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Natural and human-induced hypoxia and consequences for coastal areas: synthesis and future development

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Abstract

Hypoxia has become a world-wide phenomenon in the global coastal ocean and causes deterioration of structure and function of ecosystems. Based on the collective contributions of members of SCOR Working Group #128, the present study provides an overview of the major aspects of coastal hypoxia in different biogeochemical provinces, including estuaries, upwelling areas, fjords and semi-enclosed basins, with various external forcings, ecosystem responses, feedbacks and potential impact on the sustainability of the fishery and economics. The obvious external forcings include fresh water runoff and other factors contributing to stratification, organic matter and nutrient loadings, as well as exchange between coastal and open ocean water masses; their different interactions set up mechanisms that drive the system towards hypoxia. However, whether the coastal environment becomes hypoxic or not, under the combination of external forcings, depends also on the nature of the ecosystem, e.g. physical and geographic settings. It is understood that coastal hypoxia has a profound impact on the sustainability of ecosystems, which can be seen, for example, by the change in the food-web structure and system function; other influences can be compression and loss of habitat, as well as change in life cycle and reproduction. In most cases, the ecosystem responds to the low dissolved oxygen in a non-linear way and has pronounced feedbacks to other compartments of the Earth System, hence affecting human society. Our knowledge and previous experiences illustrate that there is a need to develop new observational tools and models to support integrated research of biogeochemical dynamics and ecosystem behaviour that will improve confidence in remediation management strategies for coastal hypoxia.

1 Introduction

Coastal hypoxia, defined in this study as natural and/or anthropogenic dissolved oxygen (DO) depletion in coastal waters to a certain level (e.g. <30% saturation or $<2\text{mg/l}=62.5\mu\text{M}$), has become recognized as a world-wide phenomenon since the late 1950s. It has caused a deterioration of a variety of characteristics important to the sustainability of marine ecosystems. The incidence and extent of coastal hypoxia has risen over the last century from ~20 sites before 1950 to ≥400 sites at the beginning of this century, mainly as a result of increasing human derived discharges of nutrients and organic matter (Díaz and Rosenberg, 2008). Similarly, there is evidence for an increased incidence of hypoxia in shelf systems, mainly in areas subject to upwelling and potentially linked to regional climate adjustments of the physical forcing factors (Grantham et al., 2004; Monteiro et al., 2006a; Bograd et al., 2008; Gilbert et al., 2005). Climate change can also influence the evolution of hypoxia/anoxia over decadal to geological time scales. However, because coastal hypoxia is closely associated with active feedbacks to atmosphere, hypoxic systems also offer opportunities to study and understand the sensitivity of ecosystems to future high CO_2 conditions (Naqvi et al., 2009; Taguchi and Fujiwara, 2009).

The earliest systematic records of coastal hypoxia appear in literature from Europe and North America in 1910–1920. Since then there have been increasing reports of hypoxia from coastal regions world-wide, e.g. the Gulf of Mexico, Black Sea, and Baltic Sea (Rabalais and Gilbert, 2008; Oguz et al., 2000; Zaitsev and Mamaev, 1997), embayments (e.g. Chesapeake Bay), estuaries and fjords, and more recently off large rivers in East Asia (cf. Li et al., 2002). In view of the adverse effects of coastal hypoxia on marine life, the Scientific Committee for Oceanic Research (SCOR) constituted in the fall of 2005 a Working Group (SCOR WG #128), whose Terms of Reference (TOR) were to:

1. synthesize the state of the science for the following aspects of coastal hypoxia:
    (a) prevalence and spatio-temporal variability,
    (b) natural and human causes,
    (c) effects on biogeochemistry and ecology, and
    (d) resistance, resilience and recovery of ecosystems.

2. identify gaps in our understanding of hypoxia and make recommendations for future research;

3. determine the requirements for observing and modeling hypoxia and its impacts in coastal systems; and

4. document the work of the group and generate synthetic publications that integrate results from the efforts listed above.

This special issue of *Biogeosciences* has been organized in accordance with these objectives. The synthesis in this special issue consists of 10 papers that deal with various aspects of natural as well as human induced hypoxia in coastal environments occurring on temporal scales ranging from episodic (irregular occurrence) to persistent (hypoxic events taking place over a time scale long enough to cause damage to the biota) and with spatial dimensions from tens to hundreds of thousands of square kilometers. This also includes retrieval of palaeo- and historical information on hypoxia from sediment cores.

2 Understanding the causes of coastal hypoxia

Dissolved oxygen concentrations in surface waters are governed by the balance between oxygen production (through photosynthesis), consumption (respiration and other chemical reactions that consume oxygen), and exchange with the atmosphere. The latter tends to thermodynamically remain close to 100% saturation of DO for a given salinity and temperature (Fig. 1). In coastal environments, heterotrophic processes by bacteria degrade organic matter using dissolved oxygen as an electron acceptor, either in the water column or in bottom sediments, or both; oxygen is also consumed during reoxidation of reduced constituents such as sulfide, methane etc. (Fig. 1). In some coastal systems, ventilation is performed mainly through horizontal advection (Gilbert et al., 2005; Monteiro et al., 2006a; Bograd et al., 2008). Coastal upwelling can bring high concentrations of nutrients to surface waters and stimulate primary production and oxygen production. However, in certain coastal regions up-welled waters also bring low DO due to local or large scale (e.g. Eastern Tropical Pacific and Atlantic Basins) oxygen demand from microbial decay of sinking organic particles (Stramma et al., 2008).

The numerous physical and biogeochemical processes determining DO concentrations make it challenging to understand coastal hypoxia based on observations alone. Biogeochemical models that include the oxygen cycle have contributed to improved understanding of diverse aspects of hypoxia such as for example, processes responsible for the development of hypoxia, controls on extent and temporal variability, its impacts on biogeochemical cycles, and predictions of climate change responses (Peña et al., 2009). Moreover, recent advances in 3-D coupled physical-chemical-biological models have contributed to the improved quantitative understanding of the physical and biological processes leading to hypoxia (e.g. Gregoire and Lacroix, 2001).

The results of individual coastal hypoxia studies have substantially increased our understanding of biogeochemical processes and ecological consequences that can be related to the dynamics of hypoxia across the world coastal ocean. These findings demonstrate the critical role of biogeochemistry and its interaction with physical ventilation, by advection in shelf systems and vertical mixing in shallow inshore systems, in understanding the evolution of coastal hypoxia in many different physical and geographical settings (Gilbert et al., 2005; Monteiro et al., 2006a).

In shallow systems (i.e. water depth is typically <50m), concentrations of DO in the water column can also be modified by turbulent mixing and biogeochemical uptake. For instance, hypoxia near the mouths of large rivers and in estuaries tends to have a seasonal character that is related to the input of fresh water, terrestrial nutrients and the nature of circulation, and hypoxia itself has an inverse relation to the stability of the water column. Enhanced vertical stratification and restricted horizontal exchange with the open ocean (i.e. long residence time) may support the persistence of hypoxia and even the development of anoxia (Rabalais and Gilbert, 2009) in bottom waters. More specifically, coastal hypoxia off the large rivers of the world responds to the steady increase of nutrients from catchment areas. In the case of the Northern Gulf of Mexico, the load of dissolved nitrogen from the Mississippi River seems most important (Justic et al., 2003), which emphasizes that eutrophication and hypoxia can be related through the complex mechanisms driving cycling of nutrients and microbial processes in coastal environments. There are comparable examples in the discharges of the Changjiang (Yangtze River) into the East China Sea (Li et al., 2002).

Detailed information about similarities and differences among hypoxic sites in the global coastal ocean gives insights into the complex cross-links with climate change and human perturbations on ecosystems both in land and marine sectors. Comparative studies also clarify how biogeochemical dynamics defines the magnitude and consequences of coastal hypoxia. High-resolution measurements have enabled the establishment of cross-boundary and mechanistic understanding of the emergent, evolving and declining phases of coastal hypoxia (Kemp et al., 2009; Monteiro et al., 2009). The episodic, periodic (i.e. hypoxic event occurs with a regular character in time) and/or persistent nature of coastal hypoxia allows an estimate of the time lag between the accumulation of organic matter in the water column, microbial consumption of dissolved oxygen and subsequent mineralization processes.

The approach of SCOR WG #128 has been to provide a platform to examine bottom-up (i.e. physical and biogeochemical processes) control on food-web structure and function in the coastal marine environment. For instance, stocks and diversity of benthic macrofauna and megafauna decrease in the regions affected by hypoxia, but a high biomass can be found at the edges of low DO areas or at the boundary between oxygen depleted and replete waters, while meiofauna may not show any change (Levin et al., 2009). Thus, unlike the situation in normoxic environments, changes in oxygenation affect the entire ecosystem (including benthic food-webs and the pelagic system), permitting an understanding of the DO history over the past decades to millennia through the use of various faunal, chemical and mineral proxies (Gooday et al., 2009). This enables assessment of the interplay of biogeochemical cycles and ecosystem functions, such as heterotrophic degradation of organic matter (e.g. denitrification) and the significance of recycled production that leads to feedbacks to the atmosphere (e.g. CH_4 and N_2O emission) (Naqvi et al., 2000).

The biogeography and/or the biogeochemical provinces of coastal hypoxia, together with the model constructions of trophic dynamics, enable a comparison to be made of ecosystem functioning in low-oxygen settings across the world ocean. Such syntheses are required for linking present ocean processes to paleo-oceanographic records and for predicting future states. Together, the world-wide occurrence and spreading of coastal hypoxia create an imperative for improved biogeochemical modules and understanding of coupling with ecosystem processes, which in turn will guide the development of new models and observational tools. It is expected that coupling of pelagic and benthic biogeochemical dynamics and ecosystem responses will be cross-linked in the next generation of models (e.g. Soetaert and Middelburg, 2009), and interaction with the atmosphere incorporated in coupled Earth Systems Models. Such an approach requires an increase in spatial and temporal resolution of observations and improvement in numerical techniques as well. This advance will provide a better understanding of how the complex interplay of physical, biogeochemical and ecological processes affect the temporal evolution of ecosystem functioning in various bio-geographical provinces and within the context of changing climate.

