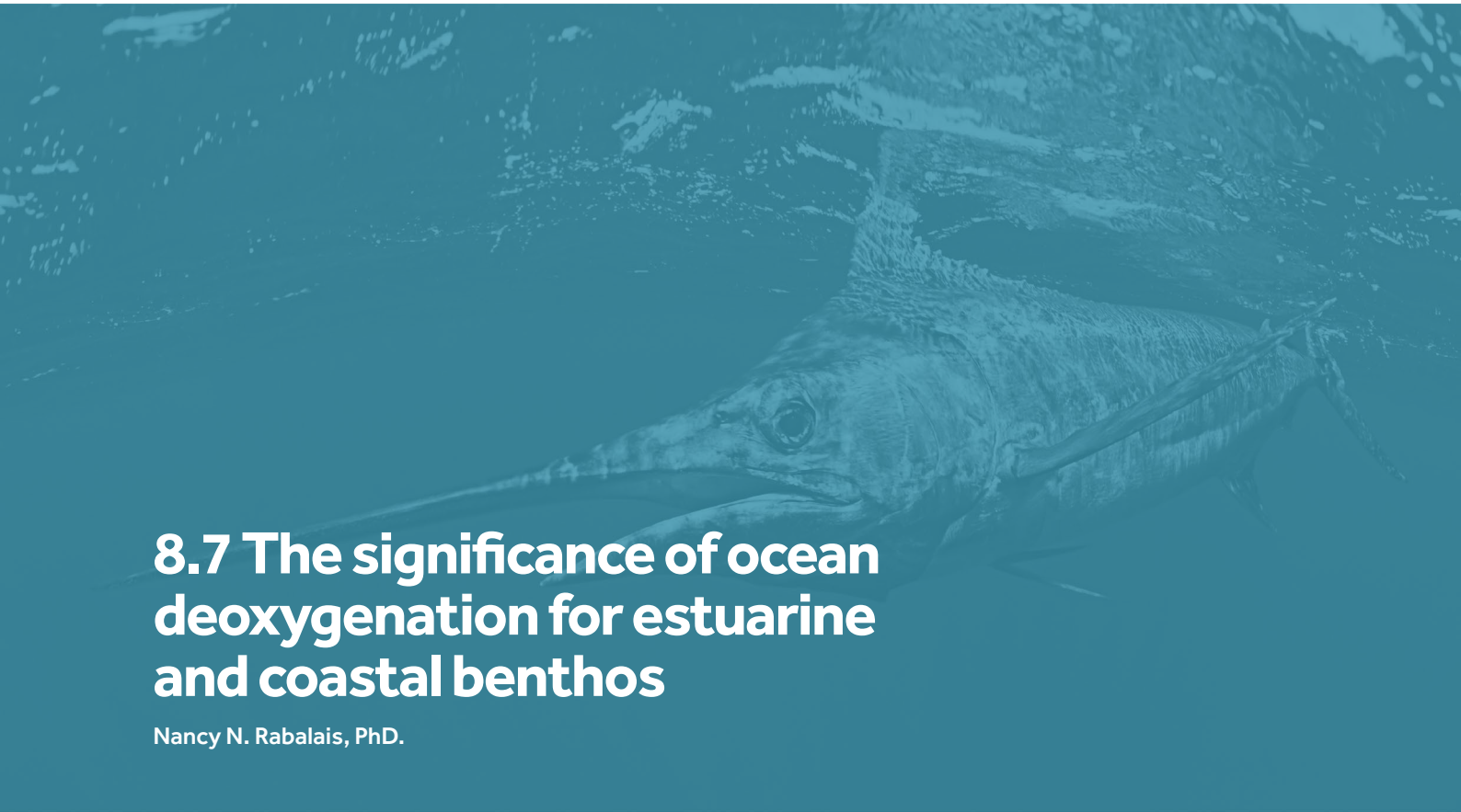




Ocean deoxygenation: Everyone's problem

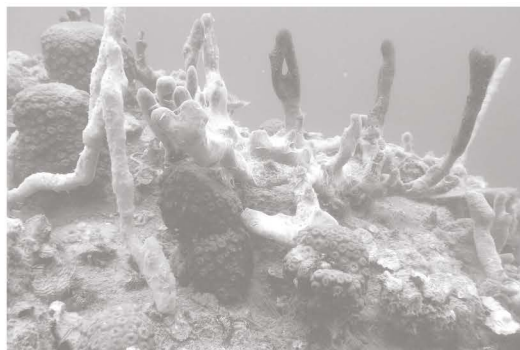
Causes, impacts, consequences and solutions

