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Abstract. Coastal hypoxia (defined here as $<1.42\,\mathrm{ml\,L^{-1}}$; $62.5\,\mu$M; $2\,\mathrm{mg\,L^{-1}}$, approx. 30% oxygen saturation) develops seasonally in many estuaries, fjords, and along open coasts as a result of natural upwelling or from anthropogenic eutrophication induced by riverine nutrient inputs. Permanent hypoxia occurs naturally in some isolated seas and marine basins as well as in open slope oxygen minimum zones. Responses of benthos to hypoxia depend on the duration, predictability, and intensity of oxygen depletion and on whether H_2S is formed. Under suboxic conditions, large mats of filamentous sulfide oxidizing bacteria cover the seabed and consume sulfide. They are hypothesized to provide a detoxified microhabitat for eukaryotic benthic communities. Calcareous foraminiferans and nematodes are particularly tolerant of low oxygen concentrations and may attain high densities and dominance, often in association with microbial mats. When oxygen is sufficient to support metazoans, small, soft-bodied invertebrates (typically annelids), often with short generation times and elaborate branchial structures, predominate. Large taxa are more sensitive than small taxa to hypoxia. Crustaceans and echinoderms are typically more sensitive to hypoxia, with lower oxygen thresholds, than annelids, sipunculans, molluscs and cnidarians.

Mobile fish and shellfish will migrate away from low-oxygen areas. Within a species, early life stages may be more subject to oxygen stress than older life stages.

Hypoxia alters both the structure and function of benthic communities, but effects may differ with regional hypoxia history. Human-caused hypoxia is generally linked to eutrophication, and occurs adjacent to watersheds with large populations or agricultural activities. Many occurrences are seasonal, within estuaries, fjords or enclosed seas of the North Atlantic and the NW Pacific Oceans. Benthic faunal responses, elicited at oxygen levels below $2\,\mathrm{ml\,L^{-1}}$, typically involve avoidance or mortality of large species and elevated abundances of enrichment opportunists, sometimes prior to population crashes. Areas of low oxygen persist seasonally or continuously beneath upwelling regions, associated with the upper parts of oxygen minimum zones (SE Pacific, W Africa, N Indian Ocean). These have a distribution largely distinct from eutrophic areas and support a resident fauna that is adapted to survive and reproduce at oxygen concentrations $<0.5\,\mathrm{ml\,L^{-1}}$. Under both natural and eutrophication-caused hypoxia there is loss of diversity, through attrition of intolerant species and elevated dominance, as well as reductions in body size. These shifts in species composition and diversity yield altered trophic structure, energy flow pathways, and corresponding ecosystem services such as production, organic matter cycling and organic C burial. Increasingly the influences of nature and humans interact to generate
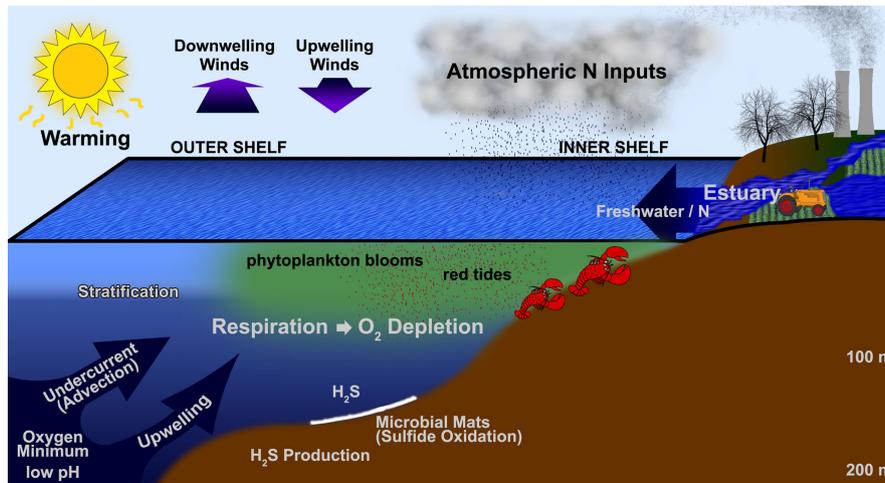
Fig. 1. Schematic diagram illustrating the mechanisms underlying the formation of hypoxia experienced by benthos along continental shelves.

or exacerbate hypoxia. A warmer ocean is more stratified, holds less oxygen, and may experience greater advection of oxygen-poor source waters, making new regions subject to hypoxia. Future understanding of benthic responses to hypoxia must be established in the context of global climate change and other human influences such as overfishing, pollution, disease, habitat loss, and species invasions.

1 Introduction

1.1 Sources of coastal hypoxia

Hypoxia, a shortage of dissolved oxygen, can originate in the ocean naturally, from human influences, or increasingly, from interactions between human activities and natural processes that make estuarine and coastal waters more susceptible to oxygen depletion. Fundamentally, the same processes are at work in most instances of natural and human-induced hypoxia. Biological oxygen demand exceeds the supply of oxygen from surface waters, typically as a result of increased microbial respiration, stimulated by accumulated carbon from enhanced primary production in surface waters. The enhanced production results from increased nitrogen (and sometimes phosphorus) availability. Nutrients are injected into surface waters either as a result of upwelling (a natural process driven by winds that occurs along continental margins) or via air and rivers as a result of anthropogenic activities. Cultural eutrophication (sensu Nixon, 1995; Diaz and Rosenberg, 1995, 2001, 2008) typically occurs where human population or agricultural production is high (Rabalais, 2004). Nutrient enhancement stimulates excessive phytoplankton growth. When the resulting organic matter exceeds the capacity of metazoan consumers to metabolize it,

the remaining organic matter settles to a pycnocline or the sediments, where it is decomposed, mainly by heterotrophic bacteria. This decay depletes the dissolved oxygen at a rate faster than resupply from surface, well-oxygenated waters because of the inhibited diffusion of dissolved oxygen across a sharp density difference, i.e. pycnocline.

Oxygen depletion is exacerbated in situations where water masses are highly stratified or isolated from oxygenated water bodies. Stratification results from strong thermal or salinity gradients including freshwater lenses formed from excessive rain or runoff from land. In many instances, warming or intense rainfall (e.g. monsoons) are seasonal events, and act to create seasonal hypoxia. Most of the time stratification is a natural process, but long-term warming trends in the ocean, climate-related precipitation changes, and altered riverine input can insert a human element (Fig. 1). Land-enclosed water bodies, such as estuaries, the Black or Baltic seas, fjords, silled basins and even the Arabian Sea, have a long residence time and little exchange with sources of oxygenated water. In regions and at water depths where well-oxygenated currents prevail, hypoxia is rapidly dissipated. The interaction of such currents (e.g. the California Current, the Humboldt Current, the Benguela Current) with strong upwelling and high primary production creates sharp natural oxygen gradients along the coast and continental margin.

Additional factors contributing to the development of natural hypoxia include the age, temperature and salinity of the water mass. Much of the ocean's new water is formed at high latitudes in the North Atlantic and Southern Ocean, and is supersaturated with oxygen due low surface temperatures that facilitate greater dissolution of oxygen. This oxygen-rich water sinks and begins a long "conveyor-belt" like trek through the interior of the oceans (Rahmstorf, 2006). Oxygen is slowly used up over periods of over 1000–2000 years,

leading to much lower base oxygen levels in the northern Pacific and Indian Oceans, than in the Atlantic and Southern Oceans. Hypersaline waters and warm waters hold less dissolved oxygen than cold, fresher water. Where warm, saline waters (e.g. from the Red Sea) enter the ocean (e.g. the Arabian Sea) or where waters are very old, hypoxia is more likely.

Finally, many continental shelf systems experience variable advection (or bathing) of low-oxygen waters from adjacent or deeper water masses or systems. Seasonal wind reversals can shift the relative influence of undercurrents that transport such waters, leading to seasonal hypoxia or even anoxia. Remote forcing of these currents, combined with warming and reduced wind stress (that normally drives ventilation), appear to dominate oxygen dynamics on the shelves of the central Benguela ecosystem off Namibia (Monteiro et al., 2008) and Oregon (Grantham et al., 2004), and off India (Naqvi et al., 2006). Larger-scale climate modes associated with Kelvin waves such as El Niño Southern Oscillations (ENSO Schaffer et al., 2002) and the Benguela Niño (Monteiro et al., 2008) force decadal shifts in shelf oxygenation by altering relative advection of equatorial water masses, although the oxygenation effects can be in opposite directions.

The factors described above (Fig. 1) can come together in different ways, over a range of space and time scales, to generate oxygen depletion of varying intensity, duration and recurrence. Within a single region, hypoxia severity can vary over time as a function of amount of productivity and degree of stratification (Rabalais and Turner, 2001; Naqvi et al., 2006; Rabalais et al., 2007b). How hypoxia affects benthos, and whether the effects vary fundamentally under conditions of human-caused versus natural hypoxia, will be the focus of this paper. Our goals are to (a) briefly review the time scales and sources of natural and human-induced hypoxia experienced by coastal benthic communities, (b) present case studies that illustrate benthic responses to hypoxia in estuarine, enclosed sea, inner shelf and outer shelf/slope environments, (c) provide a synthetic overview of oxygen thresholds and gradients responsible for population, community and ecosystem-level responses to hypoxia, distinguishing human and natural forcing where possible and (d) evaluate recovery potential, the influence of concurrent stresses, and future prospects for benthos subject to hypoxia. We treat all major benthic life forms, with the exception of microbial responses other than those of macroscopic, mat-forming sulfur bacteria.

1.2 Coastal hypoxia: environments and time scales

Coastal hypoxia will be treated here in three settings: estuaries and embayments, enclosed seas, and open continental shelves. Often there is a distinction between processes controlling hypoxia on the inner shelf ($\sim$0–100 m), and those on the outer shelf/ upper slope (100–400 m). Where appropriate we have tried to emphasize this distinction (Fig. 1). In

areas with deep shelves or steep continental margins, even depths below 200 m can be considered coastal. Open ocean, deep-water oxygen minimum zones (OMZs, $<0.5\,\mathrm{ml\,L^{-1}}$) occur permanently at depths between 100 and 1200 m in the Arabian Sea, the Bay of Bengal, the E South Pacific and E Subtropical North Pacific, and seasonally in the Gulf of Alaska and W Bering Sea. The world's OMZs have a surface area of 30.4 million km^2 (8% of ocean area) (Paulmier and Ruiz-Pino, 2008), and where they intercept the slopes, confer hypoxia on about 2% or 1.15 million km^2 of the continental margin (Helly and Levin, 2004). These settings and deep, silled basins subject to permanent hypoxia, though significant in area, will not be considered directly except where they impinge on the shelf or provide relevant ecological or evolutionary insight.

Different settings experience hypoxia on different time and space scales. Estuaries for example, are often subject to seasonal (on an annual basis) or episodic hypoxia (Diaz and Rosenberg, 1995, 2001). Sometimes hypoxia is localized within a specific tributary or in the shallow reaches of an estuary and affects only selected components of the benthic community. In shallow, well-mixed settings subject to nutrient loading, hypoxia may occur over diel cycles, with supersaturation resulting from primary production in daylight hours and anoxia resulting from heterotrophic respiration at night (Verity et al., 2006; Tyler et al., 2009). In contrast, enclosed seas are more likely to experience either permanent or long-term hypoxia over larger spatial scales. The Black, Baltic, and Azov seas encompass massive hypoxic regions. When the hypoxia is the result of eutrophication, as on the Black Sea shelf, active reductions in nutrient inputs can reverse low dissolved oxygen trends and reduce or eliminate hypoxia (Mee et al., 2005). Continental shelves receiving input from large rivers (e.g. Mississippi, Po, Rhine), or near large population centers, are bathed in nutrients from land, wastewater, or from atmospheric deposition. These coastal areas are likely to experience hypoxia during summer when high temperatures strengthen salinity stratification. In the Gulf of Mexico, this affects up to 22 000 km^2 each summer, in waters mainly shallower than 45 m (Rabalais and Turner, 2001; Rabalais et al., 2007b). Outer shelves are subject to the influence of interannual and decadal climate cycles as well as seasonal winds, through their effects on upwelling, downwelling and advection. On the Pakistan and West India margins there is a monsoon-driven seasonal shoaling of the oxygen minimum zone and additional development of inshore hypoxia (Naqvi et al., 2000, 2006; Brand and Griffiths, 2008). Similar conditions have developed in recent years on the Oregon inner shelf, although for different reasons (Grantham et al., 2004; Chan et al., 2008). On the Chile margin the inner shelves are seasonally hypoxic with low dissolved oxygen in austral summer (Sellanes et al., 2003). Outer shelves off Peru and Chile are subject to the pervasive influence of ENSO cycles. During normal and La Niña years production is high there and the regions below 100 m

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are permanently hypoxic. During El Niño events, strengthened influence from equatorial water masses oxygenates the shelf and deepens the upper boundary of the OMZ off Peru (Helly and Levin, 2004), whereas El Niño causes a shoaling of the OMZ and oxygen depletion on the southern California shelf (McClatchie et al., 2009).

1.3 Oxygen thresholds and levels deleterious to benthos

Dissolved oxygen (DO) concentrations are typically measured in units of $mg L^{-1}$, $ml L^{-1}$, micromolar ($\mu M = \mu mol L^{-1}$) or percent saturation. From here on we will either present oxygen concentrations as $ml L^{-1}$, or present parallel conversion to these units when data are originally given in other units. Shelf hypoxia is often defined as oxygen levels of $<2 mg L^{-1}$, $1.42 ml L^{-1}$, or $62.5 \mu M$; in contrast, much lower concentrations of $0.5 ml L^{-1}$ are used to identify permanent oxygen minimum zones (Helly and Levin, 2004; Paulmier and Ruiz-Pino, 2008). However, at $2 mg L^{-1}$, DO shortages can induce avoidance, or altered behavior, growth, reproduction or survivorship in taxa for which normoxia is the rule. Hypoxia represents the degradation of water quality for an average species. Among fishes and invertebrates, different taxonomic groups, body sizes and skeletal types have different oxygen tolerances and thresholds (Diaz and Rosenberg, 1995; Wannamaker and Rice, 2000; Rabalais et al., 2001a; Karlson et al., 2002; Vaquer-Sunyer and Duarte, 2008), so that no single definition of hypoxia fits all organisms.

Mobile nekton on the northern Gulf of Mexico continental shelf will avoid oxygen levels $<2 mg L^{-1}$ ($1.4 ml L^{-1}$) (Pavela et al., 1983; Renaud, 1986). Fish avoidance generally occurs at oxygen concentrations 0.5 to $2 mg L^{-1}$ (0.35 to $1.4 ml L^{-1}$) higher than the LC 50s, when tolerance has been tested (Vaquer-Sunyer and Duarte, 2008). Within estuaries, reduced densities of hogchoker (*Trinectes maculates*) occur at $<1 mg L^{-1}$ ($0.7 ml L^{-1}$), for spot (*Leiostomus xanthurus*) at $<1.5 mg L^{-1}$ ($1.1 ml L^{-1}$) and for Atlantic croaker (*Micropogonius undulates*) at 3 to $5 mg L^{-1}$ ($2.1–3.5 ml L^{-1}$). Lethal oxygen levels are $0.4 mg L^{-1}$ ($0.28 ml L^{-1}$) for hogchoker and $0.7 mg L^{-1}$ ($0.5 ml L^{-1}$) for spot (Pihl et al., 1991); Atlantic croaker in the Gulf of Mexico avoid oxygen concentrations of less than $2 mg L^{-1}$ ($1.4 ml L^{-1}$) (Rabalais et al., 2001a; Craig and Crowder, 2005). In Long Island Sound, 15 out of 18 fish species occur more frequently and at higher densities at sites with DO $>3 mg L^{-1}$ ($> 2.1 ml L^{-1}$) than at sites with DO $<2 mg L^{-1}$ ($1.4 ml L^{-1}$) (Howell and Simpson, 1994). We note that hypoxia associated with diel cycling may be less effectively avoided by fish and could provide chronic exposure that affects reproduction.

Some invertebrates may experience mortality at $<4 mg L^{-1}$ ($2.7 ml L^{-1}$), with larval stages being the most sensitive (Gray et al., 2002). A meta-analysis by Vaquer-Sunyer and Duarte (2008) revealed that the median oxygen concentration eliciting sublethal effects in 62 invertebrate species (265 experiments) was $2.13 mg L^{-1}$ ($1.5 ml L^{-1}$; $67 \mu M$). This value is close to the standard definition of hypoxia. Crustaceans are more sensitive to low oxygen than fishes, which are more resistant to hypoxia than molluscs. At $2 mg L^{-1}$, crustacean mortality occurs on average within 119 h of exposure, perhaps explaining why piles of dead crabs or lobsters are often the first sign and a common feature of hypoxia (Officer et al., 1984; Chan et al., 2008). Thresholds are clearly affected by temperature and the presence of H_2S (Vaquer-Sunyer and Duarte, 2008).

Thresholds are lower for animals that have evolved in permanently hypoxic settings such as oxygen minimum zones ($O_2 < 0.5 ml L^{-1}$), which drape margins of the eastern Pacific, the Arabian Sea and West Africa (Levin, 2003). Within OMZs, invertebrate species composition and diversity are affected at DO concentrations below 0.4 to $0.5 ml L^{-1}$ (Levin and Gage, 1998; Levin et al., 2000). Little is known about species-specific thresholds in OMZs but clearly some metazoan populations can survive at oxygen levels close to the limits of detection (e.g. Levin et al., 2003). Studies on Volcano 7 off Mexico (Levin et al., 1991) and the Pakistan margin (Levin et al., 2009) suggest that multispecies macrofaunal communities occur down to an oxygen threshold of around $0.1 ml L^{-1}$, but exceptions (where animals thrive at lower levels) have been found off Peru (Levin et al., 2002) and recently off India (Kitazato et al., unpublished data).