The cumulative number of hypoxic systems has risen exponentially over time, with a dramatic increase since the 1980s (Díaz and Rosenberg, 2008). Before 1980, over half (52%) of literature records of hypoxia originated from Europe, more than 4 times the number in Asia (10%, mostly from Japan). Since the 1980s, the number of hypoxic sites in North America (43%, mostly from the United States) has become greater than in Europe (39%), as shown in Fig. 2. Moreover, before 1980, episodic events accounted for 13% of the total number of hypoxic systems, while periodic and seasonal hypoxic systems accounted for 66%, followed by persistent hypoxic events at 19% (Fig. 2). After the 1980s, there has been a reduction relative to the pre-1980s for episodic (11%), periodic and seasonal (55%) and persistent (3–4%) hypoxia, while the proportion of hypoxic events for which the frequency of occurrence remains unknown has increased (Fig. 2). About 30% of hypoxic systems reported in the literature after 1980 have causal mechanisms that remain unknown (Fig. 2). By comparing oxygen concentration trends from the 1951–1975 period with the 1976–2000 period, Gilbert et al. (2009) showed that the proportion of negative trends was significantly higher in 1976–2000, indicating a degradation of oxygen conditions in recent years.

3 Hypoxia in coastal upwelling systems

Natural hypoxia has long been known to occur in most coastal upwelling systems e.g. off Namibia (Copenhagen, 1953), western India (Banse, 1959; Carruthers et al., 1959) and Peru (Dugdale et al., 1977). However, the number of reports of hypoxia and ecosystem impacts from such systems has increased since the 1980s (Díaz and Rosenberg, 2008). Tropical and subtropical eastern boundary upwelling systems are usually associated with oceanic boundary currents owing to the combination of the Coriolis effect and wind-forcing (Lass and Mohrholz, 2008). Nutrient enrichment of the euphotic zone caused by upwelling makes these systems highly productive, which in turn leads to high oxygen consumption rates in subthermocline waters. Oceanic Oxygen Minimum Zones (OMZ) form the shadow of the subtropical gyral circulation, where subsurface waters are less vigorously ventilated (Lass and Mohrholz, 2008; Karstensen et al., 2008). Cross-shore exchanges of water mass properties through extra-tropical Rossby waves or mesoscale eddies between the ventilated coastal region and the open ocean may provide a mechanism for maintaining extended oxygen minimum zones in these eastern boundary current systems. This results in the formation of extensive oxygen minimum zones (OMZs) in the mesopelagic realm, particularly in the Humboldt (Peru-Chile) Current and California Current systems in the eastern Pacific Ocean (Deuser, 1975; Helly and Levin, 2002; Paulmier and Ruiz-Pino, 2008). In the Indian Ocean, the most vigorous upwelling occurs in the north (i.e. in the Arabian Sea) and not along its eastern boundary (e.g. off Western Australia), where upwelling is suppressed by the pole-ward Leewin current. The OMZ of the Indian Ocean is therefore found in its northern basins (Arabian Sea and Bay of Bengal). In the Atlantic Ocean, severe oxygen depletion is restricted to the Benguela system off Namibia, while the Canary Current System (off Mauritania-Morocco) is not known to support hypoxia. Upwelling of oxygen-depleted water in these regions, with the exception of Northwest Africa, is the primary cause of the development of hypoxic conditions in shelf waters.

Where upwelling is more or less perennial (e.g. off Peru), hypoxic conditions may persist throughout the year. More often, upwelling intensity varies seasonally, resulting in marked seasonal changes in coastal hypoxia (e.g. off southern Chile, Namibia and western India). Thus, in all these and other similar systems, physical processes play a key role in controlling the vertical structure of hydrographic parameters and the supply of water masses with low DO (Grantham et al., 2004; Monteiro et al., 2006; Bograd et al., 2008). The uniqueness of the eastern boundary upwelling system is their connection with equatorial variability (Pizarro et al., 2002; Rouault et al., 2007) which allows for a remote control of hypoxia events through the pole-ward propagation of equatorial Kelvin waves that may act on the oxycline along the coast (Monteiro et al., 2006a; Guttierez et al., 2008). In the Humboldt system, along-shore wind variability associated to the South Pacific Anticyclone activity also induced Ekman pumping and transport off central Peru and central Chile (Renault et al., 2009) that may favor the occurrence of hypoxia events. Compared to other coastal hypoxic areas, oxygen depletion in upwelling systems may occur in sub-surface waters, mostly due to the presence of a pole-ward undercurrent lying on the continental slope that carries poorly oxygenated waters from the equatorial OMZs (Monteiro et al., 2006a; Mohrholz et al., 2007; Guiterrez et al., 2008). On the shallow continental shelves, hypoxia events induced by upwelling can cause mass mortality of benthic fauna and diminish ecosystem services (Carruthers et al., 1959; Cockroft, 2001; Grantham et al., 2004). The large scale characteristics of the oxygen minimum layer and shelf hypoxia have a direct impact on fisheries by changing boundary conditions for spawning and early life history of economically important species (Ekau et al., 2009).

This may result in the occurrence of denitrification in the water column (Naqvi et al., 2000, 2009). It has been suggested that, in addition to denitrification, the anaerobic ammonium oxidation (e.g. anammox) is an alternative mechanism regulating nitrogen cycling in the bottom waters of coastal upwelling systems (Kuypers et al., 2005). Complete consumption of nitrate triggers the onset of sulphate reduction (Dugdale et al., 1977; Naqvi et al., 2000, 2006). Upwelling induced hypoxia may also cause massive release of hydrogen sulphide and methane from the sediments as happens in the Namibian coastal system (Weeks et al., 2002; Lavik et al., 2009). Sediment underlying hypoxic upwelling systems often support microbial communities comprising large, nitrate-storing bacteria because of high bottom-water nitrate concentrations (e.g. Schulz and Jørgensen, 2001). Deeply hypoxic or anoxic upwelling systems can also be significant CO_2 sources to the atmosphere in contrast to comparable aerated systems which are typically CO_2 sinks (Santana-Casiano et al., 2009).

Like other coastal areas, upwelling systems have been impacted by human activities such as eutrophication to varying degrees. For example, the world's largest natural hypoxic zone that develops seasonally over the Western Indian continental shelf appears to have intensified over the last three decades (Naqvi et al., 2000, 2009). Given the huge increase in fertilizer consumptions in South Asia, this region is expected to receive large amounts of anthropogenic nutrient loading through land runoff and atmospheric deposition (Seitzinger et al., 2002; Duce et al., 2008). Thus, the combination of upwelling and eutrophication is probably the major cause of the observed increase in hypoxia. However, variability of hydrography and circulation as an alternative or additional causative mechanism cannot be ruled out. Such changes have been invoked to explain the intensification of hypoxia in the California Current System in the last few years (Grantham et al., 2004; Bograd et al., 2008). However, the relative importance of eutrophication and physical changes, as well as human-induced effects and natural variability in driving hypoxia variability in various upwelling systems are still not fully established.

Note that Eastern Boundary Current systems of the Southern Hemisphere may be very sensitive to climate change due to their connection with equatorial variability and to change in land-sea thermal contrast associated with a warmer atmosphere and driving upwelling-favorable coastal winds. This is likely to translate into changes in hypoxia event statistics (i.e. occurrence and magnitude) in these regions. Moreover, climate models predict expansion of the eastern boundary oxygen minimum zones under global warming conditions (Matear and Hirst, 2003).

4 Hypoxia off river mouths and in estuaries

Hypoxia in the Adriatic Sea off the River Po was among the first cases attributed to human activities (Justić et al., 1987). Coastal hypoxia that develops in coastal areas off the large rivers, notably the Mississippi River, Changjiang (Yangtze River), Pearl River (Zhujiang), and Danube River (Zaitsev, 1992; Turner and Rabalais, 1994; Li et al., 2002; Rabalais et al., 2002; Yin et al., 2004; BSC, 2008), usually has been related to anthropogenic activities in the catchment areas on land. In particular, changes in land-use and agriculture (e.g. application and substantial loss of chemical fertilizers), combustion of fossil fuel, and release of municipal and animal waste to the environment have resulted in large increases in nutrients (mostly nitrogen and phosphorus) loads of rivers world-wide. Several models have been developed to understand the mechanisms that link river discharge and nutrient concentration to hypoxia development and cessation (Peña et al., 2009). These models have been useful for planning and forecasting possible responses of marine ecosystems to different management scenarios and for providing guidelines in setting goals of nutrient reduction. It is estimated that riverine nutrient fluxes to the world ocean have increased by a factor of two to four in the 20th century relative to the pre-industrial period. The increase in nitrogen load may have been even higher for some regions, 5 to 10-fold in Europe and North America (Boesch, 2002; Howarth et al., 2002) (Fig. 3). The number of coastal hypoxic systems and the amount of industrially fixed nitrogen have increased rapidly since the 1960s, with both trends showing a similar pattern (Fig. 3). However, a closer examination of

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the data indicated that such a rapid increase of industrial nitrogen, mainly of chemical fertilizers, is largely responsible for the increasing numbers of coastal hypoxic sites, but with a delay of ca. 5–10 years (Díaz, 2009).

Coastal eutrophication develops in the area adjacent to the river discharge, when nutrient over-loading results in increased productivity that provides abundant organic matter for microbial degradation (Fig. 1). Organic matter photosynthesized under eutrophic conditions is labile and can be readily degraded, while that derived from soils and terrestrial vegetations tends to be much more refractory because of degradation during transport to the sea (Wu et al., 2007). Inputs of fresh-water through river runoff also enhance stratification in adjacent marine water bodies, which reduces vertical mixing intensity and oxygen penetration into subsurface waters and promotes low-oxygen waters near the seafloor. Low oxygen in the deep part of the water column can also arise from incursion of offshore oceanic waters naturally low in dissolved oxygen. Examples include the influence of the Western Current, Kuroshio on the East China Sea, particularly the area offshore the Changjiang; the sub-surface waters of the Kuroshio have relatively low dissolved oxygen (ca. 125–150 μM) (cf. Li et al., 2002; Zhang et al., 2007). Mesoscale intrusions of subsurface suboxic waters from the Rim Current of the Black Sea general circulation system also modulates episodically the near-bottom oxygen structure of northwestern shelf (BSC, 2008). Long-term observations show that coastal hypoxia off large river mouths and in estuaries/bays has an important seasonal (Rabalais et al., 2001) and/or inter-annual component (Gilbert et al., 2005) that can be related to climate variability as well.

