly due to insufficient oxygen to support their sulphide- or methane-oxidizing symbionts within the OMZ or the inability of their larvae to survive low-oxygen waters (e.g. Levin et al., 2016). Expanding oxygen minimum zones, or the creation of new hypoxic areas is likely to affect seep diversity and function by suppressing the occurrence of hypoxia-intolerant foundation species.

8.5.4.4 Thresholds and tipping points

Animal exposure history, and basin-wide differences in oxygenation appear to influence oxygen tolerance thresholds (Chu & Tunnicliffe, 2015). For example, oxygen thresholds that induce migration for demersal fish in the NE Pacific occur at $44\text{--}53 \mu\text{mol } O_2 \text{ kg}^{-1}$ ($1.0\text{--}1.2 \text{ ml } L^{-1}$) (Chu & Tunnicliffe, 2015; Vaquer-Sunyer & Duarte, 2008,) but are several times higher in the Atlantic (Chu & Gale, 2017). There is also considerable variation in tolerance related both to taxonomic group and mobility; mobile fish and crustaceans that can move away from hypoxia exhibit higher thresholds (greater sensitivity) (Vaquer-Sunyer & Duarte, 2008). Tolerance thresholds for most infaunal invertebrates (macrofauna) occur at much lower oxygen concentrations, with values between $5\text{--}10 \mu\text{mol } O_2 \text{ kg}^{-1}$ (0.1 and $0.2 \text{ ml } L^{-1}$) (Levin et al., 2009; Sperling et al., 2016), or in some cases less

than 20 $\mu\text{mol O}_2 \text{ kg}^{-1}$ (Levin & Gage, 1998). However, some fish and invertebrate species can survive at 1–2 $\mu\text{mol O}_2 \text{ kg}^{-1}$ (Gallo & Levin, 2016; Gallo et al., 2019; Levin, 2003).

8.5.4.5 Lessons from the past

Oxygen regimes in the ocean have changed multiple times through geological history, providing a record to help understand how periods of high and low oxygen influence marine communities (Sperling et al., 2015). Changes in global oxygen conditions are associated with major extinctions or radiations of benthic marine fauna (Moffitt et al., 2015a) and the expansion and contraction of oxygen minimum zones through time are hypothesized to have played an important role in the modern-day distribution and diversity patterns of deep-sea species (Rogers, 2000; White, 1988). During the Cretaceous/Paleogene Event, bottom waters underwent severe oxygen depletion due to accumulation of organic matter (de Oca et al., 2013), at the same time aerobically active predatory fishes exhibited particularly large losses (Friedman, 2009). However, fishes in the open ocean, far from coastal oxygen minima, appeared to be more resilient to the extinction event (Sibert et al., 2014).

8.5.4.6 Changes over the last 25–50 years

Long-term records documenting changes in species distributions over the past 25–50 years on deep margins are rare. Catch records for hypoxia-intolerant groundfish off British Columbia show they have moved shallower by 2–3 m each year over a decade (Whitney et al., 2009) as hypoxia has expanded on the British Columbia coast (Whitney, 2009). Off Southern California, echinoid distributions have expanded for some species and contracted for others (Sato et al., 2017) (Figure 8.5.6). Where long-term, fisheries independent survey data exist (e.g. Sato et al., 2017) or detailed catch records are kept, data could be mined for this type of information to better understand the influence of changing oxygenation on margin ecosystems and their services.

8.5.4.7 Variability, tolerance and adaptation potential

There is a general belief that those ocean ecosystems subject to greatest variability in climate drivers will host species most adaptable and least vulnerable to negative climate impacts (Henson et al., 2017). Continental shelf and slope settings subject to seasonal, wind-driven