The severity of hypoxia experienced by coastal benthic ecosystems is determined by the nature of the exposure in addition to the actual DO concentrations. At the community and ecosystem level, the area affected, the frequency and duration of exposure and the evolutionary history of exposure will all determine the "severity" of impacts and the nature of the response, making prediction of standard successional patterns difficult (Conley et al., 2007).

2 Regional studies of benthic responses

2.1 Estuaries and bays

Estuarine hypoxia, where present, is most often seasonal, due to increased temperature and salinity stratification between late spring and early fall. Exposure to low oxygen conditions may be aperiodic (not every year; lasting for tidal cycles, days or weeks), episodic (following flooding) and restricted to specific regions (a tributary), so that normoxic refugia may remain elsewhere in the estuarine complex. Estuaries are also subject to harsh extremes of salinity and temperature. In studies of multiple stressor effects on macrofaunal distribution and abundance, dissolved oxygen explains more of the variability than temperature or salinity (Rainer and Fitzhardinge, 1981; Flemer et al., 1999). In addition, organic loading often interacts with DO, and together they explain much of the variation in species presence and density (Flemer et al., 1999). Factors such as reduced solar radiation

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(reducing phytoplankton oxygen production), reduced tidal range (enhancing haline stratification), and precipitation (inducing runoff) can contribute to estuarine hypoxia in tidally mixed estuaries.

Detailed lists of estuaries and bays subject to human-induced hypoxia and faunal responses are summarized in Diaz and Rosenberg (1995, 2001, 2008) and Gray et al. (2002). The majority of hypoxic estuaries are reported from the North Atlantic Ocean and adjacent seas (Diaz and Rosenberg, 2008). Over 46% of US estuaries are subject to seasonal hypoxia in one or more localized regions (Gray et al., 2002; Bricker et al., 2007). Of these, the majority occur on the US East and Gulf Coasts. The US West Coast appears more resistant, although hypoxic events have been recorded from Hood Canal (Puget Sound), Los Alamitos and Newport Bay, with nutrient enrichment implicated. Estuarine hypoxia is of widespread concern because estuaries support major shellfisheries (oysters, scallops, clams), provide nursery habitat to numerous finfish and shellfish species harvested commercially, and are key sites for aquaculture.

2.1.1 Chesapeake Bay

Chesapeake Bay is one of the largest estuaries in North America, with a length of 320 km. Episodic hypoxia has occurred in Chesapeake Bay since at least 1600 and seasonally since 1900 (Zimmerman and Canuel, 2002; Willard and Cronin, 2007; Gooday et al., 2009). Seasonal hypoxia increased in extent, duration and intensity during the 20th century (Breitburg et al., 2001; Cronin and Vann, 2003, Hagy et al., 2004).

Hypoxia is restricted to the mesohaline regions within the main stem below the pycnocline, and to tributaries such as the Patuxent and Rappahanock Rivers. When the water column is stratified in summer, about 40% of Chesapeake Bay lies below the pycnocline. The volume of hypoxic water in summer has tripled in the last 40 years and may comprise up to 25% of the mainstem Bay waters (Hagy et al., 2004). Sediment laminations occur in the deep central bay sediments, indicating that macrofauna are absent and permanent hypoxia may have existed for ∼100 years (Schaffner et al., 1992).

Demersal dwellers and feeders, such as blue crabs, croaker and spot, are particularly susceptible to the effects of hypoxia (Caddy, 1993). Death of crabs in pots, disappearance of crabs in deep water below 4–6 m, and shoaling of crabs during summer have been noted since the 1950s (Officer et al., 1984). In Chesapeake Bay bottom fishes experience habitat compression and potentially reduced access to food (Officer et al., 1984; Breitburg, 1992; Breitburg et al., 2001). However, macrobenthos experiencing hypoxia in the York River migrate to the sediment-water interface and may enhance, at least temporarily, food supply for higher trophic levels (Pihl et al., 1991, 1992).

The combined factors of extensive overfishing, diseases (*Perkinsus marinus* and *Haplosporidium nelsoni*), and oxy-gen depletion have had cascading consequences for the bay's ecosystem. Oyster reefs in particular have been decimated in the shallower waters of Chesapeake Bay. In the lower Rappahannock, some oysters have suffocated during hypoxic events, yielding "black bottoms" (Officer et al., 1984; Breitburg et al., 2001). Loss of oysters led to diminished filtration of phytoplankton and consequently reduced light transmission and declines in submerged aquatic vegetation (Newell, 1988; Newell and Koch, 2004). Loss of oyster reef substrates required for benthic life stages of sea nettles led to declines in this key plankton predator that controls ctenophores within the Bay (Breitburg and Fulford, 2006). Bottom-dwelling fishes on the remaining viable oyster reefs were often killed during intrusions of hypoxic water into shallow waters. (Officer et al., 1984; Breitburg, 1992; Breitburg et al., 2001).

The response of benthic communities to hypoxia depends on the severity in terms of DO concentrations, persistence, and temporal sequence. Near total faunal depletion in summer has been recorded for over 30 years in parts of the Patuxent estuary (Mountford et al., 1977; Holland et al., 1977, 1987), followed by fall recolonization. At oxygen concentrations $< 1.4\,\mathrm{ml\,L^{-1}}$, macrobenthic communities in the Rappahannock River show reduced species diversity (50% lower), lower biomass (70% lower), and loss of deep-dwelling, long-lived species (Dauer et al., 1992). Shallow-dwelling, short-lived opportunist species dominate under hypoxic conditions. These include the polychaetes, *Paraprionospio pinnata, Polydora ligni, Streblospio benedicti, Mediomastus ambiseta, Leitoscoloplos fragilis, Glycinde solitaria, Eteone heteropoda* and *Asabellides oculata,* and the bivalve *Mulinia lateralis* (Dauer et al., 1992).

In the York River, benthos was resistant to periodic hypoxia (0.2–$0.8\,\mathrm{ml\,L^{-1}}$) of short (6 to 14-d) duration that affects mainly areas deeper than 9 m. There were few permanent effects of hypoxia on macrobenthos (Dauer et al., 1992). Epifaunal communities tolerated hypoxic events of up to 1 week in the York River but exhibited behavioral responses including migration up in the water, development of resting stages in sessile taxa, and reduced feeding and growth by mobile taxa (Sagasti et al., 2001). Evidence of long-term changes in benthos of the York River suggests that hypoxia has shaped the benthic communities (Boesch et al., 1976). Observations of macrobenthic and epibenthic resistance and resilience to short-term hypoxia (Pihl et al., 1991; Dauer et al., 1992; Sagasti et al., 2001) have led to speculation of long-term conditioning of the community to episodic oxygen depletion (Diaz and Rosenberg, 1995).

2.1.2 Changjiang (Yangtze River) estuary and inner shelf of the East China Sea

The Changjiang (Yangtze River) is among the five largest rivers in the world with $928.5 \times 10^9\,\mathrm{m^3\,yr^{-1}}$ of water discharged historically, and 0.4–0.5×10^9 tons $\mathrm{yr^{-1}}$ of sediment (Qu et al., 2005). The river is ca. 6400 km in length with

a drainage area of 1.81×10^6 km^2. In the East China Sea, the dilute riverine waters (i.e. river effluent plumes) can disperse over ∼10^4 km^2 across the broad shelf in summer when the Changjiang reaches its maximal water discharge (e.g. 40–50×10^3 m^3 s^{-1}). Water circulation in the East China Sea is dominated by complex interactions of water masses and/or currents under the East Asia monsoon climate, including the Kuroshio Surface (KSW) and Sub-surface (KSSW) waters, Taiwan Strait Warm Water (TSWW), East China Sea Coastal Current (ECSCC) and Changjiang Diluted Water (CDW) (cf. Zhang and Su, 2006). These play a crucial role in regulating biogeochemical processes (e.g. hypoxia) on the shelf (Zhang et al., 2007).

Seasonal hypoxia off the Changjiang Estuary is found in summer and sometimes early autumn (i.e. July–September), presumably owing to the stratification that is induced by the buoyancy effect following increase in riverine water influx and high production in surface waters fueled by terrestrial inputs of nutrients. The hypoxic water (i.e. DO≤1.4 ml L^{-1}) is mainly constrained near the 20–75 m isobath about 10–20 m beneath the sea surface, with a minimum DO level of ca. 0.35 ml L^{-1}. Over the last several decades the area of hypoxia off the Changjiang Estuary has tended to increase by a factor of 5–10. The hypoxic area in the inner shelf of the East China Sea was ca. 1800 km^2 in August of 1959, approximately 13 700 km^2 in August 1999 (Li et al., 2002) and >15 400 km^2 in August 2006 (Zhu, 2007). Owing to the very dynamic character of circulation in the East China Sea, the coastal hypoxia off the Changjiang Estuary has strong temporal and spatial variability. The center or core of hypoxia, where minimal DO was observed in near-bottom waters, ranges from 29° N to 33° N in the area of the 40–50 m isobaths. Sometimes, two hypoxic cores can be identified offshore of the Changjiang Estuary (Li et al., 2002).

Total organic carbon (TOC) of bottom sediments (i.e. 0–5 cm) can be as low as 0.1–0.3% in areas affected by seasonal hypoxia off the Changjiang Estuary, then increase to 0.5–1.0% further offshore. Similarly, Chl-*a* in bottom sediments is 50–100 ng g^{-1} (dry weight) in areas of summer hypoxia, whereas it can be 200–400 ng g^{-1} in offshore regions (Zhu, 2007). The benthic fauna in this region is composed of Polychaeta (e.g. *Glycera chirori*), Crustacea (e.g. *Callianassa japonica*), Echinodermata (e.g. *Ophiura sarsii vadicola*) and Mollusca (e.g. *Thyasira tokunagai*) (Tang, 2004). Seasonal hypoxia in this region causes changes in the species abundance and community structure of benthic fauna, with impaired function of the East China Sea ecosystem via food-web alterations. Abundance of sessile species that have limited mobility can be considerably reduced when summer hypoxia prevails in the water column. The densities of sessile species do not fully recover in late autumn after hypoxia disappears. At this time strong mixing and water column instability associated with increasing northeast winds may prevent settlement. This is in contrast to the open shelf area outside the hypoxic waters, where animal abundance is

higher but exhibits less seasonal variability. The outer shelf meiofaunal (i.e. <0.5 mm) abundance in surface sediments (i.e. 0–5 cm) is depressed (0.5–1.0×10^6 individuals m^{-2} [=500–1000 ind 10 cm^{-2}]) but doubles in autumn when hypoxia starts to fade owing to wind-induced vertical mixing; higher meiofaunal abundance (e.g. 2.0×10^6 ind m^{-2} [2000 ind 10 cm^{-2}] occurs in areas where normoxic conditions dominate in the water column (Tang, 2004). Macrobenthic densities in hypoxic surface sediments reach 100–200 ind m^{-2} in spring before the development of seasonal hypoxia, but are <100 ind m^{-2} in autumn when the normoxic conditions recover; outside the hypoxic area abundances are 2–3 times higher (Zheng et al., 2003; Tang, 2004, 2006).

Fish species dwelling in near-bottom waters avoid and/or escape from the hypoxic conditions offshore of the Changjiang Estuary. However, because this region is a traditional spawning and hatching grounds for some economically important fish species (e.g. *Trichiurus lepturus*, *Larimichthys polyacti* and *Portunus trituberculatus*), persistent hypoxia in summer can cause damage to early life-history stages, leading to reduction of recruitment of crucial marine resources (Zheng et al., 2003; Qu et al., 2005). Adults of benthic invertebrates and fish exhibit higher biomass outside the hypoxic zone, with aggregations along the fringe of normoxic waters. Densities (i.e. kg h^{-1} of trawling) of yellow croakers, hairtail and crabs in the hypoxia region off the Changjiang Estuary can be 5-fold lower than in normoxic areas further offshore on the shelf (cf. Tang, 2006). Hypoxia in this region interacts with eutrophication induced by nutrient enrichment from land, species invasion from ballast waters, and over-fishing, affecting the sustainability of the ecosystem in the East China Sea Shelf. Collapse of the benthic fauna caused by hypoxia has led to a pelagos-dominated system off the Changjiang Estuary (Zheng et al. 2003; Tang, 2006).

2.2 Fjords and enclosed seas

Enclosed water bodies such as fjords, lochs, basins and shallow seas often exhibit stratification of temperature and/or salinity with oxygen depletion in deeper waters. When thermal stratification is most intense during summer, hypoxia can be seasonal, persisting for weeks to months.

2.2.1 Fjords

Anoxia is usually a local event and does not encompass the whole water body. Mussel bed presence will enhance oxygen depletion, due to enhanced oxygen consumption. Summer anoxia typically elicits a mortality sequence. Motile species such as fish will move away from the anoxic areas. Somewhat less mobile crustaceans such as shrimp and crabs die first, followed by lamellibranch molluscs, and snails, with polychaetes often most resistant (Jørgensen, 1980). Sulfide oxidizing bacteria (*Beggiatoa, Thiovulum*) form mats at the

sediment-water interface where both sulfide and oxygen are present. Areas less affected provide source organisms for re-colonization.

Oxygen-tolerant taxa in NE Atlantic fjords typically include *Heteromastus filiformis*, *Melinna cristata*, *Spiophanes kroyeri*, *Abra nitida*, and *Thyasira equlis*. *Thyasira sarsi*, *Amphiura chiajei*, *A. filiformis*, and *Capitella capitata* are dominant at deeper stations, although they require higher oxygen levels (Josefson and Widbom, 1988; Nilsson and Rosenberg, 2000). Indices that combine animal abundance measures with sediment structure and redox potential discontinuity (RPD) depth provide good characterization of the successional response to hypoxia by fjord benthos (Nilsson and Rosenberg, 2000)

Fjords and lochs have limited flushing, and thus are susceptible to hypoxia through human inputs of organic matter via fish farming, pulp mill effluent, and sewage. Salmon farming is a common practice in high-latitude fjords and lochs. When flushing is restricted or infrequent, organic matter from the farms will sink to sediments and cause high oxygen consumption (Gillibrand et al., 1996), depleting the oxygen in bottom waters. In lochs such as Loch Ailort, subject to farming for several decades, the fish food may contribute up to 50% of the total particulate organic carbon (POC) supply. *Scalibregma inflatum* was the dominant taxon beneath fish farms in Loch Ailort. *Mellina cristata*, with the ability to build long tubes up into the water, was dominant in the Gullmarfjord after extended hypoxia. Tube extension may increase turbulence and enhance oxygen supply (Nilsson and Rosenberg, 2000). The benthic fauna was eliminated near a sulphite pulp mill in the upper reaches of the Gullmar Fjord (Leppäkoski, 1975).

2.2.2 Black Sea

The Black Sea drains areas from 17 countries, receiving input from Europe's 2nd and 3rd largest rivers, the Danube and Dnieper (Mee et al., 2005, Shapiro et al., 2006). The shallower shelf of the Black Sea has been subject to extensive eutrophication while hypoxia in the deep basin is natural and has persisted for much longer periods. Prior to 1973, the Black Sea shelf (50 000 km^2) was dominated by a red alga *Phyllophora nervosa* that supported a rich assemblage of 118 invertebrates and 47 fish species. Along a vertical oxygen gradient in the northwestern Black Sea there is a transition from *Mytilus galloprovincialis* (62 m) to *Modiolus phaseolinus* biocoeneses at 100 m. The high filtration rates of the mussels regulate phytoplankton biomass. During the 1960s agricultural and lifestyle transformations in countries surrounding the Black Sea led to increased agricultural, animal, industrial and human waste inputs to surface waters. Eutrophication and increased phytoplankton biomass resulted in light limitation that led to the die off of the macroalgal mats. As eutrophication increased, mussels were unable to regulate phytoplankton blooms and massive buildup

of detritus generated excessive oxygen demand (Mee et al., 2005). In 1973 the northwestern shelf experienced 3500 km^2 of summer hypoxia as a result of eutrophication. By 1978 this had expanded to 30 000 km^2. By 1989, mass mortalities of benthos had occurred (Zaitsev, 1992) and in 1990 the "dead zone" encompassed 40 000 km^2. Anoxia led to further release of phosphorus and ammonium from sediments, contributing additional nutrient loading. The collapse of the benthic system led to a pelagic-dominated system. Overfishing and species invasion by the comb jelly *Mnemiopsis leydi*, which attained biomass up to 5 kg m^{-2}, further impaired function of the ecosystem (Vinogradov, 1992).

Economic failure and social change in the late 1980s led to a dramatic reduction in nutrient and waste inputs to the Black Sea, and ultimately to a shift in political and management regimes. A variety of treaties and altered practices have greatly reduced eutrophication in the Black Sea and provided valuable information about capacity for ecosystem recovery. Benthic studies suggest limited recovery within 6 years, with some macroalgae and mussels present (Mee et al., 2005). However, humans cannot control all aspects of Black Sea hydrography and oxygenation. External forcing from the continental margin waters and from climate events are important in this system, along with nutrient loads. Episodic phytoplankton blooms result when cold, nutrient-rich waters from the northern slope and shelf mix with the cold intermediate layer. Winter production may rival the eutrophic production (Sorokin, 2002). In 2001 late rainfall and high temperatures triggered a hypoxic event on the northwestern shelf (Mee et al., 2005).