Díaz and Rosenberg (2008) found 60–70 hypoxia records in the literature prior to 1980, of which 18% were reported from river/estuary systems; since 1980 another 330–340 cumulative hypoxia reports have been published, of which the proportion from hypoxic river-estuary systems increased up to 22%. The actual number of hypoxic systems that can be related to land-source inputs exceeds 20–25% of recorded sites in the literature, because the ecosystem functioning of some lagoons and bays are also influenced by fresh-water influx into the system.

5 Hypoxia in semi-enclosed seas and basins

Marine basins that are semi-enclosed by land-mass may have a signature of oxygen depletion in deep and bottom waters, but that sometimes extends very close to the surface. This oxygen depletion can be seasonal or perennial, as in the Black Sea, Cariaco Basin, Baltic Sea, Kau Bay, Santa Barbara Basin and many other similar fjord-type environments (Oguz et al., 2000; Rabalais and Gilbert, 2009). Oceanographic processes that regulate hypoxia in semi-enclosed marine settings include restricted exchange with the open ocean and prolonged residence times of subsurface waters in the basins. Stratification of the water column that isolates oxygen depleted deep water from the well oxygenated surface layer and allows low oxygen conditions to fully develop in the deeper water column, and surface phytoplankton blooms that are usually induced by land-source or upwelling-derived input of new nutrients, sustain an enhanced vertical flux of organic matter to deep waters. In these semi-enclosed, hypoxic systems, the ratio of recycled to new production can be higher than in open water settings.

Semi-enclosed basins with a shallow sill at the entrance are very susceptible to hypoxia and can be found at high-latitudes (e.g. fjords in Norway, Sweden and Canada), in the temperate zone (e.g. Black Sea, which contains the world's largest body of permanently anoxic water) as well as in the tropics (e.g. Cariaco Basin and Kau Bay). Stratification can be pronounced in the case of strong salinity and temperature vertical gradients in higher-latitude systems (e.g. Baltic Sea) or more subtle in the case of tropical basins. Water renewal in these hypoxic, silled basins depends on regional processes (i.e. wind, fresh water run-off and ground water discharge) and the density of seawater just outside the silled basin. Water renewal in silled basins may be controlled by global or distant mechanisms such as El Niño (e.g. Kau Bay) or the North Atlantic Oscillation (e.g. Baltic Sea) (Hanninen et al., 2000; Gooday et al., 2009). Advection of North Sea water into the Baltic Sea anoxic basins results in a cascade of biogeochemical reactions with major consequences for food web structure and functioning. Similar processes have been reported for intrusion of Mediterranean water via the Bosporus into the upper part of anoxic Black Sea water column (Glazer et al., 2006). These natural, climate-change sensitive bottom water renewal events cause interruption of hypoxia/anoxia and the consequences are reflected in the sedimentary records (Kennett and Ingram, 1995; Gooday et al., 2009). These semi-enclosed hypoxic basins therefore amplify subtle global change effects into easily detectable and more pronounced changes in ecosystem properties and therefore represent natural laboratories.

6 Coastal hypoxia and benthic biota

Benthic ecosystems experience changes in levels of dissolved oxygen, and hence hypoxia, on different time and spatial scales and in a variety of stages of the physiology and auto-ecology of organisms. Where oxygen re-supply is slow and/or limited, damage to benthic species by hypoxia can be exacerbated. When dissolved oxygen becomes depleted in the lower part of the water column, benthic organisms show stressed behaviors with changes in community structure as well. For instance, mobile nekton will avoid an area when oxygen concentrations are too low; sessile invertebrates in near-bottom waters may undergo mass mortality and burrowing organisms escape from their burrows and lie motionless on the bottom or even disappear. However, species-specific thresholds are rarely well known, vary with body size and taxon, and thus no single definition of hypoxia fits all organisms (Vaquer-Sunyer and Duarte, 2008; Levin et al., 2009). The results of coastal water hypoxia on physiological responses and survival for benthic organisms can be very complex, depending on the structure of food webs and life histories of affected species. Larval stages are often more sensitive than adult individuals to low oxygen concentrations and hence less tolerant to hypoxia. The severity of the impact of hypoxia on coastal benthic systems is determined not only by the level of dissolved oxygen but also the temporal scale of exposure. Permanent hypoxia can have a profound impact on the species composition and biodiversity at a community level, relative to areas affected by episodic and/or periodic hypoxic events that cause damage, mostly at the species level (e.g. life history). Hypoxic areas show a trend of lower biomass/abundance of large-size organisms, a skew towards small-size organisms, and a loss of deep-dwelling and long-lived species. A reduction of species diversity is usually accompanied by dominance of one or a few oxygen tolerant species (Levin, 2003).

In ecosystems experiencing hypoxia, habitat is also compressed and/or even lost. In terms of mortality, echinoderms and crustaceans (e.g. shrimp and crabs) are typically most vulnerable, followed by mollusks, with polychaetes often the most resistant taxon to low oxygen levels (Jørgensen, 1980; Díaz and Rosenberg, 1995). The boundary areas between hypoxic waters and normal oxygen conditions, characterized by high chemoautotrophic production, may provide source organisms and food materials for re-colonization. In regions subject to episodic and/or periodic hypoxia, the damaged benthic ecosystem may not necessarily recover immediately after the return of normal oxygen conditions.

In both natural and anthropogenically caused hypoxia there is enhanced deposition of labile organic matter (e.g. phytoplankton detritus) that can cause the bottom sediments to become more heterotrophic with an increase in oxygen demand and hence an increase in re-mineralization of nutrients and certain trace elements (Middelburg and Levin, 2009). However, it is hard to distinguish whether low DO induces higher preservation of organic matter (i.e. retardation of decomposition of organic materials by heterotrophic bacteria owing to hypoxia) or if higher organic matter in bottom sediments causes a reduction of dissolved oxygen (i.e. an increase in organic-matter flux fuels heterotrophic degradation that consumes oxygen).

7 Sediment records of coastal hypoxia

Ultimately, biogeochemical dynamics in marine sediments are intimately linked to the condition of the water column. The re-mineralization of nutrients and trace elements in the upper sediment layers and at the sediment-water interface are fueled by the depositional flux of organic materials through the water column, while the oxygen supply in benthic systems can be through turbulent mixing, diffusion and bio-irrigation (Fig. 1). In hypoxic environments, anaerobic respiration results in formation of various reduced substances, such as N_2 and NH_4^+, N_2O, Fe(II), Mn(II), H_2S, intermediate oxidation state sulfur species like thiosulfate, sulfite and elemental sulfur, and metal sulfur complexes and CH_4. These products occur along with a redox cascade in the use of oxidants, which can be efficiently re-oxidized within benthic ecosystems because they contain a substantial amount of energy transferred from the original organic matter (Middelburg and Levin, 2009). In the hypoxic coastal environment, anaerobic processes dominate biogeochemical cycling, because high carbon loading creates a large oxygen demand (e.g. heterotrophic degradation) that is not balanced by oxygen supply from either the upper part of water column or exchange with other water bodies with higher oxygen content. In fact, oxygen consumption by re-oxidation processes can be 3-times higher than the amount of consumption from aerobic respiration (Glud, 2008).

In hypoxic settings, heterotrophic denitrification is favored relative to nitrification, but the rate of denitrification is regulated by the level of nitrate in near-bottom waters; an increase in nitrate concentration can dramatically promote denitrification (Middelburg and Levin, 2009). As the oxygen level in near-bottom waters decreases, Fe and Mn oxides and/or hydroxides are reduced to soluble Fe(II) and Mn(II) along with heterotrophic degradation of organic materials. Thermodynamic control means that Mn-oxides are usually utilized at higher redox conditions than Fe-oxides. Soluble Fe(II) can then combine with sulfur to form insoluble sulfides, if the system becomes anoxic. When heterotrophic respiration and degradation of organic materials consume dissolved oxygen in the water column, the pH also decreases. The pH can be as low as 7.5–7.6 in hypoxic waters (surface waters typically have pH values around 8.1), and much lower in pore waters, lowering carbonate saturations states and potentially negatively affecting species with carbonate skeletons or shells (Green and Aller, 2001). Hence, besides the direct impact of hypoxia on the ecosystem by reducing dissolved oxygen in near-bottom waters, benthic species can suffer from aggravated carbonate dissolution associated with reduced pH (i.e. corrosive water body).