upwelling are among the most variable and many taxa already experience low oxygen conditions seasonally or permanently. The East Pacific, North Indian Ocean and West Africa are such regions, as they are subject to major interannual and multi-decadal climate cycles as well as wind events that influence oxygenation (Nam et al., 2011). Communities that have evolved under these conditions usually have several species that are highly adapted to living under severely hypoxic conditions. A recent review found that at least 77 representative demersal fish species have been reported living in oxygen minimum zones (Gallo & Levin, 2016), and this group includes several species important for demersal fisheries, such as *Sebastes* spp. (thornyhead), *Microstomus pacificus* (Pacific Dover sole) and *Anoplopoma fimbria* (black cod) (Figure 8.5.10). Due to the fact that these are long-lived species, it is unlikely that increased fishing effort on these species could compensate for losses from hypoxia-intolerant fisheries species. In regions that are more highly oxygenated and less variable, declining oxygen levels could exhibit (anthropogenic) signal emergence above background variability sooner (Long et al., 2016). Oxygen loss on better-oxygenated margins such as in the Atlantic could be of greater concern as there may be less phenotypic plasticity in hypoxia response, conferring reduced adaptation capacity. On the other hand, communities in areas that already exhibit low oxygen conditions seasonally or permanently may also be closer to their tolerance limits, and therefore in some cases more vulnerable under deoxygenation scenarios.

Beyond the survival potential of hypoxia-tolerant species, physiological adaptations to declining oxygen levels may include increased concentration of blood pigments such as haemoglobin, enhanced respiratory surface areas, slowed metabolic rates, increased ventilation rates, altered muscle composition, enzymatic adaptations and energy-conserving behaviours (Gallo & Levin, 2016; Levin, 2003). A detailed listing of adaptations in fishes can be found in Gallo and Levin (2016).

8.5.5 Ecological and societal consequences

Oxygen declines (or oxygenation events) on continental margins can lead to mortality (or redistribution) of key invertebrate and vertebrate fisheries (Arntz et al., 2006; Grantham et al., 2004). Sperling et al. (2016) predict future biodiversity loss for macrofaunal invertebrates at 500–1000 m on continental margins due to combined stressor effects. As these are key to feeding demersal