Along a vertical oxygen gradient in the northwestern Black Sea, elevated meiofauna density occurs at the transition from oxic to anoxic bottom waters, which begins around 130 m ($<5\,\mu$M O$_2$, Wenzhofer et al., 2002). Some hypoxia-tolerant species persist between 130 and 185 m where the transition zone is subject to instability and appears to fluctuate vertically (Gulin and Kovalevsky, 2008). The oxic/anoxic transition interacts with methane seepage creating a complex geochemical setting inhabited largely by microbes, Foraminifera and nematodes (Sergeeva and Gulin, 2007). Larvae and adults of the polychaetes *Protodrilus* sp. and *Victorniella zaikai* (a chrysopetalid) are abundant in the transition water column and sediments, respectively (Sergeeva et al., 1999).

2.2.3 Baltic Sea

The Baltic Sea is a large brackish body of water with several basins separated by sills. Hypoxia first occurred in the Baltic Sea after its transition from fresh water to brackish water about 8000 cal. yr BP (Sohlenius et al., 2001). Hypoxia was intermittently present through the Holocene (Zillén et al., 2008), and persistently present since about 1900 (Fonselius, 1981). The Baltic Sea now has a permanent halocline that prevents mixing and oxygenation of water (Andersin et

al., 1978). The occurrence of hydrogen sulfide at depth in the Baltic fluctuates with flushing by Kattegat waters, with hydrogen sulfide present as shallow as 110 to 115 m (Fonselius, 1981). During the 20th century, nitrogen increased four-fold and phosphorus inputs to the Baltic increased eightfold (Larsson et al., 1985), which led to eutrophication and worsening hypoxia/anoxia. There is an early history of extreme fluctuation in bottom-water oxygen concentrations (>80 m) from both natural cases and human-induced eutrophication. Hydrogen sulfide was documented as early as 1931 in the Gotland Deep, and macrobenthos were reported absent from the Bornholm Basin in 1948. Episodic flushing events involving North Sea water occurred in the 1950s and 1960s causing oxygenation (3–5 ml L^{-1}) followed by rapid drops in oxygen to near 0 in the Bornholm Basin (Tulkki, 1965, Leppäkoski, 1975). During these events the normally low-diversity macrobenthos (e.g., 7–8 species) became heavily dominated in numbers and biomass by one or a few hypoxia-tolerant species (e.g. *Scoloplos armiger* in 1965; *Capitella* sp. in 1967). While macrobenthos biomass increased above the halocline, severe hypoxia and anoxia developed below (Elmgren, 1989), causing elimination of bioturbating macro-fauna and formation of laminated sediments over large areas of seafloor (Schaffner et al., 1992).

In the eastern Gotland Deep biological features and abiotic factors result in distinct faunal zones (Olenin, 1997). Up to 50 species were found at oxygenated depths <30 m, only 11–14 species were present in hypoxic waters from 50 to 124 m, and no species were recovered between 124 and 140 m. High biomass in shallow areas was associated with a hard-bottom community of *Mytilus edulis* and with *Macoma balthica* in sediment (Olenin, 1997). Among the hypoxia-tolerant taxa found at deeper depths are the ophiuroid *Amphiura sarsi*, the priapulid *Halicryptus spinulosus*, the peracarid crustaceans *Saduria entomon, Diastylis rathkei and Pontoporeia femorata*, the bivalve *Macoma balthica*, and the polychaetes *Pygospio elegans* and *Scoloplos armiger*. Hypoxia-tolerant ostracods include *Cyprideis torosa, Heterocyprideis sorbyana*, and *Candona neglecta*. These taxa reflect either omnivorous mobile (swimming) taxa, i.e. the crustaceans, or shallow infaunal deposit feeders. Both groups have minimal bioturbation capacity.

2.3 Continental shelves

2.3.1 Chilean shelf

Hypoxia on the outer Chile shelf is associated with Equatorial subsurface water. The influence of this water mass is greatest off northern Chile, where more or less permanent hypoxia occurs from the inner shelf to 400 m. Off central Chile, the outer shelf is seasonally hypoxic to 41°S due to upwelling in shallow water during spring and summer (Sellanes et al., 2003, 2007). Thick mats of sulfide oxidizing *Thioploca* and *Beggiatoa* are key features on the Chile shelf during nor-

mal summer hypoxia. These bacteria attain a wet weight of 1 kg m^{-2} between 50 and 100 m water depth (Gallardo, 1963, 1977). Associated with the bacteria mats are nematode-dominated meiofaunal assemblages (Neira et al., 2001b; Sellanes et al., 2003). Macrofauna are abundant (e.g. up to 73 900 ind m^{-2}, 68.4 g m^{-2} wet wt.) but diversity is low (Sellanes et al., 2007). Body size is reduced under hypoxic conditions on the Chile shelf (Quiroga et al., 2005). Most of the macrofauna are annelids and about half are represented by the polychaete *Paraprionospio pinnata*. This species is highly adapted for low oxygen conditions, with elaborate branchial structures that enhance oxygen diffusion and enzymatic adaptations for anaerobic metabolism (González and Quinoñes, 2000; Quiroga et al., 2007). *Mediomastus branchiferus, Aricidea pigmentata, Nephtys ferruginea* and *Cossura chilensis*, combined with the amphipod *Ampelisca araucana*, form most of the remaining macrofauna. It is hypothesized that uptake of H$_2$S by the large filamentous bacteria acts to detoxify the setting, protecting annelid prey and their predators such as red crabs (Gallardo et al., 1994).

There is a strong coupling of upwelling, primary production, oxygen budgets and benthic communities on the Chile shelf; this has been best documented off Concepcion, Chile (36° S). Bacterial mat cover and biomass is greatest after consecutive years of upwelling-favorable, highly productive, La Niña-like conditions; *Thioploca* thrives at DO levels between 0.2 and 0.3 ml L^{-1} (Gutiérrez et al., 2000). During El Niño years, when primary production declines and the shelves become better oxygenated (Schaffer et al., 1999), *Thioploca* biomass is depressed and densities of the tube-dwelling *P. pinnata* decline (Gutiérrez et al., 2000; Sellanes et al., 2007). Larger-bodied, subsurface, bioturbating species (e.g. *Cossura chilensis*) increase in density and there is an overall deepening of faunal activity within the sediments (Gutiérrez et al., 2000; Sellanes et al., 2003). This leads to greater irrigation, and more sediment reworking (Gutiérrez et al., 2000).

Meiofauna show parallel trends off central Chile during El Niño events. Meiofaunal abundance and biomass increase, dominance by nematodes is diminished, remaining nematodes dwell deeper in the sediments, and harpacticoid copepods increase in abundance (Neira et al. 2001b; Sellanes et al., 2003; Sellanes and Neira, 2006). Overall meiofaunal abundance is positively correlated with bottom-water oxygen concentration. The cumulative effect of El Niño is to attenuate seasonality and create better oxygenated, winter-like conditions on the shelf throughout the year, with effects on the benthic community lasting up to five years beyond the cessation of detectable climate shifts.

2.3.2 Peru margin

Long-term monitoring of shelf bacteria and metazoans in sediments off Peru (12° S; 94 m) shows variations in bottom-water oxygen concentrations and community structure driven remotely by coastal trapped waves originating in

the Equatorial region; these are often but not always associated with ENSO cycles. There are three community "states". Prevailing conditions involve anoxia-hypoxia (DO<10 μM) with few macrofauna and domination of biomass by nematodes. During intermediate oxygenation (10–20 μM), sulfide oxidizing bacterial mats (*Thioploca* spp.) make up much of the biomass. Under higher oxygenation levels associated with strong El Niño events (>40 μM), macrofauna are dominant. Macrofaunal dominance may persist long after reformation of hypoxia, apparently due to the bioturbation activity of nemerteans and enteropneusts, which mixes what little oxygen is available into the sediments (Gutiérrez et al., 2008). Thus different oxygen levels are not always linked to distinct assemblages and transitions are observed frequently.

Shallow waters in the Bay of Ancon, Peru (11° S) are subject to frequent hypoxia at 15 m and nearly permanent hypoxia (and sometimes anoxia) at 34 m. Macrobenthos during "normal" (non El Niño) years are characterized by low faunal densities (4000 and 425 ind m^{-2} at 15 m and 34 m, respectively), low biomass (<1.08 g and 0.2 g ash free dry wt. m^{-2}), and low numbers of species (3–17 and 0–6) (Tarazona et al., 1988a, 1988b). The numerically dominant taxa were *Owenia collaris*, *Magelona phyllisae*, *Chaetozone* sp. and *Phoronis* sp. at 15 m and *Paraprionospio pinnata*, *M. phyllisae*, *Chaetozone* sp. and *Leitoscoloplos chilensis* at 34 m (Tarazona et al., 1988a). Since monitoring of macrobenthos began in 1981 there have been four El Niño events that have raised temperatures and oxygenated the inshore waters. The community response consistently involved nearly immediate, dramatic elevation of diversity and reduced dominance, with colonization of local species (Tarazona et al., 1988a, 1988b; Arntz et al., 2006). While density and biomass increases followed oxygenation in some cases, this response was not consistent, possibly due to increased predation by megafaunal species that also recolonized. Sometimes high macrofaunal densities continued following the return of hypoxia. Similar results have been obtained for macrofauna in the Bay of Independencia (14°20′ S) (Tarazona et al., 2001; Arntz et al., 2006). Massive wash-ups of the Humboldt squid (*Dosidicus gigas*) (Fig. 6c) that occur off California, Oregon and as far north as British Columbia may also be related to inshore movement of low-oxygen water.

Numerous fisheries species on the central Peru shelf respond positively to oxygenation events during El Niño. These include the scallop (*Argopecten purpuratus*), octopus (*Octopus fontaneanus*), purple snail (*Thais chocolata*), and multiple species of shrimp (*Xiphopenaeus riveti*, *Sicyonia disdorsalis* and several *Penaeus* spp.). Other species responding positively after El Niño events include barnacles (*Pollicipes elegans*) and the hake (*Merluccius gayi peruanus*) (Arntz et al., 1988; Espino et al., 1985).

In contrast to the central Peru dynamics, at sites further north on the Peru coast (Paita 05° S, and San Jose 06°45′ S) time series of macrobenthos at 35-m and 65-m water depth reveal a negative response to El Niño conditions. Most species, except *Paraprionospio pinnata*, declined in density during the 1997–1998 El Niño. This situation was attributed to increased river runoff and reduction in food supply (Gutiérrez et al., 2005).

2.3.3 Oregon shelf

Summer hypoxia on the inner Oregon shelf (<50 m) is a recent occurrence (Grantham et al., 2004; Chan et al, 2008) and most benthic responses have yet to be quantified. Hypoxia was first reported in July to September 2002, when oxygen concentrations dipped to 0.21–1.57 ml L^{-1} over the shelf, and mortalities of schooling and benthic rockfishes were recorded (Grantham et al., 2004). Mass mortality of brachyuran crabs and absence of fishes was recorded by ROV surveys in 2006, when hypoxia covered 3000 km^2, occurred over 80% of the water column, and reached within 2 km of shore (Chan et al., 2008). The 2006 hypoxia event extended over much of the Washington shelf as well (Connolly et al., 2008). In 2007 a number of long-lived species such as large asteroids, holothurians and echinoid urchins remained absent from the system. In summer 2006 (the most intense hypoxic period to date), the benthic community at 100 m off Astoria (oxygen concentration 1.67 ml L^{-1}) exhibited high dominance by *Mediomastus* sp. and *Sphaerosyllis* sp. with *Prionospio* sp., lumbrinerids, magelonids and bivalves all abundant (>5% representation) (Levin, unpublished). No comparison data for normoxic years are available.

2.3.4 California shelf

Recent analyses of the California Cooperative Fisheries Investigation (CalCOFI) oxygen time series off southern California by Bograd et al. (2008) have documented declining oxygen concentrations over the past 22 y (1984–2006). At 200–300 m, the oxygen content of the water has declined by 20% to 30%, with a shoaling of the hypoxic boundary (1.42 ml L^{-1}) of up to 90 m within inshore regions of the southern California Current system. Both increased stratification from warming, and advection of low-oxygen equatorial waters are proposed to contribute to oxygen declines. During April 2008, oxygen was measured below 2 ml L^{-1} at 100 m depths and between 1 and 2 ml L^{-1} over much of the inner southern California shelf (J. Wilkinson, personal communication). McClatchie et al. (personal communication), suggest that similar oxygen declines associated with shoaling of the OMZ were also observed off California in 1950–60 and that hypoxia at 200–300 m is common in summer. The outer shelf provides habitat for several valuable rockfish (*Sebastes* spp.). New analyses reveal that 37% of the rockfish conservation area at 180–240 m is hypoxic during a normal summer, but this may increase to 55% during El Niño years when the California undercurrent, carrying saline low-oxygen water, is strengthened (McClatchie et al., personal communication). While the fish can migrate inshore,

this causes loss of habitat for populations already stressed by overfishing. There are few outer-shelf fish or invertebrate surveys that track changes in animal distributions in response to hypoxia. However, many changes in animal distributions are noted off California during El Niño (Arntz et al., 2006); some of these might be driven by responses to oxygen depletion in addition to warming.

Alta California (USA) has no records of shelf anoxia, but during June 2007, inshore anoxia was recorded over a 5 km stretch of coastline at Erendira, a strong upwelling region off Baja California, south of Ensenada, Mexico. Most animals died and a walkout involving many tons of lobsters was observed, similar to events off Nambia. The anoxic event was attributed to a combination of upwelling, intrusion of deep, subtropical salty, low-oxygen waters, and red tide conditions (J.M. Hernandez-Ayon et al., pers. comm.). Recent local observations of declining oxygen levels combined with ocean-scale records of expanding oxygen minimum zones in the eastern tropical Pacific (Stramma et al. 2008, and in review) suggest that hypoxia may become increasingly common on the Pacific shelves off Oregon, California and Mexico in the coming decades.

2.3.5 Northern Gulf of Mexico

The northern Gulf of Mexico hypoxic zone, adjacent to and influenced by the Mississippi and Atchafalaya Rivers, is the second largest zone of human-caused, oxygen-depleted waters in the world's coastal ocean (Fig. 2). River and landscape alterations over two centuries have significantly lessened the buffering capacity of the watershed (Turner and Rabalais, 2003), but anthropogenic additions of nutrients resulted in eutrophication and the development of hypoxia in the last half of the 20th century (Rabalais et al., 2007 a, b).

Seasonal hypoxia – spring through early fall – is the result of persistent stratification coupled with the high organic production in overlying surface waters that is fueled by river-derived nutrients (Rabalais et al., 2007a). There is a persistent haline stratification due to the high discharge of the Mississippi River, which, coupled with thermal warming in the spring and summer, intensifies the density differences. The mid-summer extent of bottom-water hypoxia ($<2\,\mathrm{mg\,L^{-1}}$; $1.4\,\mathrm{ml\,L^{-1}}$) has averaged $13\,500\,\mathrm{km^2}$ since 1985, and reached its maximal size of $22\,000\,\mathrm{km^2}$ in 2002. Hypoxic waters are most prevalent at depths between 5 and 45 m.

The responses of the fauna vary, depending on the concentration of dissolved oxygen, but there is a fairly consistent pattern of progressive stress and mortality as the oxygen concentration decreases from 2 to $3\,\mathrm{mg\,L^{-1}}$ (1.4 to $2.1\,\mathrm{ml\,L^{-1}}$) to anoxia ($0\,\mathrm{mg\,L^{-1}}$) (Fig. 3). Elasmobranchs (rays and sharks) typically leave the area when oxygen concentrations fall below $3\,\mathrm{mg\,L^{-1}}$. Other demersal fishes migrate away from the area when oxygen concentrations fall below $2\,\mathrm{mg\,L^{-1}}$, although drum, red fish and snapper are oc-

Fig. 2. Hypoxic region and influencing rivers off Louisiana in the northern Gulf of Mexico.

casionally seen by divers when the oxygen concentrations are near $1.5\,\mathrm{mg\,L^{-1}}$ ($1\,\mathrm{ml\,L^{-1}}$) and the layer of hypoxic water is not thick (N. Rabalais, personal observation). Demersal fishes and crustaceans can die en masse when hypoxic water masses trap them near shore and there is no escape. Demersal invertebrates are seldom caught in bottom trawls when the oxygen levels fall below $2\,\mathrm{mg\,L^{-1}}$ ($1.4\,\mathrm{ml\,L^{-1}}$) (Pavela et al., 1983; Renaud, 1986), but are routinely seen in remotely-operated vehicle (ROV) tapes at oxygen concentrations below that level (Rabalais et al., 2001a). Some penaeid shrimp and stomatopods were observed at oxygen levels as low as 1.7 to $1.8\,\mathrm{mg\,L^{-1}}$ (1.2–$1.3\,\mathrm{ml\,L^{-1}}$) but never below $1.5\,\mathrm{mg\,L^{-1}}$ ($1\,\mathrm{ml\,L^{-1}}$). Stomatopod presence in hypoxic waters as low as $1.5\,\mathrm{mg\,L^{-1}}$ is consistent with the results of Pihl et al. (1991) who indicated that *Squilla empusa* first adapted physiologically to hypoxia and then migrated as hypoxia became more severe, a trend consistent with its more stationary and territorial behavior.