The evolution of hypoxia in the coastal ocean can be inferred from microfossils, biomarkers and the chemical and mineralogical composition of bottom sediments. However, accurate quantitative proxies for palaeo-oxygenation remain elusive and distinguishing the effects of hypoxia from those of eutrophication without DO-depletion poses a considerable challenge. Foraminifera are by far the most widely-used benthic faunal indicators for hypoxia in near-bottom waters. Some species have the physiological ability to withstand severe hypoxia or even temporary but not long-term anoxia. For example, infaunal calcareous species with thin-walled tests and flattened, elongate biserial/triserial, planispiral/lenticular or globular test morphologies, are common in hypoxic environment (Bernhard and Sen Gupta, 1999; Jorissen, 1999), although they also occur in organically-enriched sediments overlain by oxic bottom water (Jorrisen et al., 1998). Depressed species richness and diversity is another indicator of oxygen depletion (Gooday, 2003; Gooday et al., 2009). Ostracods are generally intolerant of hypoxia, and like foraminifera, species richness is depressed in oxygen-stressed situations. In hypoxic settings, benthic assemblages are characterized by the dominance of a few exceptional species. Other bottom-sediment parameters that have been used to track the evolution of coastal hypoxia include sediment texture and other properties (e.g. development of laminations and color), the chemical and mineral composition (e.g. pigments, sulfides and trace metals), and the presence of authigenic minerals (e.g. glauconite) (Gooday et al., 2009). The occurrence and evolution of hypoxia can also be inferred from the sedimentary records of planktonic organisms (i.e. diatoms and dinoflagellate cysts, indicators of high levels of primary production linked to eutrophication) and the composition of organic matter and associated stable isotopes ratios (i.e. δ^{13}C and δ^{15}N). Since CO_2 is used in photosynthesis, an increase in CO_2 in a hypoxic water column due to enhanced respiration may result in lighter δ^{13}C values for synthesized organic matter. Photosynthesis using regenerated nitrogen (e.g. NH_4^+ produced in hypoxic conditions as product of ammonification) can induce a higher δ^{15}N value (e.g. 5–10‰) in organisms relative to those that obtain nitrogen through nitrogen fixation and/or use fertilizer nitrate as a nitrogen source. Pigment and lipid biomarkers have been used to indicate the occurrence of hypoxia; for example, fucoxanthin and zeaxanthin in sediment may reflect enhanced input of diatoms and cyanobacteria, respectively, while isorenieratene and farnesol reflect oxidation of reduced sulfur in the euphotic zone of the water column. Also sterols, fatty acids and alcohols have been used to discriminate different taxa to identify changes in plankton composition, which in turn provide a powerful tool to infer the degree of oxygen depletion in the water column (Gooday et al., 2009).

8 Scaling-up the Results from coastal hypoxia studies

Coastal hypoxia is indeed a challenging topic to deal with, and the studies involve the integration of multi-disciplinary approaches as well as a combination of observations and model simulations. On one side, coastal hypoxia is affected by changes in watershed properties through coastal eutrophication (e.g. fresh water influx together with land-source nutrients, labile/marine and terrestrial organic materials). On the other side, changes in global forcings may also be important; the atmosphere can impact coastal hypoxia by changing the surface layer heat budget, wind-induced turbulent mixing, and stratification (Fig. 4). Moreover, the dimension and severity of coastal hypoxia is regulated by the variability of ocean circulation, which in turn, is affected by the changing climate (Fig. 4). Thus, the evolution and character of coastal hypoxia are tuned by the complex and interactive combinations of natural and anthropogenic forcings at regional scale (e.g. bio-geography and socio-economic factors), and the ultimate fate of a coastal hypoxic system depends on the regional manifestations of the above-mentioned forcing factors across different spatial and temporal scales.

A key issue addressed by SCOR Working Group #128 was the natural variability in, and/or anthropogenic influence on, coastal hypoxia and the consequences of these environmental fluctuations for ecosystems. We explored whether studies of coastal hypoxia could be scaled up temporally and spatially across the different geographic and oceanographic settings. It should be noted that by doing this, we had to use approaches such as integration and extrapolation in order to evaluate the role of regional biogeochemical and ecosystem functions at a global scale. However, it should also be kept in mind that the consequences of global change on regional biogeochemical cycles and food-web dynamics can be amplified as coastal hypoxia evolves.

Eutrophication and coastal hypoxia are linked through the heterotrophic degradation of organic matter, re-mineralization of nutrients and re-oxidation of reduced metabolites (Fig. 1). The organic matter that fuels heterotrophic respiration can be derived from land (i.e. riverine input) or in situ primary production. Low dissolved oxygen in the water column can be the result of upwelling of deep oceanic waters toward the coast, in which the low oxygen waters are usually characterized by high nutrient levels (Fig. 1). Global warming linked to anthropogenic CO_2 accumulation in the atmosphere will regulate ocean-wide hypoxia development on decadal to millennial time scales (Shaffer et al., 2009). Increased stratification due to surface layer warming may enhance degassing of oxygen from the sea surface to the atmosphere. Riverine influx in summer may also provide warm surface waters to the coast, owing to the more rapid warming over the watersheds, causing enhanced coastal stratification as well (i.e. density difference). In addition, large rivers carry into the adjacent coastal environment a huge amount of plant nutrients and terrestrial organic matter that can fuel photosynthesis of phytoplankton and the heterotrophic metabolism of bacteria. When the stratification is destroyed by wind-induced mixing and/or changes in circulation, greenhouse gas species (e.g. CO_2, CH_4, and N_2O) accumulated in hypoxic waters beneath the stratified surface layer can be released into the atmosphere, potentially having a strong feedback to climate change. It has been suggested that coastal hypoxic areas are important contributors to the atmospheric inventory of long-lived greenhouse gases (Naqvi et al., 2000, 2009; De Bie et al., 2002; Zhang et al., 2008). Coastal hypoxia can also influence the oceanic inventory of dissolved oxygen, nutrients and other greenhouse gases though exchange with open ocean waters and down-welling.

Several types of modeling approaches, from simple to complex, have significantly contributed to improve our understanding of diverse aspects of hypoxia (Peña et al., 2009). Models have been used to synthesize the observational findings, understand the functioning of the systems and to develop predictive capability. Typically, models developed for specific regions perform well for the particular system for which they were developed, but when applied to other systems, their performance tends to be poor even after re-parameterization. However, the recent development of a generic ecological model (GEM, Blauw et al., 2009) for estuaries integrates biological and physical processes in a simulation of basic ecosystem dynamics for generic application to coastal waters. This model has been applied in a range of scenario studies, which have formed the basis for several major policy and management decisions and infrastructural developments in coastal zones with different hydrographic and geographic nature.

9 Integration of biogeochemistry and ecosystems

The degree to which biogeochemical cycling is linked to food-web dynamics is central to determining the impact of hypoxia on the functioning and provision of services by coastal ecosystems and feedbacks to global climate change. One of the critical issues is the efficiency and role of areas with depleted dissolved oxygen on the biogeochemical dynamics (e.g. nutrient regeneration) and vice versa, that affects the ratio between recycled and new production in coastal environments. This, in turn, affects the whole ecosystem from microbes to top predators through trophic interactions (Ekau et al., 2009; Levin et al., 2009). Because hypoxia also occurred in the geological past, it is important to determine the fate of carbon cycling relative to oxygen depletion over considerable time scales (e.g. 10^2–10^3 years) (cf. Gooday et al., 2009). There are limited data sets available on the coupling of hypoxia and biogeochemistry, and particularly on the processes that bridge remineralization and food-web dynamics. Likewise, there are few models that specifically address the effect of hypoxia on a marine ecosystem (Peña et al., 2009). Hypoxia models differ markedly in the level of complexity and temporal and spatial resolutions. Biogeochemical models that include the oxygen cycle may use relatively simple mathematic formulations (e.g. modules) for food web interactions and organisms other than phytoplankton. These formulations range from simple NPZD-type models (i.e. Nutrient, Phytoplankton, Zooplankton, and Detritus) to multi-nutrient, size-structured ecosystem models.

At present, the stoichiometric relationship between oxygen, carbon and other macro- and micro-nutrients is uncertain, given the complex character of coastal hypoxia, including different remineralization and burial efficiencies of organic carbon and other biogenic elements. This can result in decoupling of nutrients and trace elements in the biogeochemical cycles and changes in apparent nutrient limitation. Hypoxia-induced changes in nutrient ratios may have far reaching ecological consequences via alterations of primary producer communities, including the proliferation of harmful algae. Data in the literature on the ratio between carbon and other nutrient species indicate that the frequency and significance of oxygen-depleted conditions in areas affected by anthropogenic activities can be more severe than in natural systems (Díaz and Rosenberg, 2008; Middelburg and Levin, 2009). For instance, climate model experiments suggest that OMZs may be sensitive to the evolution of the carbon-to-nitrogen ratio in a warming atmosphere, with a projected expansion of the marine dead zones having severe potential implications for oxygen-sensitive nutrient recycling (Oschlies et al., 2008).

Hence the overall deterioration of ecosystems affected by coastal hypoxia could be wrongly estimated, if evaluation is only based on short-term studies. Studies of episodic hypoxia events do not usually permit the consequences of such events on food-web structure to be fully assessed, and hence the ultimate effect on ecosystems has not been properly determined. Recent insight into the non-linear links between temperature, oxygen and CO_2 on the scope for growth of marine organisms opens a new way of investigating the response of ecosystems to hypoxia variability (Portner and Knust, 2007). Recent insight into the non-linear links between temperature, oxygen and CO_2 on the scope for growth of marine organisms also opens a new way of investigating the response of ecosystems to hypoxia variability (Portner and Knust, 2007; Portner, 2008). Thus the up-scaling of stoichiometry of carbon and other macro- and/or micro-nutrients at different temporal and spatial scales should be viewed with caution.

10 Impact of coastal hypoxia on pelagic fisheries and economics

Hypoxia affects several different aspects of coastal ecosystems such as the food-web structure, habitat loss and recruitment of fishery species. These changes, in turn, may have a profound impact on social (i.e. traditional catch vs. mari-culture) and economic sectors, including tourism in addition to fisheries (Ekau et al., 2009). It is known that depletion of dissolved oxygen in near-bottom waters can damage the benthic fauna by destroying habitats, which in turn imposes a negative effect on the life history of fish. Under low-oxygen conditions, the physiological processes and life cycles of biota can be disrupted (Table 1). Water-column hypoxia affects reproduction, either because fish avoid low oxygen waters for spawning, or because sperm are inactivated or the eggs will not hatch (Nissling and Westin, 1997). Hypoxia in the coastal environment can alter the development (e.g. physiology and life cycle), recruitment, patterns of species distribution and migration (cf. Bertrand et al., 2008) in coastal upwelling (e.g. Peru coast) as well as other areas, ultimately affecting the evolution of species. Adult nektonic species may avoid areas of low DO waters and develop adaptive migrational strategies; euphausiids, embryos, larvae and juveniles are less mobile and subject to damage when the concentration of DO is too low in the water column. Thus, changes in average DO levels and the amplitude of variability can have different impacts on the survival and composition of different species in an ecosystem, with consequent changes in trophic relationships and productivity. Moreover, reduction of DO and an increase in the areal extent of hypoxia can lead to cascading effects on benthic as well as pelagic species, including community and food-web structure reorganization (Bograd et al., 2008; Stramma et al., 2009). These latter effects are of particular concern in the fisheries of the coastal ocean where pelagic and benthic processes are usually tightly linked. Hypoxia in coastal near-bottom waters impacts the benthic fauna by selecting mostly low-oxygen resistant species, thus reducing the diversity. The threshold level of dissolved oxygen for the survival and metabolism seems higher for pelagic species (e.g. fish) than benthic fauna (e.g. crustacean and mollusks), because nektonic individuals can escape from hypoxic waters while sessile species have had to adapt to the low DO conditions, sometimes via specific enzyme metabolisms. Low DO levels can severely impact egg development leading to retarded hatching in fish or complete quiescence in copepods (Ekau et al., 2009). Besides the direct lethal effects of hypoxia, sub-lethal responses to low DO concentrations, such as the reduction of egg production, food-intake, sex-selection and other stress symptoms (e.g. schooling), can also have an important impact on the population and community dynamics of ecosystems.