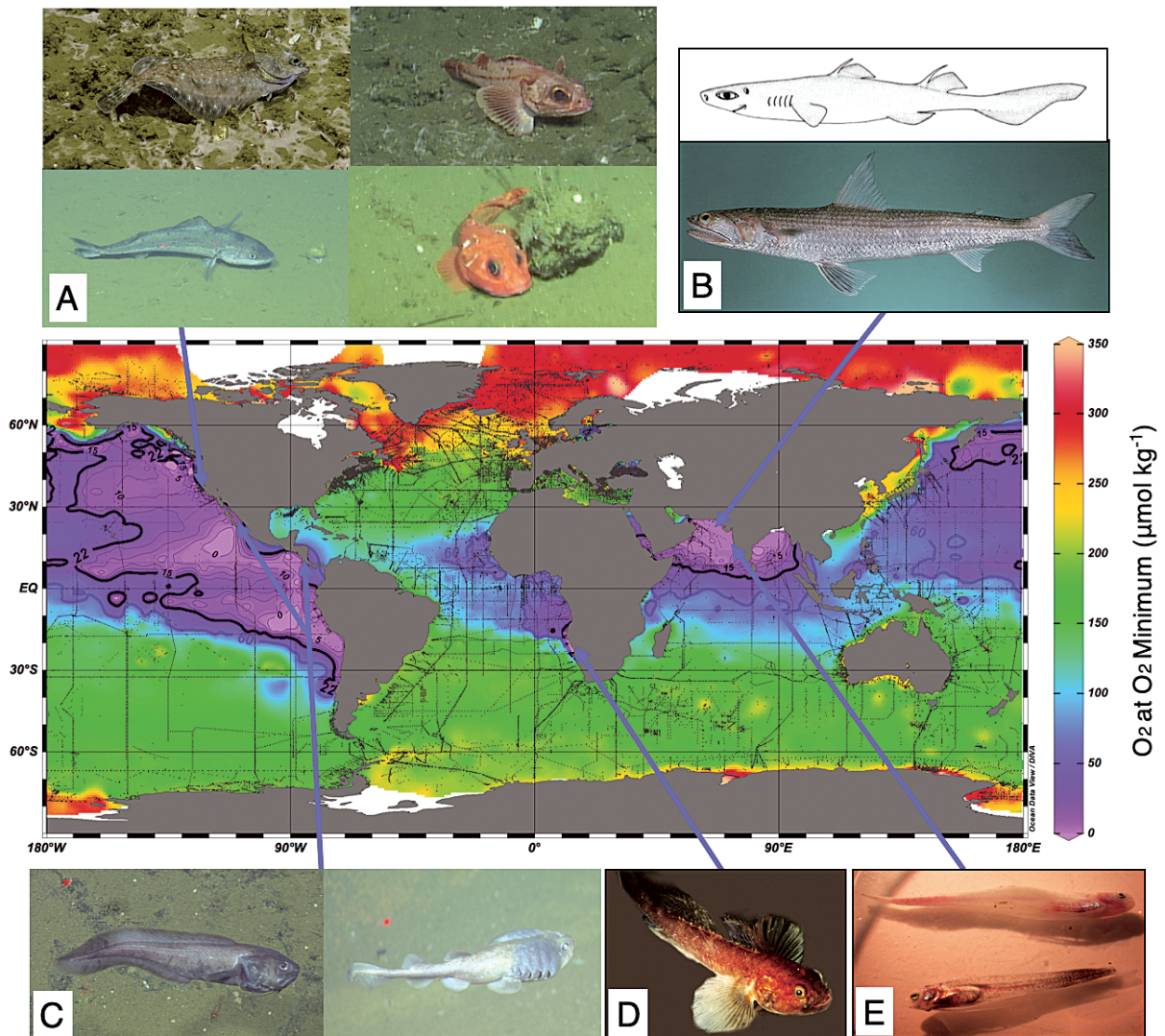


Figure 8.5.10 Global minimum oxygen concentrations within the water column and dominant demersal fish species in oxygen minimum zones (purple). Representative fish in oxygen minimum zones are shown. Modified from Gallo and Levin (2016). OMZ-adapted demersal fish species include: (A) in the Northeast Pacific—*Microstomus pacificus* (upper left), *Careproctus melanurus* (upper right), *Nezumia liolepis* (lower left), *Sebastolobus alascanus* (lower right); (B) Pakistan margin—*Centroscyllium ornatum* (upper) and *Saurida tumbil* (lower); (C) Gulf of California and central America *Cherublemma emmelas* (left)—*Cephalurus cephalus* (right); (D) Namibian margin—*Sufflogobius bibarbatus*; (E) west Indian margin—*Bregmaceros* sp.

fishes, there may be negative food web effects for demersal communities. Many demersal fish species may also rely heavily on pelagic production, which also will be influenced by changes in oxygenation (Gilly et al., 2013; see Section 8.4). Decreasing oxygen levels in the California Current Ecosystem were associated with a 63% decline in the region's mesopelagic fish larvae (Koslow et al., 2011); these species act as an important trophic linkage to seafloor communities.

Demersal fisheries on continental margins are economically valuable and deoxygenation will likely negatively affect demersal fishery catches. Catch per unit effort (CPUE) of demersal fish species along the US West Coast is tied to near-bottom oxygen concentrations

(Keller et al., 2015), which can explain up to 84% of the variation in biomass of individual fisheries species along a hypoxic gradient off Oregon (Keller et al., 2010). In other upwelling areas of the world including Peru, India, and Pakistan, the CPUE of demersal fisheries decreases when bottom oxygen levels decline (Gallo & Levin, 2016). Reductions in habitable area with warming are predicted for fish by Deutch et al. (2015) based on their metabolic index. Studies in the Southern California Bight have used projections of current trends in oxygen loss in concert with known physiological thresholds for sensitive species to project an 18% loss of habitat for rockfish (*Sebastes* sp.) in the Cowcod Conservation Area by 2030 (McClatchie et al., 2010). A number of important fisheries species in upwelling areas are not