As the oxygen level decreases from 1.5 to $1\,\mathrm{mg\,L^{-1}}$ (1 to $0.7\,\mathrm{ml\,L^{-1}}$) bottom-dwelling organisms exhibit stress behavior (Rabalais et al. 2001a). Crabs (e.g. *Libinia* sp., *Persephona* sp.) and sea stars (*Astropecten* sp.) climb on top of high spots, such as burrow excavation mounds. Brittle stars emerge from the sediment and use their arms to raise their disks off the substrate. Burrowing shrimp (*Alpheus* sp.) emerge from their burrows, and gastropods (*Oliva sayana*, *Terebra* sp., *Cantharus cancellarius* and *Distorsio clathrata*) move through the surface sediments with their siphons extended directly upward. Large burrowing anemones (*Cerianthus* sp.) become partly or completely extended from their tubes and lie on the substrate, in a flaccid and non-responsive condition. Polychaete worms emerge from the substrate and lie motionless on the surface (e.g. *Chloeia viridis* and *Lumbrineris* sp.). These behaviors are presumed to position the organisms in higher oxygen content waters, even though moving from the safety of the sediments exposes them to greater risk of predation. The presence of large, typically infaunal organisms on the sediment surface, however, supports the idea presented earlier that bottom-feeding fish are excluded from the hypoxic lower water column, unlike in
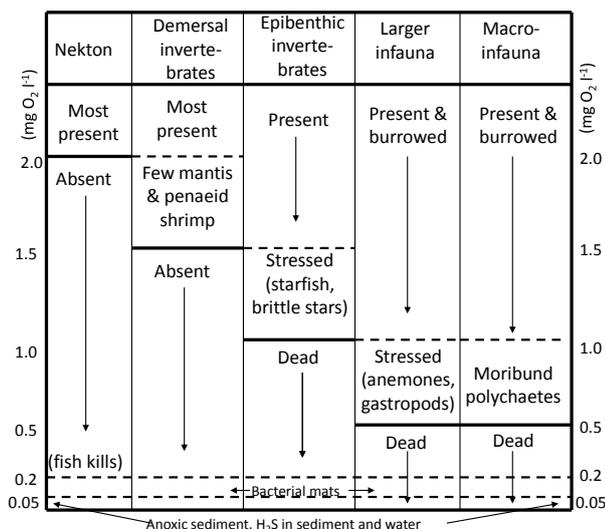
Fig. 3. Progressive changes in fish and invertebrate fauna as oxygen concentration decreases from $2\,\mathrm{mg\,L^{-1}}$ ($1.4\,\mathrm{ml\,L^{-1}}$) to anoxia ($0\,\mathrm{mg\,L^{-1}}$) on the Louisiana continental shelf (Rabalais et al., 2001a, b).

the York River of Chesapeake Bay where predators move into such areas and feed on stressed infauna (Pihl et al. 1992).

As oxygen levels decrease from 1 to $0.5\,\mathrm{mg\,L^{-1}}$ (0.7 to $0.35\,\mathrm{ml\,L^{-1}}$) even the most tolerant burrowing organisms, principally polychaetes, emerge partially or completely from their burrows and lie motionless on the bottom. Several polychaetes, one hemichordate, one ophiuroid and several cerianthid anemones that appeared lifeless on the bottom became active when they were brought to the surface in sealed containers of ambient water and placed in shallow dishes with ambient water that naturally re-oxygenated by diffusion (Rabalais et al. 2001a). Jørgensen (1980) also found that many of the organisms seen lying on the bottom in hypoxic areas were moribund, not dead. If these organisms survive, they may re-enter the sediment and may partially account for the recolonization of benthos when hypoxia abates. Below oxygen concentrations of $0.5\,\mathrm{mg\,L^{-1}}$ ($0.35\,\mathrm{ml\,L^{-1}}$) there is a fairly linear decline in species richness, abundance and biomass of benthic macroinfauna (Rabalais et al., 2001b).

Benthic communities in seasonally severe hypoxic conditions on the Louisiana continental shelf are characterized by decreases in species richness, abundance and biomass of organisms relative to similar habitats without low oxygen levels (Rabalais et al., 2001b). Some macroinfauna, including the polychaetes *Ampharete* and *Magelona* and sipunculans, are capable of surviving extremely low dissolved oxygen concentrations and/or high hydrogen sulfide concentrations. The abundance of macrofauna during the period of lowest oxygen concentrations are less than comparable areas off the southwestern Louisiana coast, on the Texas shelf, and in the Chesapeake Bay mainstem and tributaries (Rabalais et

al., 2001b). Abundances of macroinfauna, primarily opportunistic polychaetes, increase in the fall following the dissipation of hypoxia, but the numbers of individuals can be only slightly greater than the summer depressed fauna and result in no or a negligible increase in biomass. Fewer taxonomic groups characterize the severely affected area throughout the year. Long-lived, higher biomass and direct-developing species are never members of the severely affected community. Suitable feeding habitat (in terms of severely reduced populations of macroinfauna that may characterize substantial areas of the seabed) is thus removed from the foraging base of demersal organisms, including the commercially important penaeid shrimps.

Murrell and Fleeger (1989) surveyed the meiofaunal assemblages at three shallow stations (8–13 m) over an annual cycle, including severe hypoxia in the summer. Total meiofaunal abundances increased through spring and ranged from approximately 800 to 3800 $\mathrm{ind\,10\,cm^{-2}}$ before a hypoxic event. Following hypoxia there were dramatic declines in abundance and diversity of major meiofauna taxa (Murrell and Fleeger, 1989). Benthic harpacticoid copepods were least tolerant to low oxygen, while nematodes and kinorhynchs were less affected. Copepods declined from high values of 100–410 to zero $\mathrm{ind\,10\,cm^{-2}}$ when hypoxia developed. Nematode abundance ranged from 600 to 3100 $\mathrm{ind\,10\,cm^{-2}}$ before hypoxia and from 500 to 1100 $\mathrm{ind\,10\,cm^{-2}}$ after hypoxia. There was clear evidence from settlement traps deployed in the area of hypoxia that nematodes migrated into the water column away from hypoxic sediments and settled to the sediments with the return of normoxic conditions (Wetzel et al., 2001). These same settling traps provided evidence that the polychaete *Paraprionospio pinnata* delayed settlement and remained in the water column until oxygen values returned to a level above $2.0\,\mathrm{mg\,L^{-1}}$ (Powers et al., 2001).

At oxygen values below $0.2\,\mathrm{mg\,L^{-1}}$ but above anoxia ($0\,\mathrm{mg\,L^{-1}}$), various sized patches of "cottony" *Beggiatoa* mats cover the sediment surface on the Louisiana shelf. Filaments of the bacteria *Beggiatoa* and other unidentified filamentous bacteria form on the surface of the sediments at oxygen levels up to $1\,\mathrm{mg\,L^{-1}}$ (L. Duet, Q. Dortch, N. Rabalais, unpublished data). The obvious *Beggiatoa* mats, observed by ROV video and divers, are present at oxygen concentrations $<0.2\,\mathrm{mg\,L^{-1}}$. Similar bacterial mats were observed by divers on the inner shelf off Freeport, Texas in June 1979 following a severe hypoxic event (Harper et al., 1981).

2.3.6 Benguela shelf, West Africa

The Benguela shelf, extending to 350 m, is among the deepest in the world outside Antarctica (Shannon, 1985). There are three distinct regimes with respect to oxygenation and sulfide production: the inner shelf with extremely oxygen-depleted bottom waters, the oxygen minimum zone on the outer shelf and upper continental slope, and

the better oxygenated continental slope (below the OMZ) (Brüchert et al., 2003). The Luderitz upwelling cell divides the outer shelf and slope into a northern region, characterized by oxygen minimum waters and a better oxygenated southern zone. Sanders (1969) conducted seminal work on macrofaunal diversity along a transect from Walvis Bay (100 m) to the open ocean (2140 m). He documented a 100-fold increase in density between 100 m and 200–300 m water depths and a 10-fold increase in diversity as oxygen shifted from just under 2% saturation to 11–15% saturation (Sanders, 1969). Most studies of the Benguela benthic ecosystem response to hypoxia conducted since that time focus on fisheries species (Sakko, 1998) or sediment microbiology (Schulz and de Beer, 2002; Brüchert et al., 2003).

Recent investigations have revealed that the central Benguela outer shelf experiences significant oxygen variability, driven by advection over both seasonal and interannual time scales (Monteiro et al., 2006, 2008; Monteiro and van der Plas, 2006; Brüchert et al., 2006, Mohrholz et al., 2007). The relatively better oxygenated Cape Basin South Atlantic central water and the warm, saline hypoxic Angola Basin Central water provide opposing biogeochemical influences that mix on the shelf after upwelling at Cape Frio and Lüderitz. Hypoxia intensifies from December to May when the poleward flow of the equatorial current strengthens and peaks in June and July due to contributions from in situ oxygen consumption. This seasonality has been intensifying due to warming trends (Monteiro et al., 2008). Interannual variability is also strong, with Benguela Niños shifting the hypoxic boundary vertically, and driving hypoxia to persistent anoxia on the central Benguela shelf (Monteiro et al., 2006). The shape of the shelf has a large influence on the sources and tempo of physical forcing by regulating influence of the ocean-shelf boundary and regional wind-stress driven advection.

Fish assemblages change along latitudinal and depth gradients on the Benguela shelf. The oxygen-depleted central inner shelf (to depths of approximately 150 m) is populated almost exclusively by the goby *Sufflogobius bibarbatus*, but diversity is much higher on the outer shelf (150–300 m) where hake and horse mackerel are found in bottom waters. Squid and cuttlefish are present to the south where oxygenation improves (Sakko, 1998). Benthic ostracods also show low diversity in the north and higher diversity to the south, corresponding to differences in water mass oxygenation (Dingle et al., 1995). Decapod crustaceans typically avoid low oxygen. The portunid *Bathynectes piperitus* avoids the low oxygen concentrations on the shelf but aggregates just below the OMZ at 300–400 m (Abello and Macpherson, 1989). Such aggregations, observed in crabs, shrimp and ophiuroids on different margins, appear to be a common feature of lower OMZ boundaries (Levin, 2003).

Biomass spectra of fishes reveal greater abundance of small species with rapid turnover rates, lower community diversity, reduced importance of elasmobranchs, and declining biomass in the central, most productive shelf areas, relative to less productive regions (Macpherson and Gordoa, 1996). Although oxygen is not mentioned by these authors, it almost certainly is a key agent producing these patterns. The dynamics of hake populations on the shelf and slope are driven largely by oxygen. The two prevalent hake species have different habitat preferences and tolerances to low oxygen; this is reflected in their temporal variability. *Merluccius paradoxus* moves N and S with the better-oxygenated Cape Basin central water. This species resides at the boundary between the equatorial and Cape Basin waters, retaining some access to oxygen but gaining protection from less hypoxia-tolerant predators (Monteiro et al., 2008). In contrast, *M. capensis* resides on the shelf and through physiological adaptation tolerates relatively lower oxygen. Severe oxygen limitation causes massive biomass fluctuations in this species rather than a redistribution of the population (Monteiro et al., 2008)

The inner Benguela shelf (to 100–125 m water depth) is distinct in having muddy, diatomaceous sediments rich in opal and organic carbon that accumulate at high rates due to elevated productivity. There are measurable sulfide fluxes to the water column, and sediments are also sulfidic (Brüchert et al., 2003). Overlying water is often hypoxic or anoxic with oxygen depletion resulting from in situ degradation of organic matter combined with periodic advection of low oxygen Angola current water. Hypoxic conditions ($<0.5 \, \mathrm{ml \, L^{-1}}$) cover almost 4700 km^2, which is 55% of the total shelf, whereas extreme anoxia (oxygen concentrations less than 1 μM ($=0.023 \, \mathrm{ml \, L^{-1}}$)) occurs over almost 900 km^2, roughly 10% of the total shelf area (Brüchert et al., 2006). There is some disagreement about the extent to which water column oxygen levels on the inner shelf are regulated by sedimentary processes versus external forcing. Both seasonal and decadal variability in oxygen on the shelf are attributed to the influence of external hypoxic boundary conditions (van der Plas et al., 2007; Monteiro and van der Plas, 2006). However, the close match between the combined sediment and water column oxygen consumption versus primary production on the inner shelf supports local, sedimentary regulation (Brüchert et al., 2006).

High rates of sulfate reduction occur within inner shelf sediments (Brüchert et al., 2003) and when sulfate is depleted, methanogenesis occurs. Sulfide removal is bacterially mediated by large, sulfide oxidizers, including *Beggiatoa* spp. and *Thiomargarita namibiensis* (Schulz and de Beer, 2002). However, both methane and sulfide may accumulate as free gas and emerge in small quantities, creating pockmarks (Emeis et al., 2004), or as massive, episodic eruptions, generating a toxic water column (Weeks et al., 2002, 2004; Ohde et al., 2007). Unlike *Beggiatoa* spp., *T. namibiensis* is not obligately microaerophilic, and can survive during outgassing events that bring them into contact with oxygenated waters (Schulz and de Beer, 2002).
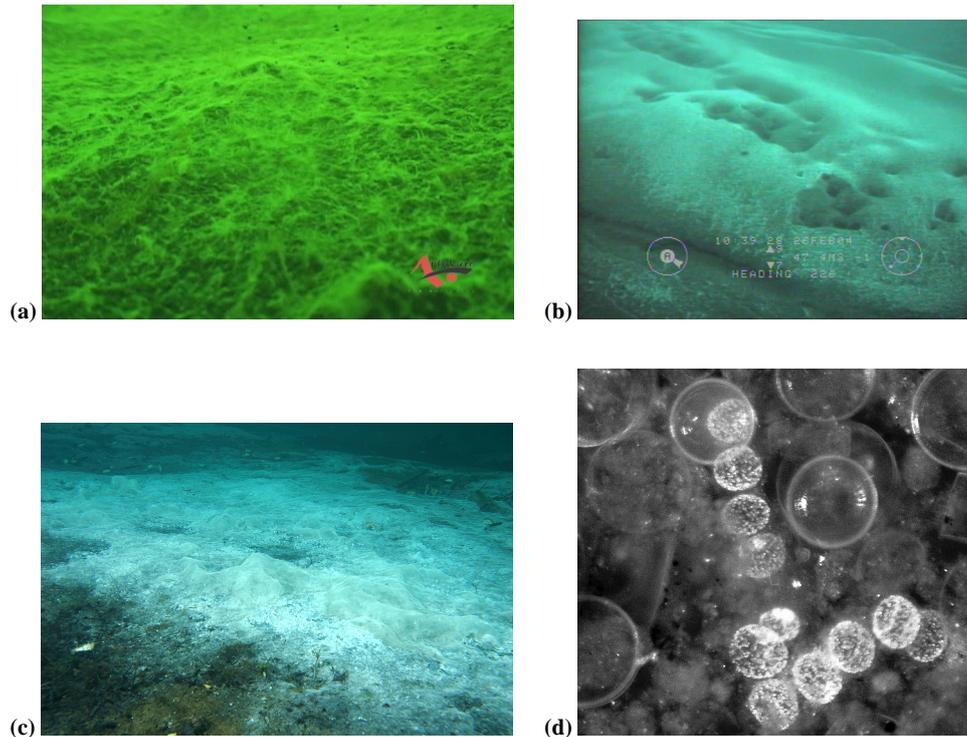
Fig. 4. Bacterial mat formation in coastal waters. **(a)** *Thioploca* mat, Concepcion Bay, Chile (10 m), Photograph by Sergio Nuño, **(b)** Bacterial mat (*Beggiatoa* and *Thiomargarita*), Namibia inner shelf (47 m, 22°58.7 S 14°22.1 E, February 2004), Note the pitting from escaped methane gas. Photograph by R. Bahlo (Institut für Ostseeforschung Warnemünde). **(c)** *Beggiatoa* mat, New Zealand Fjord (5–10 m) Photograph by S. Wing. **(d)** *Thiomargarita namibiensis* against a backdrop of centric diatom frustrules, from the Namibia shelf at 100 m (19°48.8 S 12°46.4 E, May 2008).
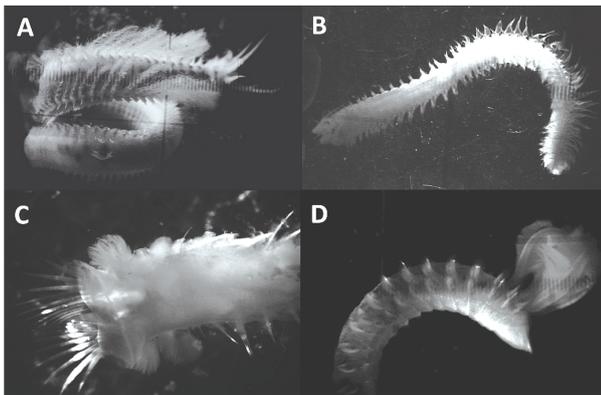

Fig. 5. Elaborate gills and branchiae on polychaetes associated with microbial mats on the Namibian inner shelf. **(a)** *Diopatra* sp.; note long spiral branchiae **(b)** Nereidae; note posterior branchial proliferations **(c)** *Pectinaria* sp.; note anterior gill filaments **(d)** *Paraprionospio* sp.