In shallow-water environments, the surface layer is used as a refuge for planktonic organisms when hypoxia occurs in near-bottom waters and hypoxia compresses the vertical and horizontal dimensions of living space; in deep-water environments (e.g. eastern boundary upwelling systems), organisms such as copepods, squids or certain fish species (e.g. horse mackerel, hake or gobies in the Benguela upwelling system off Namibia) (Ekau et al., 2009) have developed vertical migration strategies, and are able to migrate into and out of low oxygen water masses as a means to cope with OMZs.

In summary, at basin-wide macro-scales and at the ecosystem level, hypoxia can constrain the distributions of fish species both vertically and horizontally, can force organisms to depart from their normal behavior (e.g. through migration and reproduction), and can change the predator-prey relationships. At sub-basin meso-scales and at the organism level, hypoxia will cause changes in physiology (e.g. metabolism and growth rate) and alter life-cycle performance (e.g. larval settlement of benthic species) and vulnerability to perturbations (e.g. diseases and toxicity).

11 Feed-back to the Earth System

One of the distinguishing characteristics of coastal hypoxia is its potential for a strong feed-back to climate through changes in atmospheric composition (Fig. 4). The ocean is an important source of N_2O to the atmosphere, but only a moderate contributor to the atmospheric CH_4 budget. The production and consumption of both gases is strongly dependent on the ambient oxygen level, and their emissions to the atmosphere per unit area from regions experiencing hypoxia are higher than the oceanic average values (Table 2 and Fig. 5). Thus, the ongoing change (general decline) in oxygen distribution in the ocean may affect these fluxes.

Most of the CH_4 accumulating in bottom waters is believed to be derived from anoxic sediments (Reeburgh, 2007), and so the DO/redox state of bottom waters is expected to affect the rate and depth of production of CH_4 in the sediment as well as its oxidative loss in water and in the upper sedimentary column. All hypoxic systems accumulate CH_4 to varying degrees depending upon the basin morphology and the extent of oxygen deficiency in the water column (Naqvi et al., 2009). Maximal build-up (at μM levels) occurs in sulphide bearing waters of semi-enclosed basins such as the Black Sea and Cariaco Basin, followed by (in tens of nM) silled basins overlain by hypoxic/suboxic waters (e.g. in the Gulf of California). Along the open coasts (e.g. up-welling areas), CH_4 content of bottom waters responds to changes in ambient DO too. Again the sulphidic bottom waters have the highest CH_4 concentrations at hundreds of nM over the Namibian shelf (Scranton and Farrington, 1977), but comparably high concentrations could also occur in hypoxic/suboxic bottom waters not containing hydrogen sulphide, e.g. in the northern Gulf of Mexico (Kelley, 2003). However, there are two factors that introduce complexities in the interpretation of CH_4 data from coastal settings. First, the regions of freshwater influence that are often sites of coastal hypoxia (e.g. Gulf of Mexico and Indian shelf), receive large allochthonous inputs of CH_4 from coastal wetlands (Jayakumar et al., 2001). Second, despite the prevailing oxic conditions, CH_4 production still occurs in the surface layer by processes that are still not fully understood (Scranton and Brewer, 1977; Reeburgh, 2007; Karl et al., 2008). As hypoxia – both natural and human induced – occurs in regions of high primary productivity where in situ CH_4 production rate in is also high, it is difficult to differentiate such production from enhanced emissions from the sediments (Scranton and Farrington, 1977).

Due to the oxidative loss, accumulation of CH_4 in bottom waters generally leads to a modest increase in its efflux to the atmosphere. However, in the Changjiang (Yangtze River) Estuary, Zhang et al. (2008) found the sea-to-air flux of CH_4 as high as

250–400 μmol m^{-2} day^{-1}, which is twenty times higher than the flux from shelf mixed water (e.g. 10–15 μmol m^{-2} day^{-1}) and up to three orders of magnitude higher than the flux from surface waters of the Kuroshio (<0.5 μmol m^{-2} day^{-1}). However, this could also be due to enhancement of surface CH_4 concentration affected by fresh water run-off. As already pointed out, the ocean's contribution to the atmospheric CH_4 budget is relatively insignificant at <2% (cf. Reeburgh, 2007), and so unless CH_4 emissions from the global ocean are enhanced by an order of magnitude or more, expansion/intensification of coastal hypoxic zones is unlikely to match increases in atmospheric CH_4 fluxes from other anthropogenic sources (Naqvi et al., 2009).

The situation is different for N_2O, which is formed mostly in the water column, as opposed to a large part of CH_4 production occurring in the sediments, both by oxidizing (e.g. nitrification) and reducing (e.g. denitrification) processes. Moreover, N_2O loss in the water column is much more restricted. Nitrification is an aerobic process, but low DO levels cause an enhancement of N_2O yield presumably through nitrifier–denitrification (Yamagishi et al., 2007). Anaerobic denitrification involves both production and consumption of N_2O (Codispoti and Christensen, 1985). Thus, while N_2O is lost through its reduction to N_2 within the cores of the open ocean OMZs and in deep (e.g. anoxic) waters of semi-enclosed basins, highest concentrations (ca. tens of nM) are always found at the edges of the OMZs, thereby making them strong net sources of N_2O (Table 2) (Codispoti and Christensen, 1985). The extent of this build-up at the oxic-anoxic boundary in the semi-enclosed anoxic basins is much smaller, for reasons that are not yet clear (Naqvi et al., 2009). On the other hand, naturally formed hypoxic systems that periodically experience sulfuric conditions at shallow depths along open coasts, such as the western Indian continental shelf, are distinguished by abnormally high N_2O build-up (i.e. up to hundreds of nM), seemingly due to production via denitrification (Naqvi et al., 2000, 2006). Moreover, since this production occurs very close to the surface, it supports high fluxes of N_2O to the atmosphere. For example, it is estimated that the Indian shelf itself could emit as much as 0.4 Tg N_2O to the atmosphere annually (Naqvi et al., 2000).

Most of the available data on N_2O from hypoxic marine environments comes from natural systems, although it is likely that some of these systems, particularly the Indian shelf, have also been significantly impacted by human activities (Naqvi et al., 2000). In the few coastal hypoxic systems that are mostly anthropogenically formed and have been sampled for N_2O, substantial enhancement of N_2O concentration has been reported. For instance, off the mouth of Changjiang in the East China Sea, concentrations of N_2O in the hypoxic layer ($O_2<63\,\mu M$) can be as high as 40–60 nM as compared to 10–20 nM in the overlying surface waters and 5–10 nM at the surface further offshore over the open shelf (Zhang et al., 2008). Accordingly, the sea-to-air flux of N_2O from the region is 50–100 $\mu mol\,m^{-2}\,day^{-1}$, an order of magnitude higher than the N_2O flux for shelf mixed water of the East China Sea ($<10\,\mu mol\,m^{-2}\,day^{-1}$) and Kuroshio Surface Waters ($<5\,\mu mol\,m^{-2}\,day^{-1}$) (Zhang et al., 2008). Even higher fluxes are expected from hypoxic zones when the stratification is eroded by mixing caused by convection and wind/wave induced turbulent mixing, particularly during extreme events such as storms (Naik et al., 2008). This applies equally well to other greenhouse gases (e.g. CO_2 and CH_4). Oceanic contribution to the atmospheric N_2O inventory is globally highly significant, with the regions of coastal upwelling/low DO serving as disproportionately large sources (Codispoti et al., 1992; Naqvi et al., 2000; Bange et al., 2001; Nevison et al., 2004). Thus, the ongoing intensification and expansion of coastal hypoxic zones (Díaz and Rosenburg, 2008) is likely to lead to a significant increase in N_2O emission from the ocean. However, a reliable quantitative prediction of this increase is not possible at present because of uncertainties concerning the mechanisms of N_2O production as well as insufficient data from key coastal regions.

The role of expanding shelf hypoxia on the global CO_2 budget also needs to be considered. Recent work has shown that shelf systems are a net CO_2 sink with a magnitude of 0.36 $Pg\,C\,yr^{-1}$ (Chen and Borges, 2009) compared to an ocean CO_2 sink of $1.8\pm0.7\,Pg\,C\,yr^{-1}$ (Doney et al., 2009). The predicted expansion of shelf hypoxia, both natural and anthropogenically forced, will reduce the magnitude of the recently estimated CO_2 sink. The magnitude of this factor will depend on changing rates of biological production and remineralization, redox conditions and rates of physical upwelling.

In summary, profiles of CH_4 and N_2O reveal high concentrations in coastal hypoxic waters, which can considerably enhance the emission to the atmosphere, especially when stratification is broken down by turbulent vertical mixing. Such high CH_4 and N_2O stocks in deep and near-bottom waters of coastal hypoxic regions can also be exported to the open ocean by circulation and dynamic processes across the shelf break, an important component of the "Continental shelf pump" for carbon and other nutrients (Fig. 4). Thus, although coastal eutrophication may induce CO_2 uptake through enhanced photosynthesis (e.g. phytoplankton blooms), the development of hypoxia, sometimes the "Twin sister of Eutrophication", can be accompanied by production of a large amount of CH_4 and N_2O, which in turn has significant feed-backs to the atmosphere and the ocean interior, and hence contribute to changes in the global climate (Fig. 4).