Edited by D. Laffoley and J.M. Baxter



8.7 The significance of ocean deoxygenation for estuarine and coastal benthos

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IUCN GLOBAL MARINE AND POLAR PROGRAMME



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Summary

- Mobile benthic invertebrates migrate away from water masses with less than 2 mg L⁻¹ dissolved oxygen.
- Diversity in benthic assemblages decreased 13-fold; abundance of benthic infauna, 25-fold; and biomass, 10-fold as dissolved oxygen approached levels of 0.05 mg L⁻¹ in a seasonally severe coastal low oxygen zone.
- As much as 343,000 to 734,000 MT carbon in the form of secondary production is lost from ecosystems annually over 245,000 km² when bottom waters are severely deoxygenated.
- Recovery of benthic communities under improved oxygen conditions may take years to decades and may not approach pre-impact conditions.

Estuaries and coastal hypoxia effects	Potential consequences
Severe deoxygenation on a seasonal basis in coastal waters alters benthic community composition.	<ul style="list-style-type: none"> • Deeper-burrowing infauna are replaced by mostly small, opportunist, surface deposit feeders that live in the upper 2 cm of the sediment. • Diversity, number of taxonomic groups, abundance, and biomass decrease as the dissolved oxygen concentration decreases. • Sediments do not become azoic (multi-cellular organisms are mostly depleted except a few acclimated to severe hypoxia or anoxia). • Microbial communities thrive.
Levels of severity of deoxygenation affect benthos differently.	<ul style="list-style-type: none"> • Developmental life stages are more sensitive to deoxygenation than adults are. • Pericaridean crustaceans will be exterminated before many polychaete worms and sipunculans. • Of the meiofauna, harpacticoid copepods are more sensitive than nematodes.
Loss of infauna from deoxygenation affects ecosystem functioning.	<ul style="list-style-type: none"> • Loss of benthos that are bioturbators allows the redox potential discontinuity to move closer to the sediment-water interface. • Loss of benthic organisms and secondary production decreases food availability to higher consumers. • At severely low oxygen levels, there are effluxes of ammonium and ortho-phosphates from the sediments that generate a negative feedback to further deoxygenation.
Areas of deoxygenation reduce suitable habitat for commercially important species.	<ul style="list-style-type: none"> • Migration of organisms to suitable habitats is prevented and results in reduced growth. • Market prices are affected.

8.7.1 Introduction

There is little doubt that the number of human-caused coastal ocean areas of deoxygenation has increased since the 1960s (Diaz & Rosenberg, 2008) with an approximate doubling of the number of areas every decade since the 1960s through 2007 (see Section 3.2). In the case of many estuaries and coasts, the development of deoxygenation paralleled the increase in nutrient loads (nitrogen and phosphorus) and other pollutants, an increase in human population, overfishing, and dramatic habitat restructuring among others (Breitburg, 2002). Many of the watersheds and airsheds contribute two to three times more nitrogen and phosphorus to receiving water bodies since the 1950s, when landscape alterations expanded, especially for agriculture, high use of artificial fertilizers prevailed, and consumption of fossil fuels increased.

Estuarine waters from the head of tide continuing to the coastal waters of the inner and mid continental

shelf are especially affected by multiple stressors including deoxygenation. These waters are the focus of this section. Compilation of their occurrence through literature citations (Diaz & Rosenberg, 2008) and recent compilations of academic and government data in coastal areas of the Baltic Sea (Conley et al., 2011) brings the global total of estuarine and coastal areas of low oxygen to about 500. The formation of human-caused deoxygenation has occurred in the last seven decades (see Section 3.2) while oxygen minimum zones that impinge on continental margins have existed for millennia (see Section 8.6). Benthos, organisms associated with the sea bed, in the former situation have been exposed to a dramatic change in environmental conditions over the last 50 to 100 years and the consequences have been mostly death and replacement by opportunistic species, rather than evolutionary adaptation in the latter situation. Estuarine and coastal benthos are adapted to changes in salinity and temperature, but the increase in conditions of low oxygen is mostly a recent phenomenon.