Off northern Namibia the OMZ (80–120 m) assemblages are dominated by large aggregations of the molluscs *Nassarius vinctus* and *Nuculana bicuspidata*; together these form 73% of the macrofauna >1 mm. Species richness is reduced relative to inshore areas (Zettler, 2009). Further south, large areas of the inner shelf are covered by extensive sulfur bacterial mats (Fig. 4b). Here the benthic fauna of the inner shelf ecosystem include spionid, onuphid, pectinarid, hesionid, sigambrid and nereid polychaete species along with nematodes (B. Currie, unpublished data). All have elaborate branchial proliferations (Fig. 5) and most are associated with *Beggiatoa* and *Thiomargarita* mats. The bearded goby (*Sufflogobius bibarbatus*) is the only fish abundant in the mat-covered sediments, and shows remarkable capacity to tolerate anoxia (Palm et al., personal communication). The bacteria, especially the *Beggiatoa*, are capable of removing most of the sulfide using nitrate as an electron acceptor (Schulz and de Beer, 2002; Brüchert et al., 2006). Thus the microbial mats act to detoxify the sediment, permitting the goby to use the benthic habitat as a predator refuge, and providing both the goby and the invertebrates with a low sulfide (but oxygen-depleted) habitat. The gobies migrate to oxygenated waters and feed diurnally (O'Toole, 1978), providing key
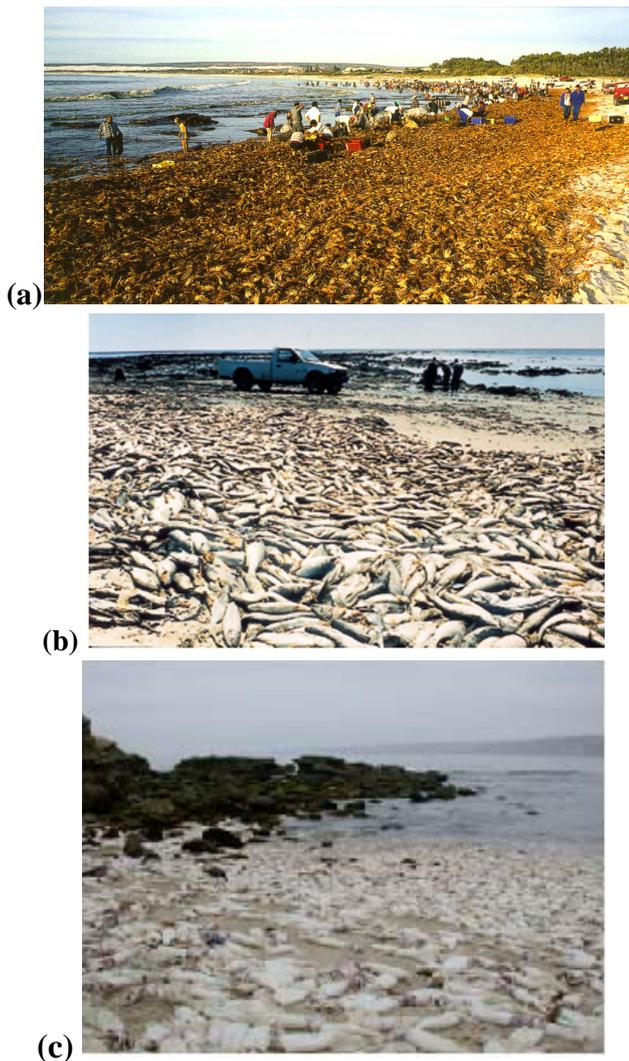
Fig. 6. Mass mortalities. **(a)** Rock lobster walkout in April 1997 at Elands Bay, South Africa, following water column anoxia induced by decay of a bloom of *Ceratium furca*. Elands Bay, South Africa. Photo by G. Roland Pitcher **(b)** Massive fish mortality associated with hydrogen sulfide production following anoxia induced by decay of *Ceratium furca* and *Prorocentrum micans*, March 1994, St. Helena Bay, South Africa. Photo by G. Roland Pitcher. **(c)** Humboldt squid (*Dosidicus gigas*) swimout on the La Jolla, California shoreline. Photo by Lisa Levin. Similar wash ups have occurred on the Oregon shoreline in 2004 and 2008. The role of hypoxia is uncertain.

food for hake, seabirds and seals in the ecosystem (Crawford and Dyer, 1995; Cury and Shannon, 2004; Palm et al., personal communication).

In general, diversity of intertidal and subtidal benthic algae and invertebrates decreases from the southern to the northern part of the Benguela shelf (Saako, 1998). Pelagic hydrozoans and scyphozoans have recently increased in abundance on the Benguela shelf, possibly in response to reduced abundance of clupeid fishes (Bakun and Weeks, 2006) or in response to eutrophication or climate change. In Walvis Bay they prey extensively on bottom organisms and on larvae of benthic invertebrates and thus are considered part of the benthic ecosystem (Flynn and Gibbons, 2007).

Water column sulfur patches on the Namibian coast are detectable by satellite; these may persist between 1–6 days and extend up to 21 km (Ohde et al., 2007). Seasonal mortality of fishes in Walvis Bay, and the possible involvement of algal blooms, were noted very early by Copenhagen (1953). Algal blooms contribute to oxygen depletion and hasten sulfide and methane eruptions. Mass migrations and/or mortality of cape hake (*Merluccius capensis*) in response to shifting oxygenation was recorded in the 1990s (Hamakuaya et al., 1998) and up to the present (Fig. 6b) (Monteiro et al., 2008). One of the most dramatic responses of inshore species to hypoxia and sulfide events in the Benguela system involves the activities of rock lobsters (*Jasus lalandii*). They aggregate inshore (within a mile of shore) where the surf oxygenates the water (Baily et al., 1985) and under extreme conditions will "walk out" (migrate) onto the shore in mass strandings (Fig 6) that lead to extensive mortality over days to a month. Recovery time varies with the area affected and whether hydrogen sulfide was produced (Cockcroft, 2001).

2.3.7 Pakistan shelf – Arabian Sea

The Pakistan shelf is subject to seasonal, monsoon-driven hypoxia. An order of magnitude drop in oxygen (from 2.12 to 0.11 ml L^{-1}) was observed on the outer Pakistan shelf (140 m) between pre-monsoon and late southwest monsoon periods in 2003, reflecting an upward shoaling of the OMZ. This was accompanied by a 4.1°C drop in temperature and a 0.4 reduction in salinity, due to either a shoaling of the thermocline or possibly contributions from a northward extension of the West India Undercurrent (Brand and Griffiths, 2009). A low-diversity foraminiferal assemblage (>300-μm fraction) is present at this site, consisting mainly of calcareous species (60%) that are largely restricted to the upper 1 cm. Foraminiferal densities increased at this shelf site and in the OMZ core at 300 m (0.09 ml L^{-1}) following the 2003 southwest monsoon, largely as a result of population increases in the phytodetritus-consuming *Uvigerina* ex. gr. *semiornata* (Larkin and Gooday, 2009). The macrofaunal community structure at 140 m exhibited little response to the southwest monsoon and concomitant oxygen decline. No significant changes in biomass, individual body size, number of polychaete families (21 vs. 25), H', J' and Rank 1 dominance were observed (Hughes et al., 2009). However, lower oxygenation was associated with a reduction in macrofaunal density, burrow counts, and number of polychaete species, with spionid and flabelligerid polychaete densities decreasing. Cirratulid polychaetes remained dominant (about 20% of the total polychaetes) (Hughes et al., 2009). Macrofauna

are extremely rare at 300 m where oxygen remains low and laminations persist (Hughes et al., 2009). Isotope enrichment studies tracking the fate of ^{13}C-labeled phytodetritus at 140 m demonstrated a strong shift in C processing pathways, with macrofauna responsible for most of the non-bacterial ^{13}C consumption during oxygenated conditions and protozoans (Foraminifera) responsible at 0.11 mL L^{-1} (Woulds et al., 2007, 2009). Additional tracer experiments show corresponding differences in metazoan vs protozoan C consumption in comparison with the better oxygenated (940 m; 0.2 ml L^{-1}) and poorly oxygenated (300 m; 0.09 ml L^{-1}) sites on the Pakistan margin, suggesting oxygen thresholds influence C cycling pathways (Woulds et al., 2007, 2009).

2.3.8 West Indian Shelf – Arabian Sea

The outer Indian shelf and slope are affected by the flow of the West India Undercurrent that is slightly better oxygenated than the waters it mixes with, thus preventing bottom waters over the outer shelf and slope from turning anoxic at least to the south of Goa (15° N). Nevertheless, the OMZ is still quite well-developed in the region throughout the year (Naqvi et al., 2006). Mazumder et al. (2003) observed high abundance of benthic Foraminifera belonging to the genera *Bolivina*, *Cassidulina*, *Lernella*, *Uvigerina* and *Eponides* in surface sediments exposed to the OMZ (depth 150–1500 m) off Goa. Interestingly, *Bulimina marginata*, which is abundant in other OMZs, accounted for only about 2% of the total benthic foraminiferal population in this region; instead, *Bulimina costata* constituted more than 15% of the total Foraminifera. Nigam et al. (2007) observed high abundance (>40% of benthic Foraminifera) of rectilinear benthic Foraminifera (RBF; e.g., *Bolivina, Brizalina, Uvigerina*) within the 90–1200 m depth range in the same region, and proposed that the increased abundance of RBF may be used as an indicator of oxygen-depleted conditions in the Arabian Sea.

Hypoxia (and anoxia) on the West India inner shelf exhibits pronounced seasonality due to upwelling associated with southward movement of the West India coastal current during the southwest monsoon. From July to November subsurface oxygen concentrations over the inner and mid-shelf regions are <10 μM (<0.23 ml L^{-1}). Upwelling of nutrient-rich subsurface waters fertilizes the euphotic zone, increasing oxygen demand while a lens of low-salinity water (from rainfall) maintains stratification and reduces ventilation. Sustained observations off Goa show that denitrification becomes the dominant metabolic pathway in mid-summer (July–August) resulting in a removal of NO$_3^-$ and the accumulation of intermediates NO$_2^-$ and N$_2$O, followed by sulfate reduction sometime in September, as evident from the buildup of H$_2$S and NH$_4^+$ in the bottom waters (Naqvi et al., 2006). The intensity and duration of anoxia varies annually. The oxygen-deficiency is most intense along the central west coast (the Konkan coast) that receives maximal SW

monsoon precipitation, and it is less intense south of about 12° N (the Malabar coast). The latter region, however, experiences massive dinoflagellate or coccolithophorid blooms during the SW monsoon (Naqvi et al., 1998; Ramaiah et al., 2005). Upwelled water reaches the surface along the Malabar coast more often than it does along the Konkan coast because of a more important role of local wind forcing, resulting in greater eutrophic zone nutrient enrichment and better subsurface ventilation. There is evidence that the extent of hypoxia has increased over the last 40 years and that H$_2$S production is most likely a recent phenomenon. This change corresponds to a 46-fold increase in N use by South Asian countries as synthetic fertilizer over the same time period (Naqvi et al., 2006).

Few quantitative data document benthic responses to hypoxia on the inner Indian shelf, although the paucity of organisms was noted as early as 1959 by Carruthers et al. (1959) off Bombay. Surface sediments off Goa show the presence of numerous shells but not live bivalves (B. Ingole, unpublished data) supporting an intensification of oxygen deficiency in the recent past. No dense mats of sulfur bacteria, as occur off Chile or Namibia, have been noted on the inner west Indian Shelf, possibly due to lack of free sulfide. Measured sulphate reduction rates are anomalously low in the inner-shelf sediments (Naqvi, unpublished). *Thioploca* are present elsewhere in the Arabian Sea at deeper depths (Levin et al., 1997; Schmalljohan et al., 2001).

An experimental study by Panchang et al. (2006) involved incubating sediment cores, collected from the mid-shelf (depth 50 m) in the Konkan region, under near in situ temperature-salinity conditions but with varying overlying-water oxygen levels (fully oxygenated to almost completely oxygen depleted). The experiments revealed that changes in overlying-water oxygen levels (from an initial concentration of 68 μM$\approx$1.54 ml L^{-1}) invariably resulted in a decrease in foraminiferal counts. In the natural environment, living Foraminifera were confined to the upper 5 cm of sediments with the most common genera in order of decreasing abundance being *Fursenkoina, Nonion, Rotalia* and *Reophax,* with *Bulimina, Cancris, Ammotium* and *Globobulimina* also present in smaller numbers. *Fursenkoina* and *Nonion* were found to be more tolerant of changes in oxygen than bolivinids and rotaliids. Experimental results implied strong seasonality in the vertical distribution, species composition and counts of Foraminifera (Panchang et al., 2006)

In addition to the afore-mentioned peak in RBF in the outer shelf-slope region that is exposed to the open ocean OMZ, Nigam et al. (2007) documented a secondary peak in RBF at 50–60 m off Goa, where they form over 78% of the benthic Foraminifera. This *Bolivina-Bulimina*-dominated assemblage is indicative of organic enrichment, as a similar assemblage occurs in sediments overlain by oxygenated waters on the Florida continental shelf (Sen Gupta et al., 1981). The macrobenthos in the same region show elevated dominance and reduced species richness at this depth (Jayaraj et al.,

2007) although oxygen levels were high during winter sampling. Macrobenthic densities were unusually low at 30 m, which falls within the zone of seasonal sulphate reduction (Naqvi et al., 2006). Among polychaetes, three species in the spionid genus *Prionospio*, cirratulids (*Cirriformia afer*), *Cossura coasta* and *Sternaspis scutata* are abundant on the inner shelf (<50 m). These deposit feeders are replaced by more carnivorous species including *Lepidonotus carinulatus, Ancistrosyllis constricta,* and *Syllis spongicola*, as well as by *Amphicteis gunneri*, *Notomastus aberrans* and *Cirratulis cirratus* on the outer shelf (>100 m). Dissolved oxygen was found to be a contributing but not overriding factor controlling assemblage structure (Jayaraj et al., 2007). Many of the inshore regions exhibit poor water quality due to extensive domestic and industrial waste disposal; very low dissolved oxygen occurs post monsoon in fall, which is mainly due to anoxia developing along the open coast. *Prionospio pinnata* is dominant in these open coastal areas when oxygen declines to 2 ml L^{-1} or lower (Varshney et al., 1988).

Demersal fish and shellfish species disappear seasonally from the outer shelf off Cochin (along the Malabar coast), and often aggregate in estuarine waters along the west coast. Solar prawns (*Metapenaeus dobsoni*) are caught in large quantities during such events. Critical oxygen levels for the dominant fish *Synagris japonicus*, expected to be most tolerant to hypoxia, are 0.25–0.50 ml L^{-1} (Banse, 1959)

Inner- and mid-shelf hypoxia is distinct from the deeper offshore suboxic zone, in part due to the presence of the above-mentioned better oxygenated West India Undercurrent, which flows along the continental margin between the two systems. Sometimes during anoxic inner shelf events, fish appear to aggregate on the outer shelf, as intense trawling is observed. At other times fish kills occur when escape from anoxic waters is not possible. The demersal fish catch along the west coast has undergone large fluctuations over the past decade, apparently related to changes in bottom-water oxygen and H$_2$S levels. The conditions were most severe in 2001, when the temperature of the upwelled water was lowest, and the prawn fishery nearly collapsed. The landing in Goa, for example, fell by a factor of ten, as H$_2$S was present at depths up to 65 m (Naqvi et al., 2009). However, a recovery to the "normal" level has since occurred (especially after 2005). Although H$_2$S is still present, the duration of complete anoxia is shorter than in the early 2000s.

2.3.9 East India shelf – Bay of Bengal

The East Indian shelf in the Bay of Bengal is not subject to hypoxia at very shallow depths as happens in the Arabian Sea, despite intense river runoff. Weaker upwelling and limited DIN loading are believed to be responsible (Naqvi et al., 2006). Despite the consequently lower primary productivity of the Bay of Bengal, the biomass and population density of benthic organisms over the eastern and western shelves of India are similar, although most of the data were gener-

ated before the intensification of hypoxia over the western shelf (Ansari et al., 1977; Ansari et al., 1982; Parulekar et al., 1982). The density of infauna is especially high close to river mouths [meiofauna: 226–967 10 cm^{-2}; macrofauna: 90–4785 m^{-2}; Ansari et al., 1982]. Among the various taxonomic groups of macrobenthos, polychaetes, bivalves and crustaceans were the most abundant. The meiobenthos is dominated by Foraminifera and nematodes followed by polychaetes and ostracods (Ansari et al., 1977, 1982; Parulekar et al., 1982).

Below the surface mixed layer (which is deeper over the eastern Indian shelf), as in other parts of the North Indian Ocean, oxygen declines sharply from saturated values to concentrations between ~0 and 0.5 ml L^{-1} at depths of 150–200 m. Recent investigations on the shelf between 16° and 20° N reveal steep drops in macrofaunal diversity (H') and evenness (J') and a rise in dominance ($> 90\%$), mirroring oxygen declines across the shelf. These also parallel a rise in sediment organic matter content up to 6% TOC on the outer shelf. At oxygen concentrations below 0.10 ml L^{-1}, the polychaetes *Prionospio* sp. and *Cossura coasta*, and nemerteans comprise most of the macrobenthos (Raman and Rao, unpublished data).

3   Synthesis: general benthos responses to hypoxia

The sections below summarize general hypoxia responses of different benthic size or taxonomic groups. Table 1 provides an overview of the characteristic genera and species common to hypoxic regions around the world and Table 2 summarizes the community-level responses across major size groups. We attempt to assess whether the cause of hypoxia (human vs natural) affects these responses, but caution that often interactions between the two types of forcing as well as site-specific environmental differences prevent a clear assessment of this issue.