12 Key questions and topics for future research

Coastal hypoxia can be considered as a transitional state of marine ecosystems passing from normoxia to anoxia, and vice versa, although complex forcing and feed-back relationships can be involved, like threshold and hysteresis in the shift from one quasi-stable regime to another (Fig. 6). Key findings of SCOR Working Group #128 offer insights that are relevant for both observational work and modeling. However, our currently limited knowledge does not allow a direct link to be established between modern hypoxia and geological records, in part owing to uncertainties in our understanding of biogeochemical processes associated with coastal hypoxia and of the physical processes involved in the transport of water mass properties, in eastern boundary current systems in particular. Some of the key issues center on questions such as evolution of hypoxia and the responses of ecosystems. The following observations and hypotheses merit future attention:

- With respect to nutrient dynamics in coastal hypoxia, the stoichiometry and different rates of cycling between macro- and/or micro-nutrients and their link to the carbon cycle are of critical importance in determining consequences for ecosystems. This in turn will dictate the change in food-web structure that develops and the subsequent biogeochemical balance between cycling of carbon within the system, export to the open ocean, and feed-back mechanisms to the atmosphere.

- Although the external nutrient supply from land-sources is important, the intrinsic factors that influence biogeochemical cycling in coastal hypoxic systems are critical. We hypothesize that the development of hypoxia is determined by the rate and magnitude of mineralization of macro and micro-nutrient species and in particular by their retention in the water column. For nutrient supply in upwelling systems, these processes include mixed-layer water residence time, climatic forcing such as the monsoons or equatorial oceanic waves, and the variability and characteristics of deep water that up-wells over the shelf (e.g. concentration of DO).

- It has been realized that coastal hypoxia can have a strong impact on the function of other compartments of the Earth System in the context of global change. For instance, data from this SCOR Working Group #128 have shown that sea to air emission flux of certain greenhouse gases from coastal hypoxic regions can be much stronger than in other parts of ocean, which in turn, affects the radiative heat balance of the atmosphere. Also, chemical species produced in hypoxic waters (e.g. CH_4, N_2O, Fe^{2+}, nutrients and CO_2 etc.) can be advected to the open ocean through the mechanism of the continental shelf pump.

Regarding the issue of multi-stressors and responses of the coastal environment such as hypoxia, the marine ecosystem is poorly known compared with its terrestrial counterpart. The relative importance of the processes that underpin coupling between biogeochemistry and physics and the driving mechanisms, either regional or remote or both, will vary temporally and spatially. These processes, which regulate the export of nutrients and carbon, include the differential rates of degradation of organic matter in subsurface waters. Each of these, in turn, will be determined by a range of factors such as remineralization rates, food-web interactions and composition and properties of organic matter and their transformation (e.g. sinking and export efficiency) (Table 3). Sensitivity analysis using coupled physical and biogeochemical models can be performed for evaluating separately the roles of increased freshwater discharge (i.e. buoyancy forcing) and increased nutrient loading from the watershed on the extent and duration of hypoxic conditions.

The future development of hypoxia in coastal waters will inevitably reflect interactions among the multiple effects of climate change. Ocean warming leads not only to increased stratification and sea level rise, but also to reduced oxygen solubility in seawater and oxygen out-gassing, enhanced respiratory rates (Q10 effects), and reduced thermal capacity of organisms. Reduced oxygen supply to tissues can be the first mechanism to restrict whole-animal tolerance to thermal extremes (Portner and Knust, 2007). In certain parts of the world, atmospheric warming will lead to increased inputs to the coastal zone of river-derived freshwater and nutrients, exacerbating eutrophication and algal blooms, and oxygen demand (Rabalais et al., 2009a). Warming can also alter wind patterns with changes in coastal circulation, upwelling and downwelling that reduce open coast oxygen levels through advection or mixing suppression and lead to expansion of oxygen minimum zones onto continental shelves (Stramma et al., 2008; Bograd et al., 2008; Stramma et al., 2009). Concomitant effects of increased dissolved CO_2 in the ocean are causing acidification and declining carbonate saturation. The interactive effects of regional hypoxia and large scale ocean acidification (i.e. lower pH in hypoxic and anoxic waters) are unknown, but much of the Northeastern Pacific Shelf is bathed seasonally by up-welled corrosive waters (Feely et al., 2008), undoubtedly adding stress to calcifying organisms already exposed to episodic hypoxia. These climate-related modifications of hydrography also interact with pollution, over-fishing, exotic species invasions, and various forms of coastal habitat loss. Understanding of hypoxia in the future ocean must involve a holistic perspective that recognizes linkages among various forms of anthropogenic forcing and ecosystem responses.

Most of the eastern boundary current systems (e.g. Benguela, Peru/Chile and California, etc.) are influenced to a large extent by the tropical climate and ocean variability, which make them sensitive to climate change in two ways: 1) regional change in atmospheric circulation may lead to change in upwelling conditions (Bakun and Weeks, 2008) and 2) change in tropical (Vecchi et al., 2006; Yeh et al., 2009) or subtropical (Garreaud and Falvey, 2009) circulation may have also a direct impact on the upwelling variability by modifying the energy spectrum of the remote (equatorial Kelvin wave activity) and local (atmospheric coastal jet) forcing. Both of these processes will have a profound influence on the severity and expansion of hypoxia and hence the structure and function of ecosystems.

The case studies of this SCOR WG #128 indicate complex mechanisms involved in the relationship between causative factors (e.g. conditions that cause hypoxia) and ecosystem responses (e.g. food web structure and function). Analyses of historical data suggest that response trajectories can be system specific, either simple linear or non-linear, or both (Kemp et al., 2009 and Fig. 6). While there is a socio-economic commitment to remediation of coastal hypoxia (e.g. reducing nutrient loading from the adjacent watersheds), a system specific "threshold" in ecosystem function may exist in the recovery from coastal hypoxia through reduction of nutrient loadings, with a hysteresis and possibility of regime shifts (Fig. 6). In some of the coastal ecosystems experiencing multiple perturbations (e.g. species invasion, fishing harvest and climate alteration), the "baseline conditions" (i.e. background in Fig. 6) can be changed when the stressors are released, which leads to situations where complete recovery of hypoxia to pre-disturbed conditions can not be achieved simply by reducing the driving forces (e.g. nutrient loading) (Van de Koppel et al., 2009; Kemp et al., 2009). Moreover, since an ecosystem usually responds to the external forcings from a combination of stressors and complex interactions within the system, removal of a single forcing factor (e.g. reduction of nutrient input) may not necessarily be followed by the return of the ecosystem to its pristine state.

Testing these processes will require both system specific examinations and multidisciplinary studies that link biogeochemistry and global change across different oceanographic settings. Several approaches can be proposed:

- Modeling studies to incorporate our understanding of coastal hypoxia in the modern ocean to reconstruct conditions back in time to the beginning of the Anthopocene and to predict future states. Coupled physical-biogeochemical-ecosystem models will allow to better address several important questions, including causes of the observed worldwide increase in hypoxic conditions, and future changes in the intensity and spread of coastal hypoxia. Model simulations can be used to capitalize on the complementary approaches obtained by previous studies into pulsed anthropogenic perturbations vs. sustained climate variability. Considering the rather coarse resolution of the current generation coupled ocean-atmosphere-biogeochemical models, dowsnscalling experiments using high-resolution regional models should be promoted in order to provide background materials for the understanding of coastal hypoxia, in particular in the context of climate change.

- Improved experimental and/or observational designs to overcome limitations of individual and discrete studies, and additional measurements that will provide insight into the impact of nutrient enrichment on climate change (e.g. biogenic gases) and biogeochemical cycling (e.g. link between coastal and open ocean). Carefully designed comparative studies between different ecosystems that are affected by coastal hypoxia will help better determine the influence of supply and regeneration of nutrient species on global biogeochemistry. Such approaches rely, however, on innovative technologies (e.g. Argo and sensor arrays), and should be managed in a way that links them to circulation models with embedded biogeochemical modules.

- Biogeochemical studies that jointly measure key parameters in coastal hypoxia, such as nutrients (e.g. C, N, Si, P, and Fe etc.), phytoplankton and microbes, will require specific investigations of typical hypoxic systems, such as coastal upwelling systems, areas off large rivers, and semi-enclosed basins. This, in conjunction with improved observational techniques, will indeed advance our knowledge of temporal and spatial controls on the occurrence and evolution of hypoxia and its impact on ecosystems across the global coastal ocean.

Despite its limited lifetime, SCOR Working Group #128 was able to address the major issues of coastal hypoxia across different types of ecosystems within the global ocean (Table 3). The series of 10 papers in this Special Issue of *Biogeosciences* on "Coastal Hypoxia" provide a snap-shot of our experiences dealing with the global significance of coastal hypoxia under the influence of multiple natural (e.g. climate variability) and anthropogenic (e.g. nutrient loading from watersheds) stressors. Such an approach will contribute to our understanding of how entire marine ecosystem functions are affected by coastal hypoxia on time scales of a few years to thousands of years and on spatial scales from small estuaries and embayments to the open ocean, as well as improving our confidence in the remediation measures applied to coastal hypoxia.

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Table 1. Comparison of behaviors of biota in marine areas affected by coastal hypoxia.