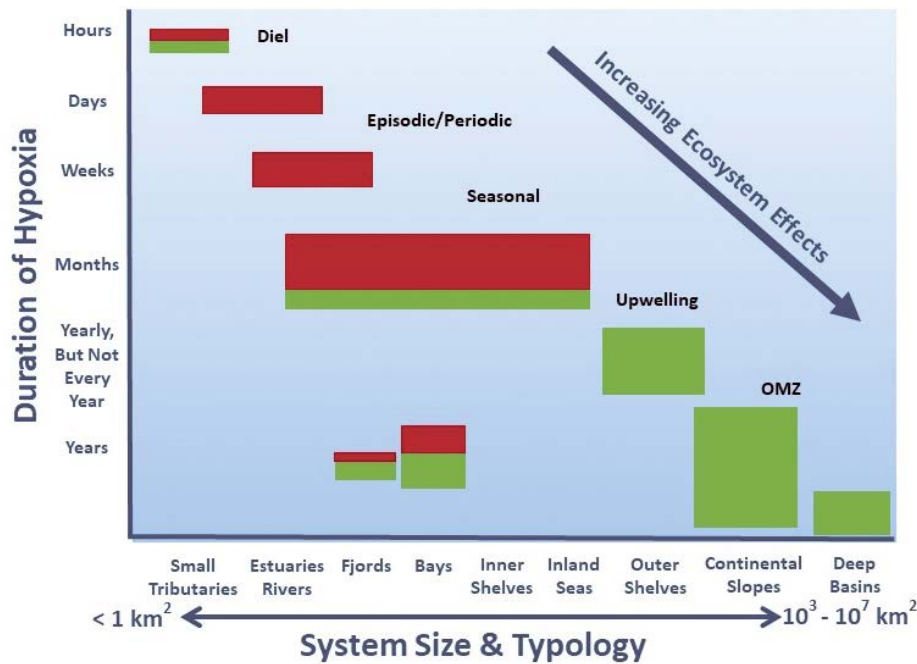


Figure 8.7.1 A synthesis of the variability of temporal, spatial, and typological categories for environments with deoxygenation (modified from Rabalais et al., 2010). The scales are without units but go from lower to higher. The red and green colours represent the relative ratio of human versus natural influences, respectively.

The additional nutrient loads stimulate primary production, the excess carbon from which falls to the lower water column and sea bed and is decomposed by aerobic bacteria that utilize oxygen in the process. The resupply of oxygen is prevented most often because of a temperature- or salinity- (or both) driven density difference (pycnocline). In some instances, a bathymetric shallow feature or sill prevents horizontal renewal of oxygenated waters into those basins that are depleted of oxygen. Estuaries may be microtidal or macrotidal, with the former more likely to have longer water residence times than the latter (Warwick et al., 2018). Coastal waters with a long residence time support the development of stratification, high primary production, and flux of carbon. Circulation or tidal cycles may push the low dissolved oxygen water mass laterally or onshore and offshore, periodically worsening low oxygen conditions or encroaching into better-oxygenated waters. Many shallow estuarine waters host stands of rooted seagrasses or attached macroalgae. The diel cycle in these systems involves high photosynthetic activity and generation of dissolved oxygen during daylight hours, then a period of respiration in the dark results in an oxygen-deficiency occurring late in the night or early morning (Tyler et al., 2009).

Amidst the milieu of physical, chemical and biological processes that generate deoxygenation in estuarine and coastal waters are living biota. The increasingly higher

loads of nutrients and development of deoxygenation, however, have put living resources at risk, including commercially important ones, such as penaeid shrimp, cod, and striped bass. The worsening of eutrophication and hypoxia have been blamed for shifts in community structure and/or declines in abundance of phytoplankton, benthos and fishes (Caddy, 1993; Hagerman et al., 1996; Turner et al., 1998). Benthic organisms reflect the environmental parameters to which they are exposed because of their relative inability to move great distances (e.g. polychaetes, molluscs, and echinoderms) or not at all (e.g. sponges, corals, burrowing crabs, and shrimp). Infauna, living in the sediments, are useful in studies of polluted waterways (Tweedley et al., 2015), and as indicators of ambient dissolved oxygen concentrations. Indicators of stress include community composition changes, food web alterations, loss of biodiversity, and shifts in functional groups.