3.1   Mat-forming microbes

Microbial responses to hypoxia are intimately tied to geochemistry, in both sediments and the water column. Although this review does not treat these interactions (see Middelburg and Levin, 2009), we consider mat-forming microbes to be a fundamental macroscopic feature of benthic ecosystems subject to severe hypoxia. These mats are formed largely of filamentous sulfide oxidizing bacteria in the genera *Beggiatoa*, *Thioploca,* or *Thiomargarita*, although sulfate reducing and methane oxidizing bacteria are often intermixed (Graco et al., 2004; Ding and Valentine, 2008). Primary differences among the dominant genera involve the presence of a sheath and multiple filaments (*Thioploca*) or bead-like construction (*Thiomargarita*), and their ability to function in the presence or absence of oxygen (Jørgensen and Gallardo, 1999; Brüchert et al., 2003, 2006). All are capable

Table 1. Characteristic fauna of hypoxic coastal settings. See text discussions for citations.

Location	Mat-Forming Microbes	Foraminifera	Polychaetes	Molluscs	Crustaceans	Other Invertebrates	Fishes	Notable Phenomena	Exacerbating Factors
Seasonal									
Louisiana Shelf	*Beggiatoa*	*Pseudononion atlanticum, Epistominella vitrea, Buliminella morgani* (mid shelf); *Ammonia parkinsoniana* (inner shelf)	*Ampharete, Magelona* tolerant through hypoxic months, *Paraprionospio pinnata, Mediomastus ambiseta, Sigambra tentaculata*, at initiation and end of hypoxia			*Aspidosiphon* sp. (Sipuncula)		Hypoxia is a summer phenomenon, areal cover of hypoxia varies each summer. Hurricanes reduce hypoxic area.	Nutrient inputs from the Mississippi River watershed
Chesapeake Bay		*Ammonia parkinsoniana* (*Elphidium selseyensis, Ammobaculites exiguus* intolerant)	*Paraprionospio pinnata, Polydora ligni, Streblospio benedicti, Mediomastus ambiseta, Leitoscoloplos fragilis, Glycinde solitaria, Eteone heteropoda Asabellides oculata.*	*Mulinia lateralis*	Ostracod - *Cytheromorpha curta*		Spot (*Leiostomus xanthurus*), Croaker (*Micropogonias undulatus*)	Habitat compression of fishes, prey behavior enhances food for fishes, oyster reef loss with cascading effects on community and trophic structure. Loss of biomass, biodiversity and long-lived macrofauna	Eutrophication, overfishing (oysters)
Changjiang Estuary & Inner Shelf			*Glycera chirori*	*Thyasira tokunagai*	*Callianassa japonica*		*Trichiurus lepturus, Larimichthys polyacti* and *Portunus trituberculatus*	Macro and meiofaunal density drops in hypoxic area, aggregations of megafauna at edges. Collapses of benthos and conversion to pelagic system	Eutrophication, invasions via ballast water
Scandinavian and Scottish fjords		*Stainforthia fusiformis, Spiroplectammina biformis, Bulimina marginata*	*Heteromastus filiformis, Melinna cristata, Spiophanes kroyeri, Capitella capitata, Scalibregma inflatum* (fish farms)	*Abra nitida, Thyasira equlis. Thyasira sarsi*		*Amphiura chiajei, A. filiformis* (Ophiuroidea)		Limited flushing increases influence of human activities, mussels can exacerbate hypoxia	pulp mill, aquaculture, sewage inputs
Chilean Shelf	*Thioploca* spp.		*Paraprionospio pinnata, Mediomastus branchiferus, Aricidea pigmentata, Nephtys ferruginea* and *Cossura chilensis*					ENSO cycles modify seasonal patterns. El Niño improves oxygenation, attenuating seasonality and favoring larger, deeper-dwelling taxa	La Niña
Peru Shelf, Ancon Bay 15 m			*Owenia collaris, Magelona phyllisae, Chaetozone* sp. and *Phoronis* sp.		*Ampelisca araucana*				
Pakistan shelf, 140 m	*Thioploca* spp.	*Uvigerina semiornata*	Cirratulidae and Spionidae dominant					Seasonal, order of magnitude decline in oxygen following SW monsoon, corresponds to density declines in Spionidae and Flabelligeridae	
W. Indian Inner Shelf			*Prionospio, Cirriformia afer, Cossura coasta, Sternaspis scutata*		*Metapenaeus dobsoni*		*Synagris japonicus*	Monsoon driven upwelling, seasonal sulfide exposure	Atmospheric nutrient enrichment, domestic and industrial waste disposal
W. Indian Outer shelf		Rectilinear bi- and tri-serial taxa (e.g. *Bolivina* and *Bulimina, Fursenkoina*)	*Prionospio pinnata, Lepidonotus carinulatus, Ancistrosyllis constricta, Syllis spongicola, Amphicteis gunneri, Notomastus aberrans* and *Cirratulis cirratus*						
Benguela Outer Shelf							*Merluccius paradoxus, M. capensis*	Benguela Niños can move the system from seasonal to persistent hypoxia	Ocean warming trends may be intensifying seasonality
Japanese Bays		*Ammonia beccarii, Trochammina hadai, Eggerella advena, Uvigerinella glabra.* Also *Virgulinella fragilis* in sulphidic habitat (Namako-ike, Japan)			Ostracods- *Bicornucythere bisanensis, B.* sp., *Cytheromorpha acupunctata, Loxooconcha viva*				
Permanent									
Black Sea		*Ammonia*, Monothalamous taxa including *Psammophaga*	*Protodrilus* sp. and *Victorniella zaikai*	*Mytilus gallo-provincialis*				Mussels keep phytoplankton blooms in check. Loss of mussels led to cascade, shift to domination by comb jellies *Mnemiopsis leydi*	Overfishing, species invasion
Baltic Sea			*Scoloplos armiger, Capitella* sp., *Pygospio elegans*	*Macoma baltica*	*Saduria entomon, Diastylis rathkei* and *Pontoporeia femorata.* Ostracods *Cyprideis torosa, Heterocyprideis sorbyana, Candona neglecta*	*Halicryptus spinulosus* (Priapula)			Eutrophication
Peru, Ancon Bay (34 m and below)			*Paraprionospio pinnata, M. phyllisae, Chaetozone* sp. and *Leitoscoloplos chilensis*					El Niño improves oxygenation and leads to colonization by scallops, octopus and whelks	
Benguela Inner Shelf	*Beggiatoa, Thiomargarita namibiensis, Thioploca*	*Virgulinella fragilis* occurs in Walvis Bay, Namibia. Characteristic species for sulphidic environments (Tsuchiya et al., 2008)	*Diopatra* sp., *Paraprionospio* sp. *Nephtys* sp., *Sygambra* sp., *Pectinaria* sp., Hesionidae	*Nassarius vinctus Nuculana bicuspidata*	*Bathynectes piperitus*		*Sufflogobius bibarbatus*	Eruptions of hydrogen sulfides create anoxic water columns and gas release visible from satellites. Microbial mats are capable of consuming much of the slow sulfide flux	Algal blooms occur coincident with hypoxia. Lobster 'walkouts' generate mass mortality of a key fisheries species

Table 2. Summary of benthic community responses to severe coastal hypoxia.

Attribute	Microbial Mat	Foraminifera	Metazoan Meiofauna	Macroinfauna	Megafaunal Invertebrates	Demersal Fish and Shellfish
Abundance	High	High	High	Reduced	Reduced	Reduced
Biomass	High	Reduced	Reduced	Reduced	Reduced	Reduced
Body Size	Large	Small, thin walled	Small, some large in the OMZ	Reduced		Reduced
Dominant (Hypoxia-tolerant) Taxa	*Beggiatoa*, *Thioploca*	Hyaline, calcareous forms	Nematodes	Annelids (Spionidae, Capitellidae, Magelonidae), Sipunculans, Priapula	Cnidarians, Ophiuroids (OMZ)	Gobies (Namibia), hogchoker (Chesapeake Bay)
Species Richness		Reduced	Reduced	Reduced	Reduced	
Evenness		Reduced	Reduced	Reduced	Reduced	
Dominance		High	High	High	Mostly intolerant	Mostly intolerant
Behavior	aggregate at sediment surface	Shallow dwelling in sediments	Migrate upward within sediments	Migrate to surface, reduced dwelling depths, suface feeding	Move away, emerge from sediments, Evisceration, depart from shell	Swim away/Avoidance, Impaired reproduction
Functional effects	Sulfide removal, dominate C flow	Dominate C cycling	Reduced micro-scale bioturbation, C processing	Reduced bioturbation, C processing		
Recovery following hypoxia	Disappear	Rapid	Rapid	Mixed	Slower	Mixed

of using nitrate as an electron acceptor. Biomass of these mega-bacteria can be unusually high; *Thioploca* reaches 120 g wet wt m^{-2} (Gallardo, 1977) and *Thiomargarita namibiensis* reaches 47 g wet wt m^{-2} (Shulz et al., 1999). Mats of *Thioploca* form permanently on the Peru shelf and seasonally off central Chile, as well as on the upper slope of Oman and Pakistan (Jørgensen and Gallardo, 1999) and off Namibia (Gallardo et al., 1998). However, *Beggiatoa* and *Thiomargarita* are the primary mat-forming taxa on the inner Namibian shelf (Schulz et al., 1999; Brüchert et al., 2003, 2006).

Thioploca mats appear to be more commonly characteristic of naturally occurring hypoxic systems associated with upwelling and high nitrate concentrations. In contrast, microbial mats caused by mass degradation of macroalgal or phytoplankton blooms in eutrophic settings (e.g. Graco et al., 2001; Glud et al., 2004) or of animals that have died in response to hypoxia in estuarine, inner shelf, and basin settings are most often formed by *Beggiatoa* and *Thiothrix*. Recently another diverse group of filamentous "macro" bacteria have been described from sulfidic shelf sediments in the eastern Pacific Ocean off Chile, Peru, Panama and Costa Rica. They appear to be sulfide oxidizers and can be associated with sheaths of *Thioploca*, but are an order of magnitude smaller, (i.e. 10 s instead of 100 s of microns in length) (Gallardo and Espinoza, 2007).

Many protozoans and metazoan animals live in association with mats of mega- and macro-bacteria, including some eukaryotes with symbiotic bacteria (Bernhard et al., 2000; Gallardo and Espinoza, 2007). An active hypothesis is that large mat-forming, sulfide- oxidizing bacteria detoxify sediment by removing sulfide, and thus facilitate metazoan habitation. In this regard, a positive correlation between *Thioploca* and meiofaunal biomass was observed on the central Chile shelf during non-El Niño conditions when *Thioploca* was abundant; after El Niño, when *Thioploca* declined, no relationship was found. Although this evidence does not verify a detoxification role for *Thioploca* mats, *Thioploca* presence is thought to have had a positive influence on meiofauna (Neira et al., 2001b). The different bacterial taxa exhibit differences in their sulfide removal capacity (Brüchert et al., 2006), but the extent to which

these differences control animal distributions, and whether they are related to the source of hypoxic conditions, requires further study.

3.2 Plants and algae

The response of benthic primary producers (seagrasses, macroalgae and microalgae) to eutrophication has been studied extensively (e.g. Duarte, 1995; Valiela et al., 1997). The current conceptual model involves a shift in dominance from seagrasses and perennial macroalgae to initially ephemeral bloom-forming macroalgae and epiphytes and ultimately to phytoplankton dominance. Eutrophication and hypoxia cause large benthic macrophytes with high biomass, high light requirements and low nutrient turnover to be replaced by small pelagic algae with lower light requirement, low biomass and high turnover (Duarte, 1995; McGlathery et al., 2007). This shift from benthic to pelagic primary producers has been attributed primarily to competition for light. Increasing nutrients stimulate phytoplankton with the consequence that underlying vegetation is shaded. Although the response of microphytobenthos (benthic microalgae and cyanobacteria) to nutrient addition has been studied extensively, there are few data on their response to eutrophication at an ecosystem scale. One would expect a decrease in microphytobenthos importance as a system becomes eutrophied because of shading by phytoplankton (Vadeboncoeur et al., 2003). However, benthic microalgae are adapted to photosynthesize in very low light levels, as low as 5–10 μE m^{-2} s^{-1} and 1% surface incident radiation (Sundbäck and Graneli, 1988; Cahoon et al., 1994). Their numbers are high below phytoplankton-shaded waters on the Louisiana continental shelf (Baustian, unpublished data).

The effect of hypoxic and anoxic waters on seagrasses has been studied extensively (Burkholder et al., 2007). Hypoxia impedes respiration and many metabolic functions including nutrient uptake by seagrasses (Smith et al., 1988). Although short-lived extreme events may result in seagrass shoot die-off, colonization by surviving seedlings may provide some resilience (Plus et al., 2003). The consequences of consecutive short-term hypoxic events need to be investigated. Bottom-water hypoxia, high organic carbon loading and lack of sediment reactive iron alone or in combination (Middelburg and Levin, 2009) may cause high concentrations of sulfide in sediments with adverse effects on seagrass functioning and survival (Burkholder et al., 2007).

Larson and Sundbäck (2008) experimentally investigated the effect of short-lived hypoxic events on microphytobenthos. They found that benthic microalgae can show high resilience after hypoxic events (i.e. high rates of recovery) and suggested that the recovery time is related to the duration of the hypoxic event. Montserrat et al. (2008) defaunated intertidal estuarine sediments by covering them with polyethylene sheets for 40 days causing anoxia in the sediments. Following removal of the sheets, microphytobenthos recovered

rapidly and showed extensive growth of cyanobacteria and diatoms. Extensive mats of microphytobenthos developed in one month, partly or perhaps mainly due to the absence of grazers. This high resilience of microphytobenthos has been attributed to the capability of these organisms to enter dormant stages, thereby minimizing respiration losses (Larson and Sundbäck, 2008).

3.3 Foraminifera

The interest of palaeoceanographers in developing proxies for palaeo-oxygenation and productivity, together with studies of oxygen minimum zones and hypoxic basins, have generated a substantial body of data on Foraminifera in naturally hypoxic systems (Sen Gupta and Machain-Castillo, 1993; Bernhard and Sen Gupta, 1999; Gooday et al., 2009). A fundamental problem in these studies has been to distinguish the effects of organic enrichment from those of oxygen depletion. Many of the changes in foraminiferal community structure and composition seen in hypoxic environments are likely to reflect changes in the quantity and quality of the organic matter supplies to the sea floor. Species that are less resistant to a shortage of oxygen begin to disappear only when oxygen concentrations fall below a critical level, possibly $\sim$0.5 ml L^{-1} or less, leading to reduced species richness and a change in species composition (Gooday, 2003; Jorissen et al., 2007). Some species are able to tolerate prolonged anoxia. Short-term tolerance of sulphide is also reported, based on experimental studies in which rose Bengal staining was supported by live observations (Moodley et al., 1998).

Foraminifera possess a number of ultrastructural and biochemical features which may help them to survive in extreme hypoxic/sulphidic environments (Bernhard and Sen Gupta, 1999). These include the presence of bacterial symbionts (Bernhard, 2003) and sequestered chloroplasts (Bernhard and Bowser, 1999), as well as peroxisomes that facilitate the respiration of oxygen derived from the breakdown of hydrogen peroxide (Bernhard and Bowser, 2008). In addition, at least some hypoxia-tolerant species are able to respire nitrate (Risgaard-Petersen et al., 2006). It should be remembered that the majority of Foraminifera live some distance below the sediment/water interface. Unlike most macro- and megafaunal organisms, which are in contact with bottom water, Foraminifera are surrounded by sediment pore water. As a result, species that live deeper in the sediment are exposed to hypoxic and anoxic micro-environments, even when the overlying bottom water is well oxygenated.

Reviews of Foraminifera in oxygen-depleted habitats are provided by Sen Gupta and Machain-Castillo (1993), Jorissen (1999), Bernhard and Sen Gupta (1999), Gooday (2003), Murray (2006), Jorissen et al. (2007), and Gooday et al. (2009). Assemblages typically exhibit a number of characteristics, which can be summarised as follows.

(1) As a group, Foraminifera are more tolerant of hypoxia than most metazoans. Their standing stocks are often

very high, probably reflecting a rich food supply combined with a scarcity of competitors and predators in these habitats (Phleger and Soutar, 1973; Phleger, 1976). In hypoxic areas where they are the most abundant eukaryotic organisms, Foraminifera dominate carbon uptake and cycling (Woulds et al., 2007, 2009).

(2) Although most Foraminifera tolerate fairly low oxygen concentrations, a relatively small number of genera and species dominate the assemblages in strongly hypoxic conditions. Elongate, sometimes flattened, biserial or triserial morphotypes (RBF, e.g. *Brizalina, Bolivina*) are often common, but a variety of spiral and other test shapes (e.g. *Cassidulina, Epistominella*) are also found (Bernhard and Sen Gupta, 1999; Jorissen et al., 2007). However, few Foraminiferal taxa or morphotypes are restricted to hypoxic environments (Sen Gupta and Machain-Castillo, 1993; Murray, 2001, 2006). An exception may be *Virgulinella fragilis,* which appears to be a sulfide specialist (Tsuchiya et al., 2008).

(3) Fauna of hypoxic settings are usually dominated by taxa with hyaline, calcareous tests (rotaliids, buliminids). In many cases, the tests are small and thin-walled. Agglutinated and organic-walled taxa are less common, although they are by no means absent (Gooday et al., 2000; Bernhard et al., 2006).

(4) In hypoxic environments, Foraminifera typically live close to the sediment-water interface. This applies even to taxa that live deeper in the sediment in well-ventilated settings, presumably because deeper layers have become too inhospitable. Some of the most tolerant species are considered to be deep infaunal species because they occupy microhabitats well below the sediment/water interface in sediments overlain by oxic seawater. However, in some areas, hypoxic assemblages are dominated by species with planispiral test morphologies, typical of niches close to the sediment surface. These taxa, which appear to be especially adapted to hypoxia at the sediment-water interface, are rare in well-oxygenated settings (Jorissen et al., 2007).