Category	Description of Behavior	Examples
Pelagic systems		
Up-welling region	Change in vertical migration of pelagic species, increase in possibility of prey – predator encounter within the compressed habitat and reduction of bio-mass	Benguela current – Namibia, Humboldt Current – Peru
Large river estuary	Increase in ratio of heterotrophic bacteria to autotrophic species, reduction of fish biomass, and change in biodiversity and dominance of economic species	Changjiang (Yangtze River) – East China Sea, Mississippi River – Gulf of Mexico
Fjord and semi-enclosed basins	Increase in recycled relative to new production and change in community composition, enhanced diversion of energy flows into microbial pathways to the detriment of higher trophic levels	Baltic Sea, Black Sea
Benthic fauna		
Up-welling region	Habitat compression, increase in mortality of benthic species, and shift of food web structure	California Current off Oregon, Central Peru system
Large river estuary	Lower abundance and species biodiversity, change in benthic fauna composition, and size spectrum	Changjiang (Yangtze River) – East China Sea, Mississippi River – Gulf of Mexico
Fjord and semi-enclosed basins	Change in redox conditions and mineralization for nutrients and trace elements, habitat compression, and increase in nutrient flux from sediment to near-bottom waters	Baltic Sea, Black Sea

Table 2. Emission fluxes of CH_4 and N_2O (unit: μmol m^{-2} d^{-1}) from major coastal hypoxic zones.

	CH_4 flux (μmol m^{-2} d^{-1})	
Region	Range	References
Northwest Africa (Canary Current)	0.4–1.7	Kock et al. (2008)
Southwest Africa (Benguela Current)	30.1–60.2	Scranton and Farrington (1977)
Northern Indian Ocean (Arabian Sea and Northern Bay of Bengal)	0–63.7 0.2–24.9	Naqvi et al. (2005), Berner et al. (2003)
Eastern North Pacific (California Current)	0.77–3.0 0.5–5.9	Sansone et al. (2001), Sansone et al. (2004)
Eastern South Pacific (Humboldt Current)	0.86–18.7	Farias et al. (2009)
Baltic Sea	30.9–367	Bange et al. (1998)
Black Sea	29–450	Amouroux et al. (2002)
Changjiang (Yangtze River) Estuary and East China Sea	0.02–440	Zhang et al. (2008)

	N_2O flux (μmol m^{-2} d^{-1})	
Region	Range	References
Northern Indian Ocean (Arabian Sea and Bay of Bengal)	0.1–351	Naqvi et al. (2005)
Eastern North Pacific (California Current)	–0.8–5.5	Cohen and Gordon (1978)
Eastern South Pacific (Humboldt Current)	3.9–15.1 –9.8–195 –2.3–42.9	Bange et al. (2001), Cornejo et al. (2007), Farias et al. (2009)
Baltic Sea	1.38–581 2.75–53.8	Bange et al. (1998), Rönner (1983)
Black Sea	1.6–5.2	Amouroux et al. (2002)
Changjiang Estuary and East China Sea	–0.7–97.5	Zhang et al. (2008)

Table 3. Summary of coastal ecosystems affected by hypoxia with different natural and anthropogenic driving forces.

Category	Type of Hypoxia	Natural Forcings	Anthropogenic Factors	Potential Impact on the Ecosystem Function
Large river estuary (e.g. Mississippi River and Changjiang)	Episodic and/or periodic events	Land-source nutrients influx, change in runoff affecting stratification	Increase in nutrient and organic matter loads	Deterioration of habitats, changes in nutrient ratios affecting phytoplankton assemblages
Semi-enclosed basin (e.g. Black Sea and Baltic Sea)	Periodic and/or persistent events	Limited water exchange with open ocean (e.g. increase in flushing time)	Nutrient influx from surrounding land masses and change in nutrient ratio	Loss of some benthic species, release of toxic chemicals (e.g. H_2S into water column)
Coastal up-welling area (e.g. Namibia and Peru)	Seasonal and/or persistent events	Equatorial variability and change in local circulation pattern (e.g. coastal trapped waves, mixing and Ekman pumping); interaction of OMZ with narrow shelf with seasonal stratification and high organic matter flux	Increase in vertical organic matter flux related to high primary production that can sometimes be related to nutrient influx from land-sources	Decoupling of pelagic and benthic processes, and loss of benthic species; habitat limitation and modulation of sub-thermo-cline species life cycle, as well as periodic strandings of benthic organisms

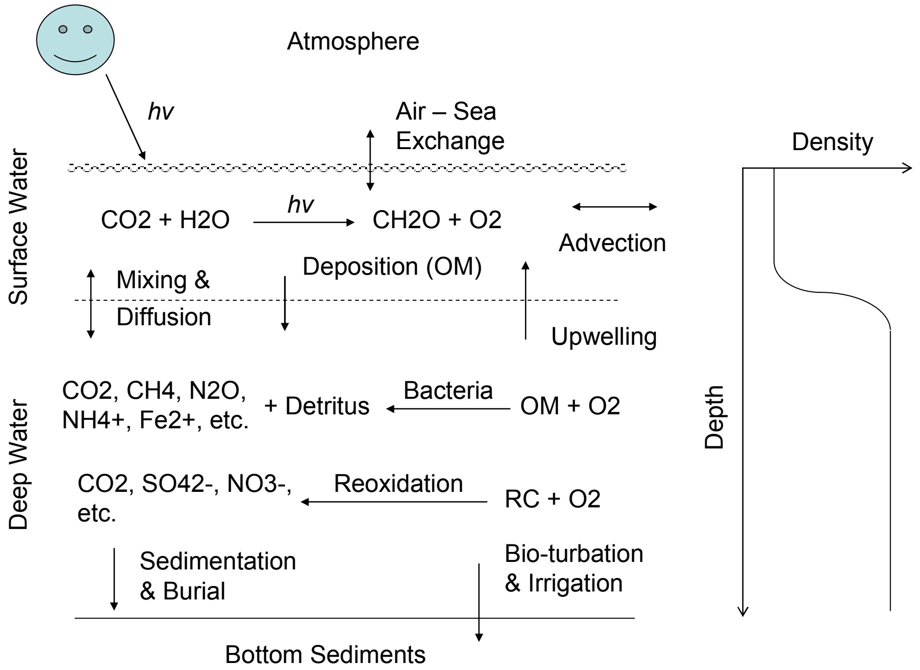

Fig. 1. Major mechanisms of production and consumption for dissolved oxygen (DO) in the coastal environment. In surface waters, high DO can be maintained by photosynthesis and exchange with the atmosphere. Advection and turbulent mixing also affect the DO concentrations for a given water mass. In the deep part of the water column (e.g. beneath the pycnocline) and in bottom sediments, heterotrophic metabolisms (e.g. respiration), degradation of organic matter (OC), reoxidation of reduced constituents (RC) such as sulfide, methane etc., as well as chemoautotrophy (e.g. oxidation of ammonium) consume DO with a variety of pathways and, when the consumption exceeds DO supply, hypoxia develops.

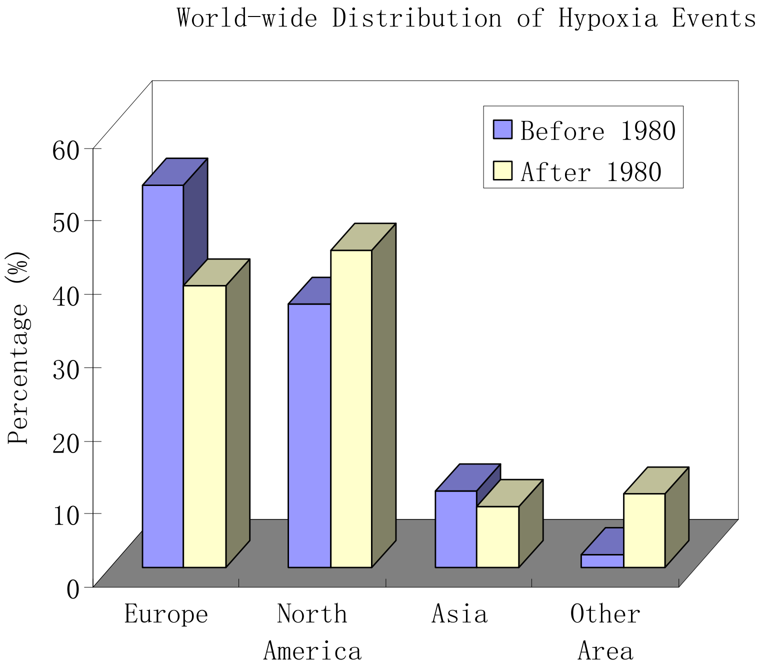

Fig. 2a. Comparison of world-wide distribution of hypoxic systems before and after 1980, with **(a)** hypoxic systems per geographic category, and **(b)** classification according to type of hypoxia: Eps – episodic, Pe/Se – periodic and seasonal, Per – persistent, and Unk – for which the hypoxia behavior is not well recognized (i.e. unknown). Data are from Díaz and Rosenberg (2008).

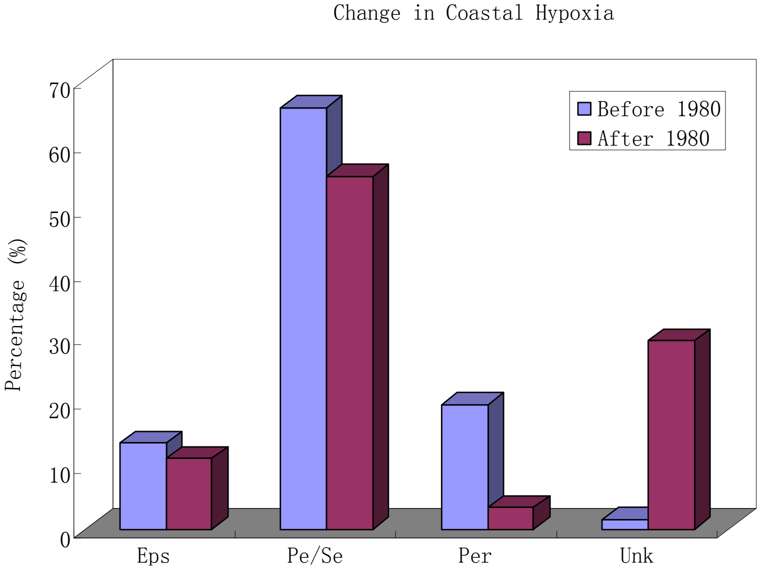

Fig. 2b. Continued.