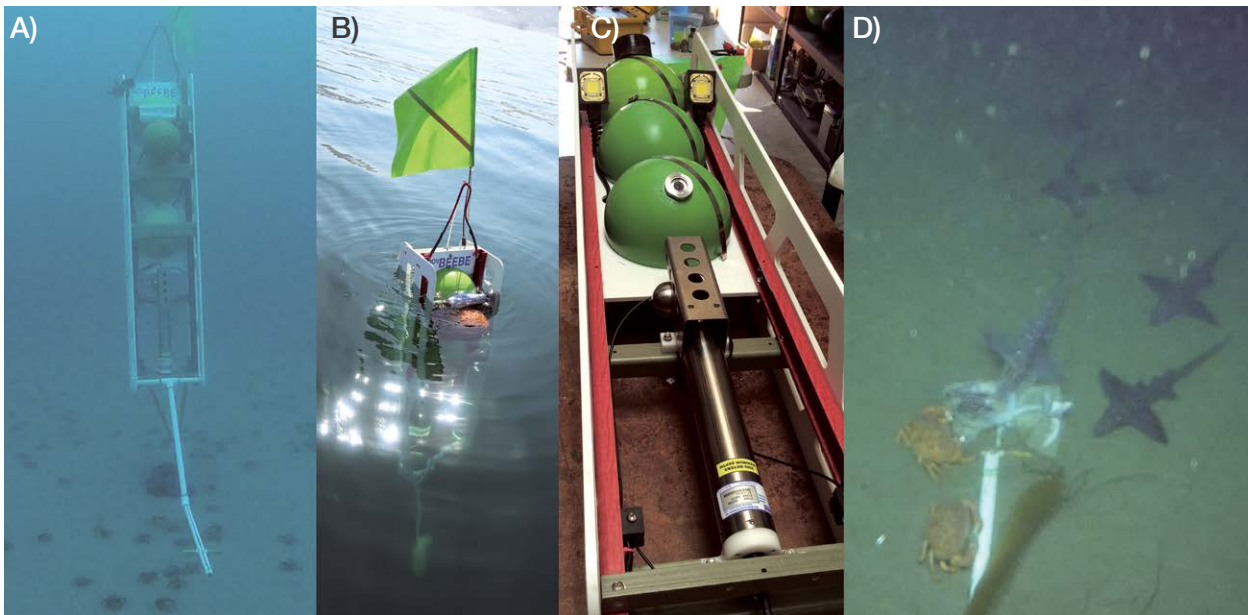


Figure 8.5.11 Autonomous landers with coupled environmental sensors and camera systems provide a low-cost framework for studying how environmental oxygen conditions affect continental margin communities. Pictured is Deep Ocean Vehicle (DOV) BEEBE, which is rated to 1000 m and collects data on environmental conditions (temperature, oxygen, salinity, and pressure) with a SBE MicroCAT ODO sensor and collects video data on the seafloor community with a pre-programmed camera system. A) DOV BEEBE deployed on the sea floor; B) DOV BEEBE at the surface during recovery; C) DOV BEEBE in the lab, showing the position of the SBE sensor and the camera sphere; D) image of seafloor community during a deployment with crabs and chimeras attracted to the bait on the drop-arm. Lander design courtesy of Kevin Hardy (Global Ocean Design).

hypoxia-tolerant and would likely be negatively impacted by deoxygenation trends (Gallo & Levin, 2016). These include *Sebastes* spp. and *Cancer magister* along the US West Coast (Grantham et al., 2004; McClatchie et al., 2010). During the 1997-1998 El Niño, local fisheries for hake, octopus, and scallop off Peru expanded in response to a significant increase in oxygen along the sea floor (Arntz et al., 2006). This suggests that future trends in hypoxia expansion may lead to reductions in these fisheries in coming years.

8.5.6 Implications of continuing ocean deoxygenation and vulnerabilities

In some developing countries, including Mexico, Peru, and India, severely hypoxic conditions can be found at upper slope and shelf depths, sometimes as shallow as 20 m (Banse, 1968). In the US, severely hypoxic conditions can also be found seasonally at inner shelf depths (20-50 m) off Oregon (Grantham et al., 2004; Keller et al., 2010). These regions, where severely hypoxic waters already occur at shallow depths, may be particularly vulnerable to continued deoxygenation trends and should be monitored closely (Hofmann et al., 2011). This is especially pertinent given that decreases in oxygen in the Southern California Bight have been most pronounced closer to shore at depths between 100-400 m (Bograd et al., 2008). These nearshore,

shallow areas are particularly vulnerable because they are likely more utilized by coastal communities for fishing. Shallower marine communities are exposed to warmer conditions which increase oxygen demand. At the same time, they likely experience habitat compression from shoaling oxyclines (Rosa & Seibel, 2011), making them more concentrated and thus susceptible to overfishing. Likely, benthic communities in areas with shallow OMZs in tropical parts of the world where water temperatures are warmer will be those most impacted by deoxygenation trends.