(5) The elimination of hypoxia-sensitive foraminiferal species leads to a reduction in species richness, while the abundance of a few hypoxia-tolerant species results in increased dominance. As a result, indices of species diversity that combine richness and dominance are depressed compared to more oxic environments (Gooday et al., 2000).

Much of our information about hypoxia-tolerant Foraminifera comes from bathyal settings where hypoxia occurs naturally, principally oxygen minimum zones, silled continental margin basins and fjords, and methane seeps (Bernhard and Sen Gupta, 1999). In most of these areas, hypoxic conditions have persisted for thousands and millions of years. Studies in shallower water have focused mainly on areas off major rivers, such as the North Adriatic (River Po) and the northern Gulf of Mexico (Mississippi River), where hypoxia is exacerbated by human influences (Van der Zwaan and Jorissen, 1991).

Since hypoxic conditions are mostly seasonal in coastal systems, the severity of oxygen depletion varies on a yearly and seasonal scale. In many cases, strong hypoxia persist for only short periods of time, which may be too short to cause the disappearance of the more sensitive species. It is therefore probable that the specific faunas of these areas are mainly a reflection of the strongly increased organic input, often with a large proportion of terrestrial components. An exception can be noted for the genus *Quinqueloculina*, which is hypoxia-intolerant and has disappeared from the foraminiferal community on the Louisiana continental shelf (Rabalais et al., 1996).

The species inhabiting these coastal and sublittoral areas are different from those found at bathyal depths; for example, deep infaunal species of *Globobulimina* and *Chilostomella* are generally absent. However, as in deeper-water settings, faunal composition changes with increasing eutrophication and hypoxia. Most miliolids disappear where hypoxia is severe (Platon et al., 2005). Species of *Ammonia*, which are very common in nearshore habitats, are particularly tolerant of eutrophic conditions whereas most species of another typical shallow-water genus, *Elphidium*, are much more sensitive. This contrast led Sen Gupta et al. (1996) to propose the ratio between the abundance of *Ammonia* and *Elphidium* (the "*Ammonia-Elphidium* index") as an indicator of hypoxia (see also Sen Gupta and Platon, 2006). Three other hyaline calcareous species, *Pseudononion atlanticum, Epistominella vitrea* and *Buliminella morgani*, flourish in low oxygen conditions on the Louisiana shelf and have been used as indicators (PEB index) of historic low oxygen in sediment core records (Osterman et al., 2003). These indices probably mainly reflect eutrophication, which is usually correlated with hypoxia.

Core records indicate that increased hypoxia/eutrophication leads to a depression in species richness and diversity in coastal and shelf areas (Nelsen et al. 1994, Platon et al., 2005), similar to that observed at upper bathyal depths (Gooday et al., 2000). Moreover, hypoxia, whether natural or human-induced, appears to impact foraminiferal assemblages in a similar way. For example, on the Louisiana shelf, Osterman et al. (2008) reported periodic peaks in the abundance of species tolerant to lower oxygen (the PEB index) extending back over the last 1000 years. These responses, which were presumably related to natural low-oxygen events fueled by terrestrial organic matter, resembled the rapid increase in the PEB index caused by the development of human-induced hypoxia since the 1950s in the same area. The current PEB index, however, is much higher than the periodic peaks in the >100 year record. In the Adriatic Sea, species typical of eutrophic conditions in front of the Po delta include *Nonionella turgida, Hopkinsina pacifica*, *Stainforthia concava* and several *Bolivina* species (Barmawidjaja et al., 1992; Jorissen et al., 1992). In a study on a sediment core taken off the Po delta, Barmawidjaja et al. (1995) tentatively explained the relative increase of these

taxa starting in the 1960s as a response to the appearance of seasonal hypoxia in this area.

3.4 Metazoan meiofauna

Ecological studies on effects of hypoxia and anoxia on metazoan meiofauna are limited (Diaz and Rosenberg, 1995). Several field studies have demonstrated the sensitivity of metazoan meiobenthic animals to bottom-water hypoxia (e.g. Coull, 1969; Elmgren, 1975; Josefson and Widbom, 1988; Murrell and Fleeger, 1989; Moodley et al., 1997). The general consensus is that meiofaunal taxa are less affected by hypoxia than macrofauna and megafauna (e.g. Elmgren, 1975; Josefson and Widbom, 1988; Levin et al., 2002). Meiofauna also seem to be less sensitive to physical disturbance and destabilization of the sediment that may accompany hypoxia (e.g. Thistle, 1980; Austen et al., 1989; Warwick et al., 1990; Neira and Rackemann, 1996).

Among the metazoan meiofauna, nematodes, the numerically dominant and least motile meiofaunal taxon in subtidal soft sediment communities, are the most tolerant to low oxygen (Giere, 1993; Cook et al., 2000; Neira et al., 2001a). Several species are able to withstand anoxic conditions for over 60–78 days, although their densities decline (Wieser and Kanwisher, 1961; Moodley et al., 1997). Recent meiofaunal studies at three shelf and upper slope sites off Chile (north, off Antofagasta at 309 m; central, off Concepcion at 366 m; south, off Chiloe at 296 m) (0–10 cm; Veit-Kohler et al., 2009), and off Callao, Peru (94 m) (0–1 cm; Gutiérrez et al., 2008) confirm previous observations for the region (Neira et al., 2001a, 2001b) that nematodes are the dominant meiobenthic group at these depths and that they reach highest densities and biomass during periods of strong oxygen deficiency. Time series data off Callao, Peru (94 m), indicate fluctuations in nematode density and community dominance (up to 100%), with a "nematode state" suggested to occur under extreme La Niña conditions when bottom-water oxygen concentrations are <10 μM (0.22 ml L^{-1}) and macrofaunal densities are reduced (Gutiérrez et al., 2008). Similar nematode trends have been observed in relation to low oxygen off central Chile (Neira et al., 2001a; Sellanes and Neira, 2006) and off Callao at 305 m (Neira et al., 2001b; Levin et al., 2002) during and after El Niño events.

In contrast, copepods and other crustaceans appear to be the meiofaunal groups most sensitive to anoxia (Coull, 1969; Elmgren, 1975; Heip, 1980; Murrel and Fleeger, 1989; Moodley et al., 1997). During 1985/1986, summer hypoxic conditions on the Louisiana shelf led to complete loss of harpacticoid copepods within a month, with lesser declines in nematode and kinorhynch densities. Copepods were slow to recover following return of normal oxygen conditions in the spring of the following year, further suggesting the sensitivity of copepods to hypoxia (Murrel and Fleeger, 1989).

Hypoxia can affect the vertical distribution and composition of nematode fauna. On the Swedish west coast,

Sabatieria pulchra, a species associated with the redox potential discontinuity, migrates vertically and is the only metazoan species present after summer hypoxia (Hendelberg and Jensen, 1993). Species of the same genus dominate bathyal sediments (500 m and 1000 m) off the Kenyan coast in the W Indian Ocean (Muthumbi et al., 2004). Subsurface fauna appear to be affected by hypoxia only in a narrow, shallow depth range, suggesting an upwards migration in response to increasing sulphide concentration (Hendelberg and Jensen 1993). Beneath fish farms in the western Mediterranean (Tyrrenian Sea), 74% of the meiofauna was concentrated in the top 1 cm compared to only 42% after the cages were removed (Mazolla et al. 2000).

In surface sediments, food availability is thought to play a more important role in regulating meiofaunal communities than oxygen, whereas oxygen supply is often the limiting factor in deeper sediments (Vanreusel et al., 1995). Organic load biodeposition of mussel and fish farms can also lead to oxygen depletion of bottom waters (e.g. Tsutsumi et al., 1991; Mazzola et al., 1999; Mirto et al., 2000, 2002). Because they are sensitive to changes in the environment, meiofauna have been suggested as initial indicators of benthic community structural response to fish farm biodeposition (Duplisea and Hargrave, 1996). In the Western Mediterranean (Tyrrhenian Sea), a strong impact on meiofauna assemblages was observed beneath fish cages. Meiofaunal densities (top 10 cm) dropped about 3 fold as compared with a control site during the 8 months of sampling (Mazzola et al., 1999). Copepods and ostracods exhibited a significant decline in the farm sediment in the first three months; kinorhynchs disappeared completely at the farm site, whereas polychaete density did not vary (Mazzola et al., 1999). The nematode assemblage was highly impacted, with reduced densities, diversity and richness in sediment beneath the farm. There were also changes in functional indices; after 45 days of farming there was an increase in individual biomass and a different nematode assemblage. In another study in the same area, meiofaunal densities beneath a mussel farm were significantly lower (1551 ind 10 cm^{-2}) than at a control site (2071 ind 10 cm^{-2}) over 12 months. In this setting turbellarian, ostracod, and kinorhynch densities significantly decreased compared with a control site, while copepod densities remained constant or increased, possibly benefiting from enhanced microphytobentic biomass (Mirto et al., 2000). The observed changes in meiofaunal community structure are a combined response to increased organic load along with reduced oxygen penetration at the water-sediment interface.

3.4.1 Meiofaunal recovery following hypoxia

Meiofaunal organisms are known to be characterized by high turnover rates and hence rapid or short recovery times (e.g. Chandler and Fleeger, 1983; Alongi et al., 1983; Danovaro et al., 1995). Meiofaunal crustaceans such as copepods and

ostracods can rapidly recover due to their motility. However, the speed and extent of meiofaunal colonization of defaunated sediments vary greatly. For example, Chandler and Fleeger (1983) showed that copepods and nauplii recolonized azoic estuarine sediments (15×28 cm chambers) in only two days, whereas nematodes required 29 days. Subtidal experiments placing azoic sediment trays (29×34 cm) revealed that copepods required five days to reach background densities, while for nematodes it took seven days (Alongi, 1981). Neira and Rackeman (1996) reported that meiofauna recolonized "black spots" (1 m^2 patches of buried algae with reduced sediments lacking fauna) only after re-development of an oxidized sediment layer. In those places where the surface remained "black", the meiofauna did not re-establish or their abundances and taxon richness were very low for almost one year. Differences in recolonization modes of the meiofauna may be attributed to their motility, ability to become suspended, active swimming, as well as their vertical distribution in the sediment column (Jensen, 1983; Chandler and Fleeger, 1983; Bowman et al., 1984; Powell, 1989). Experimentally-induced hypoxia, created by covering 4×4 m sediment plots with a polyethylene sheet, caused strong changes in nematode community composition on a tidal flat but did not result in complete nematode mortality (Van Colen et al., 2009), as was observed for the macrobenthos (Van Colen et al., 2008). Nematode recovery was rapid (1 month) but was strongly influenced over the long term by the dynamics of the macrobenthic bioturbation, grazing and resuspension (Van Colen et al., 2009).

The re-establishment of meiofauna in sediments previously affected by hypoxic bottom waters may occur by a combination of passive transport of sediment particles, and selective re-entry into the sediment, which is influenced by the physico-chemical features of the substrate (Palmer, 1988; Fleeger et al., 1990). Meiofauna, primarily copepods, ostracods, turbellarians, polychaetes and juvenile bivalves, are known to respond to environment deterioration by active migration away from the sediment (Bell and Sherman, 1980; Armonies, 1988, 1994; Wetzel et al., 2001). Nematodes are predominantly dispersed either passively by resuspension by currents, by locally restricted movements within the sediment, or by active swimming (Hagerman and Rieger, 1981; Chandler and Fleeger, 1983; Walters, 1988; Armonies, 1990, 1994). Thus it is not surprising that meiofauna are commonly early colonists (Rhoads et al., 1977), and that the most mobile and sensitive taxa (i.e., copepods) rapidly colonize sediments after favorable conditions return.

3.5 Macrofauna and megafauna

Detailed reviews of macrobenthic responses to hypoxia can be found in Wu (2002), which addresses molecular responses, Grieshaber et al. (1994), which considers physiological and metabolic responses, Diaz and Rosenberg (1995),

which focuses on physiological and species-level attributes, Rosenberg (2001), which addresses functional groups and community succession, and Levin (2003), which reviews benthos within permanent oxygen minimum zones. Organism tolerances to hypoxia are treated in Rosenberg (1991) and Gray et al. (2002). Often the ecosystem responses are associated with organic enrichment; these are synthesized by Pearson and Rosenberg (1978, 1987) and Gray et al. (2002). Below we briefly review community changes and the ecosystem-level consequences expected along gradients of increasing hypoxia (decreasing oxygen) and recovery (increasing oxygen), and assess whether the source, frequency or intensity of hypoxia influences macrobenthic response.

First responses to hypoxia are usually behavioral or physiological. Tube lengthening or body extension into the water column occurs in a variety of polychaetes and amphipods (Tyson and Pearson, 1991; Nilsson and Rosenberg, 1994, 2000; Rosenberg et al., 2002). Related responses include shallowing of burial depth (Long et al., 2008), emergence from the sediment (Rabalais et al., 2001a), and the formation of aggregations that raise individuals into the water column (Stachowitsch, 1984; Baden et al., 1990). During September 1983 anoxia occurred in the Gulf of Trieste, covering at least 50 km^2. Stachowitsch (1984, 1991, 1992) made careful observations of sequential responses by epibenthos at 20–25 m water depth, providing a glimpse of relative tolerance. Initially brittle stars (*Ophiothrix quinquemaculata*) and holothurians (*Cucumaria planci*) detached from sponges and other hard substrate; some holothurians eviscerated. Burrowing holothurians, echinoids, mantis shrimp and ghost shrimp emerged from the sediment. Subsequently hermit crabs left their shells, bivalves and sipunculans emerged; crabs, gobies and flatfish died. Anemones and tunicates were among the last to die. The ophiuroids *Amphiura filiformis* and *A. chiajei* emerged from the sediment in experimental tests when oxygen fell to 0.85 ml L^{-1} and 0.54 ml L^{-1}, respectively (Rosenberg et al., 1991). Ophiuroid aggregation and climbing behavior is also documented in the southeastern Kattegat (Baden et al., 1990) and Gulf of Mexico (see earlier text).

As hypoxia persists or its severity increases, mortality occurs. This can result from direct lethality, caused by low oxygen or presence of hydrogen sulfide, or from indirect causes such as increased susceptibility to predators (due to reduced burial and dwelling depths or less efficient foraging) (Long et al., 2002; Wu, 2002). Subsequent effects can be abrupt and involve sharp reductions in numbers of species, biomass and density and increased dominance by a few species (Harper et al., 1991; Rosenberg, 2001; Rabalais et al., 2001b).

Small body size, rapid growth rates, shallow dwelling zones, limited bioturbation, and annual life cycles are attributes of species that inhabit seasonally hypoxic settings. Seasonal hypoxia typically causes loss of species numbers, reduced biomass and increased dominance. Annelids (e.g. *Heteromastus filiformis, Paraprionospio pinnata*) and

certain molluscs (e.g. *Thyasira equalis, T. sarsi, Melinna cristata*) prove most tolerant although even they can disappear completely when sulfide levels increase greatly (Josefson and Widbom, 1988; Nilsson and Rosenberg, 2000; Quiroga et al., 2007).

Diversity is the biological attribute most sensitive to hypoxia. Loss of hypoxia-intolerant taxa leads to greatly reduced species richness and evenness. Typically crustaceans and echinoderms disappear first, with annelids and selected molluscs exhibiting greatest tolerance to hypoxia (Diaz and Rosenberg, 1995; Gray et al., 2002). Under extreme oxygen depletion only a few species may persist and dominance is always high. Because hypoxia and eutrophication (or upwelling production) often co-occur it is difficult to separate their effects on diversity (Levin and Gage, 1998). Organic enrichment will strongly influence evenness and dominance. Another confounding factor is that hypoxic waters typically have low pH, in part from CO_2 buildup produced by respiration. In permanently hypoxic or suboxic waters, animals may be bathed in waters of pH<7.5. Thus it is often difficult to distinguish effects of oxygen depletion from those of decreased pH on taxonomic composition in such regions. Calcifying taxa such as echinoderms, with highly soluble high-Mg calcite, usually fare poorly in hypoxic settings (Levin, 2003).

Other attributes shaped by hypoxia include body-size structure and morphology. Smaller taxa typically prevail over larger forms due to their greater surface area to volume ratios that enhance diffusion (Levin, 2003). Smaller taxa that persist in hypoxic settings tend to be opportunistic, with high larval availability, rapid growth and short generation times (Wu, 2002). Branchiate species with prolific respiratory structures (gills, brachiae, palps and tentacles; Fig. 5) such as spionid, cirratulid and ampharetid polychaetes, seem to have an advantage in both oxygen acquisition (Lamont and Gage, 2000) and surface feeding, and may explain the predominance of surface-deposit feeding annelids in many enriched, hypoxic settings.

Animal vertical distributions in the sediment are typically predicted to become shallower under hypoxic conditions (Long et al., 2008). This seems to occur when hypoxia is episodic or seasonal, as seen in the northern Gulf of Mexico (Rabalais et al., 2001b). For the most part, deep burrowers disappear under hypoxic conditions and animal activities are focused near the sediment-water interface in most estuaries and continental shelves. However, in settings where taxa are adapted to naturally occurring, persistent low-oxygen conditions, a deepening of deposit-feeder vertical distributions is observed, perhaps associated with an enhanced chemosynthetic food supply (Smith et al., 2000; Rabalais et al., 2001; Levin et al., 2003, 2009).