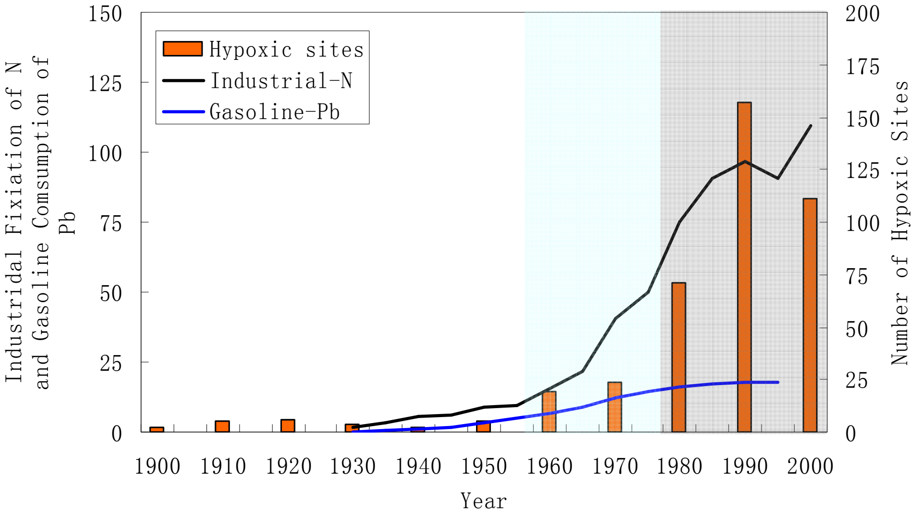

Fig. 3. Temporal relationship between the number of coastal hypoxic sites (Hypoxic sites: events/decade), accumulative industrial fixed nitrogen (Industrial-N: $\times 10^6$ tons), and alkyl Pb consumption (Gasoline-Pb: $\times 10^5$ tons) in US and major European countries (i.e. France, Germany, Italy and UK, altogether accounting for 70% of EU gasoline consumption). Gasoline-Pb is another indicator of anthropogenic perturbations on marine environment but mostly through the atmospheric pathway. The leveling-off of alkyl Pb consumption took place in the 1970–1980s because of bans against lead use in gasoline, and since then Pb level in ocean surface waters has decreased. Industrial fixed nitrogen, mainly used for fertilizer application, shows a fast increase in the 1960–1970s and a slow-down after 1980s; the number of coastal hypoxic sites per decade dramatically increased after the 1960s and reached a peak in the 1990s. It is believed that 1960–1980 was a period of explosive increase of coastal eutrophication (light green shadowed area). However, in developing and economically emerging countries, coastal eutrophication and hypoxia has become more serious in the period of 1980–2000 (grey shadowed area) (modified from Boyle, 2001; Boesch, 2002; Díaz and Rosenberg, 2008).

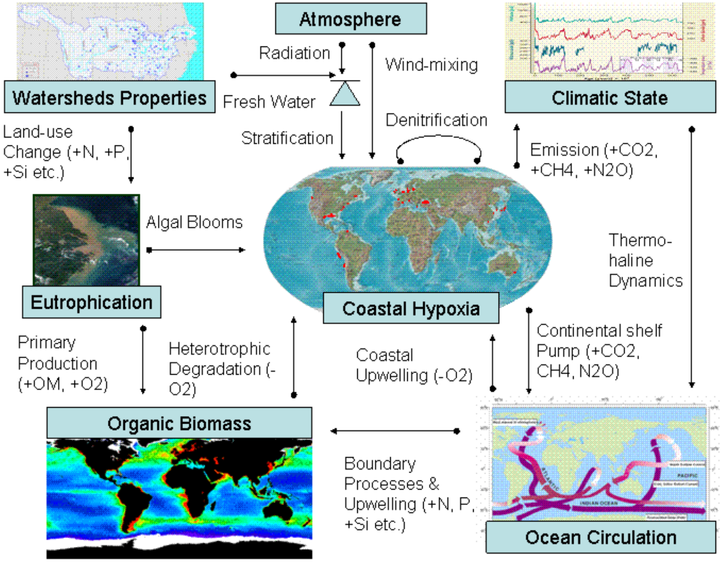

Fig. 4. Schematic view of hypoxia in the global coastal ocean, in which critical mechanisms and state of availability of nutrients, coastal hypoxia, marine primary productivity, and effect of climate change are highlighted. In the figure, the boxed variables are linked by a line terminated with a solid arrow head if the correlation is positive or with a circle if the correlation is negative. The amplification and/or regulation of driving forces are displayed with a sign of audio symbol. Usually, stratification in coastal environments is caused, and subsequently maintained, by surface-layer warming and fresh-water input from rivers (e.g. buoyancy effect), or excess rainfall (e.g. during the monsoon season off India), a combination that has a more significant effect than any single factor. Changes in land-use, application of chemical fertilizers in agriculture and hydrographic engineering (e.g. damming) can induce variations in fresh waters and nutrients influx to the adjacent marine waters. An increase in deposition flux of organic matter, either labile (e.g. plankton detritus from in situ production) or refractory (e.g. soil organic materials from watersheds), or both can stimulate heterotrophic metabolisms (e.g. respiration) and chemoautotrophy (e.g. oxidation of ammonium) in the deeper part of the water column and bottom sediments, using oxygen as electron acceptor. Climate state affects the variability of ocean circulation, and hence the development of coastal hypoxia through boundary circulation – shelf/coast interactions. All these dynamic processes affect the inventory of dissolved oxygen in the coastal environment, and hence the fate of hypoxia; the combination of different processes often has a more profound impact than any single factor on the persistence of coastal hypoxia. In terms of feed-backs to Earth System, coastal hypoxia is a source of trace gas species (e.g. CH_4 and N_2O) to the atmosphere and open ocean, and in extreme cases like in the Gulf of Mexico, CH_4 concentrations in surface waters are up to 1000 times saturation with respect to atmospheric equilibrium (Solomon et al., 2009), linked to the escape of hydrate bubbles from marine seeps. The sub-figures are from JGOFS/IGBP and Brook, 2005.

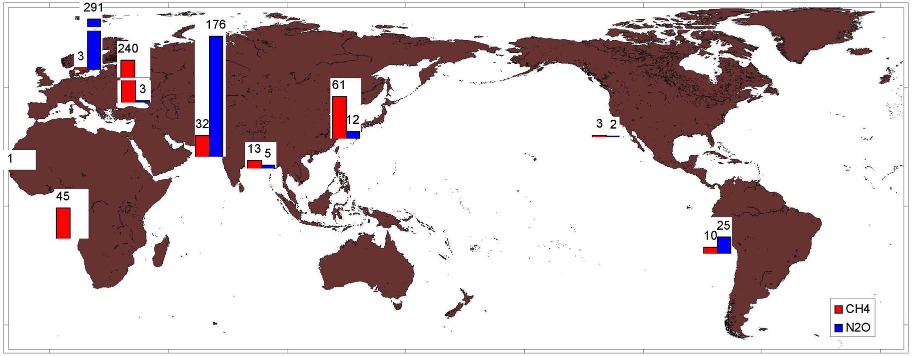

Fig. 5. Sea to air emission flux of CH_4 and N_2O (unit: $\mu mol\,m^{-2}\,d^{-1}$) from major coastal hypoxic environments of the world, including upwelling systems (i.e. Canary Current, Benguela Current, California Current, Humboldt Current), Northern Indian Ocean (i.e. Arabian Sea and Northern Bay of Bengal), Semi-enclosed basins (e.g. Black Sea and Baltic Sea), and off large river mouths and in adjacent shelves (e.g. Changjiang Estuary and East China Sea Shelf). See Table 2 for details of data source. For comparison, CH_4 and N_2O concentrations in the open ocean not underlain by oxygen-depleted waters are close to or slightly supersaturated (i.e. by a few percent) with reference to their atmospheric levels.

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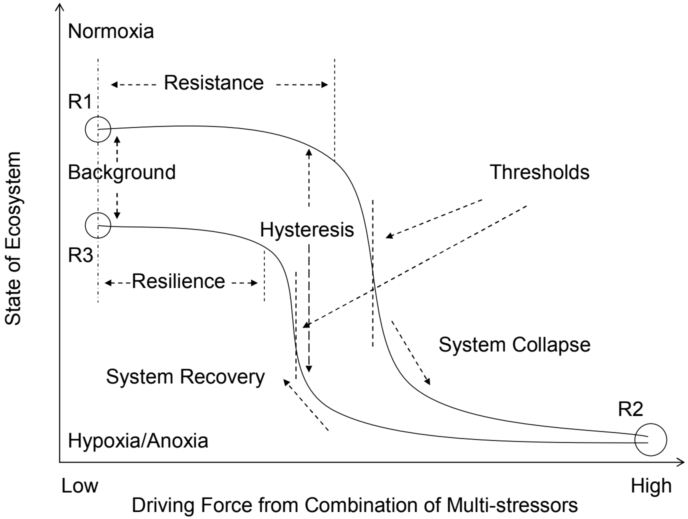

Fig. 6. Conceptual diagram for the response of ecosystems to the conditions of dissolved oxygen in the coastal ocean, along the trajectories of normoxia to hypoxia/anoxia and vice versa. In the figure, R1, R2 and R3 represent different regime states of the ecosystem that can change from one state to another. In most cases, the ecosystem is affected by a combination of multi-stressors with specific regional nature rather than by any single forcing, and hence the system response is not linear. The resistance, hysteresis, threshold, resilience and change in background conditions are characters that dictate the response processes of the ecosystem to the external forcing and/or pressure (e.g. either natural and/or anthropogenic, or both), which is usually very dynamic in the coastal environment. When the system response passes over a threshold (e.g. from R1 to R2), a new ecosystem regime can be reached (i.e. regime shift); in the case of relief from external stressors, the recovery of the ecosystem will follow another pathway and eventually, can have a different background situation (i.e. R3). The figure is a modification based on the work by Tett et al. (2007), van de Koppel et al. (2009), and Kemp et al. (2009).