Most developing countries do not have good oxygen monitoring networks in place to document declines in oxygen and impacts to marine communities, nor do they have good baseline data against which to compare future conditions. Relative to other climate impacts, deoxygenation remains an under acknowledged climate impact within the international climate policy community (Gallo et al., 2017).

8.5.7 Approaches to monitoring deoxygenation on margins

Long-term time-series are an important tool in monitoring oxygen loss and consequent biological responses. Time-series data can reveal: (i) the timing, intensity and duration of hypoxic events and the rate and

magnitude of the response in the animal communities, or (ii) the influence of the various oceanographic phenomena operating on different time scales (e.g. ENSO, seasonality, abrupt events) that can mask the long-term decline imposed by climate change. Long-term monitoring programmes such as the California Cooperative Fisheries Investigation (CalCOFI) have shown the potential importance of oxygen trends in influencing the abundance of mesopelagic fishes (Koslow et al., 2011). However, compared to pelagic time-series, benthic time-series are more limited. Key contributions have come from the VENUS Observatory in Saanich Inlet off Canada that actively monitors both environmental oxygen conditions and collects video imagery of the benthic community (e.g. Matabos et al., 2014). Additionally, landers with coupled environmental sensors and camera systems can be used to collect high-frequency data on oxygen conditions and community responses at more locations (though usually for shorter periods) than possible with cabled observatories (Figure 8.5.11; Gallo, 2018). Existing benthic time-series programmes should include oxygen monitoring if they do not do so already. Fisheries-relevant trawl studies that sample across latitudes and depths (e.g. Bianchi, 1991; Hamukuaya et al., 2001; Keller et al., 2015) can also provide important insight into the influence of oxygen on community characteristics, provided that they collect paired high-quality environmental and community data. The use of satellite archival tags that can measure dissolved oxygen concentrations *in situ* (Coffey & Holland, 2015) will also be informative in determining the oxygen niches of species and observing any changes in environmental characteristics through time. All of these monitoring tools will prove useful in attribution of ecological change to specific climate drivers (whether oxygen, temperature, pH or other) in an ocean increasingly subject to multiple stressors.

8.5.8 Conclusions / Recommendations

Although anthropogenic access to deep margins for fishing, energy extraction and scientific research has intensified significantly over the past quarter century (Levin & Sibuet, 2012; Ramirez-Llodra et al., 2011), there are relatively few seafloor observations made on appropriate long time and space scales that document the consequences of changing environmental conditions, including ocean deoxygenation. Notably, benthic ecosystems have received much less attention with regards to deoxygenation than pelagic systems; the majority of long-term coastal monitoring

programmes focus on water column measurements and do not encompass the sea floor.

Research across natural gradients on margins in space and time indicates there are dynamic and rapid responses to oxygen change at all levels of organization, from the ecosystem to the gene, on both ecological and evolutionary time scales. Deoxygenation drives changes in species distributions, assemblage composition, body size, biomass (productivity), biodiversity, and food webs. Sublethal impacts take place at much higher thresholds than lethal impacts (Hofmann et al., 2011; Vaquer-Sunyer & Duarte, 2008), so we should be conservative in identifying thresholds of concern, especially since sublethal impacts are harder to observe but impact organismal fitness. Marine environments only appear to be viable if they support metabolic indices (the ratio of O_2 supply to resting metabolic O_2 demand) of 2 to 5 (Deutsch et al., 2015), suggesting that sublethal impacts begin occurring at oxygen concentrations much higher than experimentally-determined physiological limits. To advance understanding of how deoxygenation impacts on benthic communities will affect ecosystem services, it will be necessary to understand species-specific environmental niches and physiological tolerances and predict changes in the densities of key species of interest, expanding beyond the use of broader groupings such as the meiofauna, macrofauna, or megafauna. However, species-specific information will need to be interpreted within an ecosystem-based framework, considering the role each species occupies in the food web and in mutualistic and competitive interactions with other species. Some metrics, such as carbon sequestration, will require whole community metrics.

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