Hypoxia-induced changes in the size, composition, diversity, feeding and dwelling habits of benthic macrofaunal communities have many functional consequences. These include shifts in trophic structure and food chain support func-

tions, altered organic matter remineralization pathways, reductions in bioturbation and attendant oxygenation and carbon burial, and loss of habitat heterogeneity and key biogenic structure-forming species (e.g. mussel beds, oyster reefs, seagrasses) that act as ecosystem engineers (sensu Coleman and Williams, 2002).

As oxygen is depleted suspension feeders are replaced by deposit feeders, and deep-burrowing, subsurface-deposit feeders are replaced by shallow interface feeders. Predators decline along a hypoxia gradient in Hong Kong (Wu, 1982) and in Chesapeake Bay (Breitburg et al., 1994). Macrobenthos abundances are reduced, while meiobenthos abundances remain high, and eventually protozoans replace metazoans as biomass dominants and as key recyclers of organic carbon (Woulds et al., 2007). Under extreme conditions nearly all energy flows through microbes and trophic support for fisheries is curtailed or terminated. As animal biomass declines and activities are concentrated at shallower depths in the sediment column, particle mixing and solute pumping rates and depths diminish. There is a loss of geochemical heterogeneity in sediment and a reduction in organic matter remineralization and burial (see Middelburg and Levin, 2009). Loss of large-reef forming species reduces habitat complexity and water filtration capacity, two factors that are important to maintenance of system health and biodiversity (Coleman and Williams, 2002).

3.5.1 Macrofaunal and megafaunal recovery

Recovery of macrobenthos and megabenthos following coastal hypoxia can follow variable trajectories (e.g. Gutiérrez et al., 2008), sometimes with different successional patterns occurring at nearby sites (e.g. Harper et al., 1981). Sediment profile imagery and derivation of a benthic habitat quality index from the imagery defines four distinct successional stages following a 2-year reoxygenation of the Gullmar Fjord. These involve formation of microbial mats and absence of fauna in stage 0, then increasing dwelling depths in the sediment column and degree of bioturbation. The recovery stages did not mirror the degradation stages, with *Capitella capitata*, the nemertean *Hubrechtella dubia*, and the heart urchins *Echinocardium* spp. colonizing at 85–95 m (Nilsson and Rosenberg, 2000; Rosenberg et al., 2002).

On the Texas inner shelf, recovery following acute hypoxia with hydrogen sulfide buildup involved colonization by *Paraprionospio pinnata* in deeper waters (20 m) and sequential succession of *Magelona phyllesae, Abra aequalis, Balanoglossus* sp. n., *Natica pusilla*, and *Lembos brunneomaculata* in shallower (15 m) waters. Ampeliscid amphipods, while not tolerant of severe hypoxia, are observed to be common just prior to hypoxic events (Harper et al., 1991) at oxygen minimum zone edges (Levin, 2003) and at the Mississippi River canyon (Soliman and Rowe, 2008), suggesting they may be organic enrichment opportunists that can serve as indicators of impending hypoxia. The ampeliscid

amphipods, however, did not recruit back to the hypoxic zone studied by Harper et al. (1981, 1991) for several years and were completely absent from the benthic macroinfaunal community in severely hypoxic areas of the Louisiana continental shelf (Rabalais et al., 2001b).

Annual recovery is common to sites subject to predictable, seasonal hypoxia, such as Tampa Bay, Florida (Santos and Simon, 1980). Rapid growth, reproductive timing and dispersal potential all contribute to resiliency. Kiel Bay fauna (Arntz, 1981) and Tampa Bay fauna (Santos and Simon, 1980) are considered pre-adapted to hypoxia, with recovery occurring in 1 year. However, when hypoxia is not seasonal and occurs over longer periods, recovery following hypoxia can be delayed. Recovery of macro- and meiofauna following defaunation by hypoxia can take 18 months or more in settings as diverse as fjords (Josefson and Widbom, 1988; Austen and Widbom, 1991), the New Jersey shelf (Boesch and Rosenberg, 1981), the Adriatic Sea (Stachowitsch, 1991) and Hong Kong waters (Lu and Wu, 2000). Additional factors, such as the presence of excessive organic debris and sulfide (Rosenberg, 1972, 1976; Leppakoski, 1975; Karakassis et al., 1999), limited exchange and recruit sources (Lardicii et al., 2001), altered salinity regimes, or recurring hypoxia (Gutiérrez et al., 2008), can all slow faunal recovery following hypoxia.

3.6 Benthic and demersal fisheries resources

The shelf and estuarine habitats most likely to experience hypoxia are also nutrient-rich areas that support abundant bottom fisheries, so there is strong interest in the effects of hypoxia on these resources (see review by Breitburg et al., 2009; Ekau et al., 2009). Hypoxia can affect fish and shellfish directly, by inducing behavioral avoidance, altering migration routes, reducing growth and reproduction, inhibiting immune responses or by causing mass mortality. However, often it is the indirect effects of severe hypoxia, including loss of prey and loss or compression of critical habitat including structural features that can have the greatest effect on demersal fisheries (Diaz and Breitburg, 2009).

Surprisingly, moderate or intermittent hypoxia can be linked to benefits for fishery species. The underlying source of hypoxia, nutrient enrichment, may yield elevated prey biomass systemwide, as in parts of the Baltic Sea (Elmgren, 1989). Oxygen-stressed infauna may move towards the sediment-water interface and provide an enhanced, readily accessible food supply to mobile fish and shellfish that can return to oxygenated waters after feeding. Demersal species that are able to tolerate low DO for short periods, (e.g., weakfish; Tuzzolino, 2008) can take advantage of enhanced prey availabililty. They also can obtain refuge from less tolerant predators. The widespread ability of fish and shellfish to swim away from hypoxic areas, combined with the facilitative effects described above, may explain why large-scale studies rarely demonstrate a clear negative relationship between fishery landings and extent of hypoxia (Breitburg et al., 2009). However, the proportion of demersal fish and shellfish relative to pelagic fishes typically declines under conditions of extensive or permanent hypoxia, such as found in the Sea of Azov, the Black Sea, the Skagerrak-Kattegat and the Adriatic Sea (Caddy, 2000; de Leiva Moreno et al., 2000).

There are clear cases where hypoxia induces mass mortality or reduces catches locally. Sporadic declines in oxygen concentrations connected to thermohaline stratification occur quite frequently in shallow shelf waters such as the North Sea (Westernhagen and Dethlefsen, 1983) or Mid Atlantic Bight (Mountain, 2002) and in inshore bays, such as the Limfjord in Denmark (Jørgensen, 1980). During low-oxygen events in the North Sea, fish abundance dropped to 1 to 5 kg per 30 min trawl compared to the situation after remixing with 360 to 450 kg catch per trawl. Video images revealed that most mobile animals such as fish had left the area. This was in agreement with a similar event in the New York Bight in 1976 (Sindermann and Swanson, 1979). As oxygen depletions do not happen instantly, fish and other mobile animals normally have enough time to leave the endangered areas, and can repopulate the sites after the situation has improved. For sessile species that are hypoxia-tolerant, one consequence of reduced predation by fishes and megafaunal invertebrates may be enhanced survivorship. This may explain the sustained production of the harvested quahog clam *Mercenaria mercenaria* in hypoxic settings in Narragansett Bay, Rhode Island, USA (Altieri, 2008).

Most demersal fish species are sensitive to low oxygen and react to changes at a tolerance level of about 30% saturation ($2 \, \text{ml} \, \text{L}^{-1}$). Miller et al. (2002) give an LC_{50} of 1.5 to $3 \, \text{mg} \, \text{L}^{-1}$ (1 to $2 \, \text{ml} \, \text{L}^{-1}$) for several coastal and estuarine fish. These species will readily detect decreasing oxygen and escape as early as possible. However, the less mobile members of the demersal community can experience extremely high mortality, depending on the rate of decrease of dissolved oxygen. Westernhagen and Dethlefsen (1983) observed up to 100% mortality in some ophiuroid species in their study. Some crustaceans can cope with $1 \, \text{mg} \, \text{L}^{-1}$ ($0.7 \, \text{ml} \, \text{L}^{-1}$) (Miller et al., 2002) without showing significant change in behavior (Demers et al., 2006), but crayfish and lobsters cannot escape quickly and thus are highly vulnerable to events like the hydrogen sulfide eruptions that occur on the Namibian shelf. They become trapped by the upwelling anoxic waters and pushed towards the shore. In this case mobile species like fish also sometimes get trapped and washed ashore.

Another impact of strong hypoxia or anoxia is on the early life stages of some species. The best example maybe the Baltic cod, that lives in a strongly stratified environment where more saline but poorly oxygenated waters occur at greater depths. To maintain sperm activation and egg buoyancy, cod needs a minimum salinity of 11 (Nissling and Westin, 1997). Oxygen content of waters below the
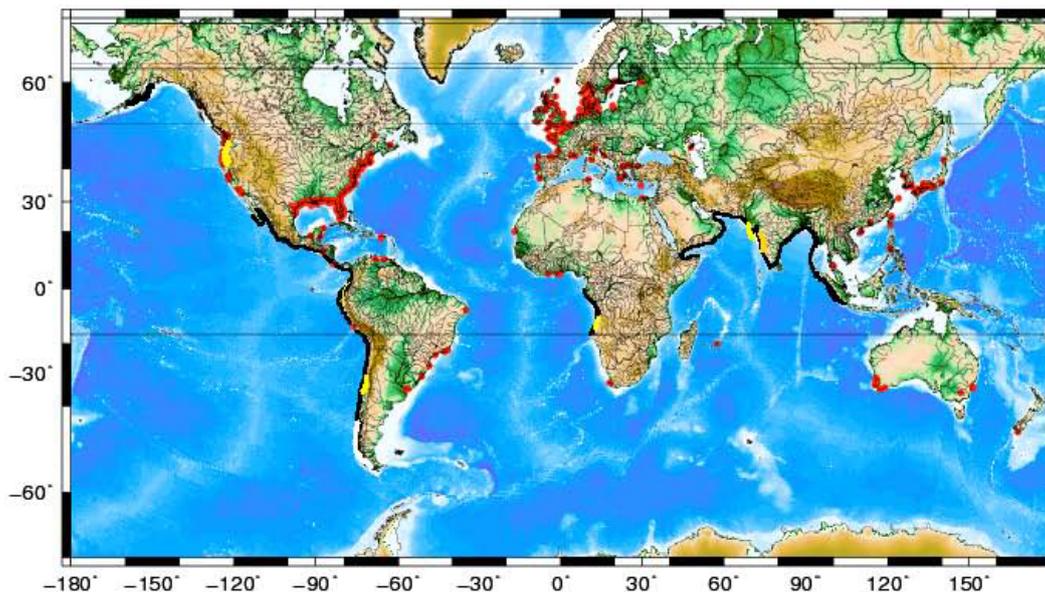
Fig. 7. World distribution of coastal hypoxia including eutrophication-induced coastal hypoxia (red, from Diaz and Rosenberg, 2008), outer shelf (200 m) hypoxia (black, from Garcia et al., 2006, World Ocean Atlas), and inner shelf hypoxia (yellow, see paper text).

thermocline has decreased in the Western Baltic Sea in recent decades (Gerlach, 1996). The habitat required for spawning (saturation >30% and salinity >11 suitable for cod development) has diminished due to a continuously rising oxycline (Lozán et al., 1996; Nausch et al., 2003). The Bay anchovy is encountering similar difficulties in weakly stratified estuaries of Chesapeake Bay, where eggs sink into lethal hypoxic waters (Keister et al., 2000).

4 Are there differences between human-caused vs. natural coastal hypoxia?

4.1 Characteristics of human-induced and natural hypoxia

To compare benthic responses to natural versus human-induced hypoxia, we must consider how the location, sources, timing, duration, areal extent, or intensity of hypoxia might differ when hypoxia is caused by human activities. Among the major factors contributing to hypoxia (nutrient enrichment, limited circulation, stratification, old water, or advection of low-oxygen water), the most direct human cause of hypoxia is nearly always eutrophication. At first glance, the occurrence of most eutrophication-related hypoxia differs in distribution from natural open shelf [OMZ- or climate-change related] hypoxia (Fig. 7). The east and west North Atlantic, along with the NW Pacific, support a majority of eutrophication-driven hypoxia records, which mainly occur in bays, estuaries, fjords and enclosed seas (Diaz and Rosenberg, 2008). In contrast, upwelling regions, including the Eastern Pacific, West Africa and Northern In-

dian Ocean are all sites of natural shelf hypoxia. One hypothesis is that long-term exposure of ecosystems to natural upwelling and high production generates resistance to eutrophication. An alternative explanation is that regions with natural shelf hypoxia support smaller human populations with a smaller N footprint, or that these ecosystems are less well studied (leading to fewer records of human-induced hypoxia).

4.2 Emergent responses to human-induced vs natural hypoxia

Eutrophication, via riverine or atmospheric input of nutrients, or particulate organic matter (e.g., from fish food or sewage) will usually select for species that are enrichment opportunists (Table 1), and high abundance and species dominance (Table 2) will persist, or precede a crash. Similar characteristics are likely for shelf fauna exposed seasonally to upwelled, natural oxygen- depleted waters.

Often organic additions by human can exacerbate conditions in areas already susceptible to hypoxia due to natural topography (silled lochs and fjords, enclosed seas, estuaries), seasonal upwelling or to advection of low-oxygen water masses. The dramatic increase in incidence of hypoxia from cultural eutrophication in recent decades must be linked to human activities in hypoxia-conducive environments (Diaz and Rosenberg, 2008).

Less direct human influences such as altered coastline configurations and circulation, changes to freshwater or sediment supply, and global warming (with associated shifts in

winds and precipitation) may generate hypoxia without massive eutrophication. Although both human and natural hypoxia can be regular, episodic or permanent, most human-induced hypoxia is seasonal and localized, but persistent in recurrence on an annual basis (Diaz and Rosenberg, 2001, 2008). Recovery is possible, and conditions should select for infaunal species with annual (or shorter) life spans or mobile taxa able to migrate away from hypoxic areas. Early successional communities should dominate in regions subject to human-induced hypoxia, and composition should be temporally dynamic. While permanent hypoxia can be induced by humans in enclosed seas (Mee et al., 2005), it is more often a natural phenomenon that generates highly adapted, co-evolved, low-diversity communities formed of species that can live and reproduce with surprisingly little oxygen (Karlson et al., 2002). The evolution of small body sizes, elaborate respiratory structures, ontogenetic migrations (into different oxygen zones), and chemosynthesis-based diets, are features of naturally hypoxic systems (Levin, 2003). Episodic re-oxygenation events are also a natural phenomenon. Hurricanes in the Gulf of Mexico or El Niño conditions off Peru and Chile all act to temporarily dissipate hypoxia. Hypoxia in the Gulf of Mexico reforms within a week once the system has re-stratified. The capability of species to respond rapidly and positively to amelioration of hypoxia appears to be much greater in areas of natural hypoxia (Arntz et al., 2006).

Human-introduced hypoxia often occurs adjacent to large human populations, ie. mainly near river mouths or in enclosed bays in the Northern Hemisphere (Diaz and Rosenberg, 2008). For many of these areas, normoxia is the historical condition, and organisms have had little prior exposure to severe hypoxia. Thus, oxygen thresholds inhibiting growth and reproduction or inducing mortality are an order of magnitude higher than where hypoxia occurs naturally, and complete mortality of metazoans is more likely. In enclosed water bodies and along the coasts of the south eastern Pacific Ocean, off West Africa, and in the northern Indian Ocean, where hypoxia occurs naturally often over great expanses (Helly and Levin, 2004), a broader range of species are able to persist at near-anoxic conditions (reviewed in Levin, 2003).

4.3 Interactions of hypoxia, climate change, and other human influences

At some point the influences of nature and humans interact and cannot be distinguished in assessing benthic responses to hypoxia. Recent observations of declining oxygen and shoaling OMZs in the tropical oceans (Stramma et al., 2008), on the Oregon Coast (Grantham et al., 2004, Chan et al., 2008), and on the California coast (Bograd et al., 2008; McClatchie et al., personal communication) all introduce the possibility but claim uncertainty about the role of global warming in observed oxygen trends. Ocean warming can exacerbate hypoxia by reducing oxygen solubility, by increasing tem-

perature stratification, by shifting upwelling or downwelling winds, and by altering circulation to enhance advection of low-oxygen water masses or reduce advection of oxygenated waters. Warming can increase storm incidence and thus increase oxygenation (Rabalais et al., 2009). It may also enhance respiration over production due to their differential temperature dependence. Untangling these different effects from each other and from human-induced eutrophication may be difficult. At the level of the individual, reduced oxygen supply to tissues can be the first mechanism to restrict whole-animal tolerance to thermal extremes. Hypoxia will exacerbate this limitation, and accelerate extinctions or relocations induced by warming (Pörtner and Knust, 2007).

In addition, hypoxia and warming will rarely be the sole factors acting to shape communities and ecosystems. Ammonium, hydrogen sulfide, organic carbon loading and acidification effects that accompany hypoxia will all have individual and synergistic effects (Wu, 2002). Hypoxia and low pH, for example, will reduce oyster defense against common diseases by lowering production of reactive oxygen intermediates (Boyd and Burnett, 1999), and increase the vulnerability of Humboldt squid (*Dosidicus gigas*) to predation by slowing metabolism (Rosa and Siebel, 2008). On larger scales, overfishing, other forms of pollution, habitat degradation and pressure from invasive species and diseases can all increase ecosystem susceptibility to disruption by hypoxia. Thus, predicting species, community or ecosystem responses to oxygen depletion in coastal settings requires a broader understanding of the context in which it occurs.

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