8.7.2 Definitions and scope

This section addresses the benthos, those organisms living in, on, or associated with the sea bed, and covers primarily multicellular invertebrates, although some information on demersal fishes is appropriate for inclusion. Benthic foraminiferans are amoeboid protists with mineral or calcium carbonate tests that allow for consistent taxonomic identification. Several species maintain unicellular algal endosymbionts or chloroplasts

from ingested algae to conduct photosynthesis, i.e. generation of oxygen, but others succumb to severely low oxygen concentrations ($\sim 0.05 \text{ mg O}_2 \text{ L}^{-1}$) (Gooday et al., 2009). Because of their complex metabolic processes (LeKieffre et al., 2017), they will not be considered here but are good indicators of dissolved oxygen concentrations over millennial time scales or more recent decades or centuries (see Chapter 5). Demersal fishes are mostly excluded from this section because of their ability to escape, but they face other sublethal effects (see Section 8.5). Benthos may be exposed permanently or over extended periods to extremely low oxygen conditions in anoxic ocean basins or semi-enclosed seas, e.g. Black Sea or Cariaco Basin, Baltic Sea proper, deep fjords, and upwelled oxygen minimum zones (OMZs) (Section 8.4; Levin et al., 2009).

The benthos in estuaries and coastal waters are exposed to deoxygenated waters on either (1) a short time period, e.g. days to weeks, (2) a seasonal basis where there are strong pycnocline(s) that prevent reoxygenation; these may be perennial or seasonal, (3) seasonally intermittent deoxygenation where physical forces disrupt longer periods of seasonal deoxygenation, or (4) a diel cycle in areas with subaquatic vegetation. Many of the deoxygenation trends in estuaries and coastal waters are expressed following eutrophication (the increase in the production and accumulation of carbon in an aquatic ecosystem). The responses to either may be similar but can be identified, especially in studies of Foraminifera in accumulated sediments where multiple productivity and deoxygenation indicators can each be identified along with biogeochemical indicators (Chapter 5; Gooday et al., 2009). As human influences increase in shallower waters of the coastal ocean, there are more ecosystem effects (Figure 8.7.1). Upwelling areas and OMZs are primarily natural, but human activities that indirectly affect global climate change are also affecting these areas. OMZs are the largest, most persistent and natural oxygen-depleted areas in the world's ocean and have the greatest ecosystem changes relative to oxygen conditions, but these are the result of adaptation over geological time.

Studies of benthos exposed to lower dissolved oxygen conditions than what is sustainable for life processes take many approaches: use specific groupings by body size (e.g. meiofauna versus macrofauna, dependent on sediment sieve size for collection), employ different collection techniques (e.g. sediment corers, trawls, dredges, video or photographic transects, and digital

imagery), assign isotopic signatures to infer food web changes, apply categories of functional groups or the ratio of one functional group to another, and many others. Measurements of stress may be determined from taxonomic composition changes over time, metabolic stress under hypoxic conditions, behavioural changes, and reproductive physiology. Necessary data to complement studies of benthos responses to lower oxygen levels are the actual dissolved oxygen concentrations. Depending on logistics and resources, records may be for the duration of the experiment, minimal oxygen measurements at the time of study, inferred levels from other studies, or quality-controlled, long-term *in situ* deployed instrumentation. The more ancillary data that are available, the better is the understanding of the results and their implications.

Most multicellular aquatic organisms require dissolved oxygen to live. Physiologists often measure the partial pressure of oxygen available for transfer to tissues (measured in milli-atmospheres, matm , or kPa) to determine the effects of lower than optimal oxygen conditions (Hoffman et al., 2011; Seibel, 2011). Environmental data for aquatic systems, however, measured in units of $\text{ml O}_2 \text{ L}^{-1}$ or $\text{mg O}_2 \text{ L}^{-1}$ are often converted to percentage oxygen saturation to compensate for temperature and salinity (Rabalais et al., 2010). The most commonly used and agreed-to value of dissolved oxygen for estuarine and coastal waters that affects the benthos is 2 mg L^{-1} (equivalents are 1.4 ml L^{-1} , $63 \mu\text{M}$, or 30% saturation).

8.7.3 Range of responses

While the typical value for responses of benthic organisms to oxygen deficiency is 2 mg L^{-1} , there is a continuum of decreasing dissolved oxygen concentrations starting at about 5 mg L^{-1} down to 0 mg L^{-1} where organisms succumb to insufficient oxygen or are affected physiologically or behaviourally (Gray et al., 2002; Vaquer-Sunyer & Duarte, 2008). There is variability in these responses according to the severity, the duration of the exposure, the presence of toxic hydrogen sulphide, the taxon or taxonomic group, the life history stage, and the organism's physiological capacity. Effects on a species are not all the same, but on average result in population effects, and eventually community effects. These responses are mostly determined by the duration and severity of the decrease in oxygen concentration.

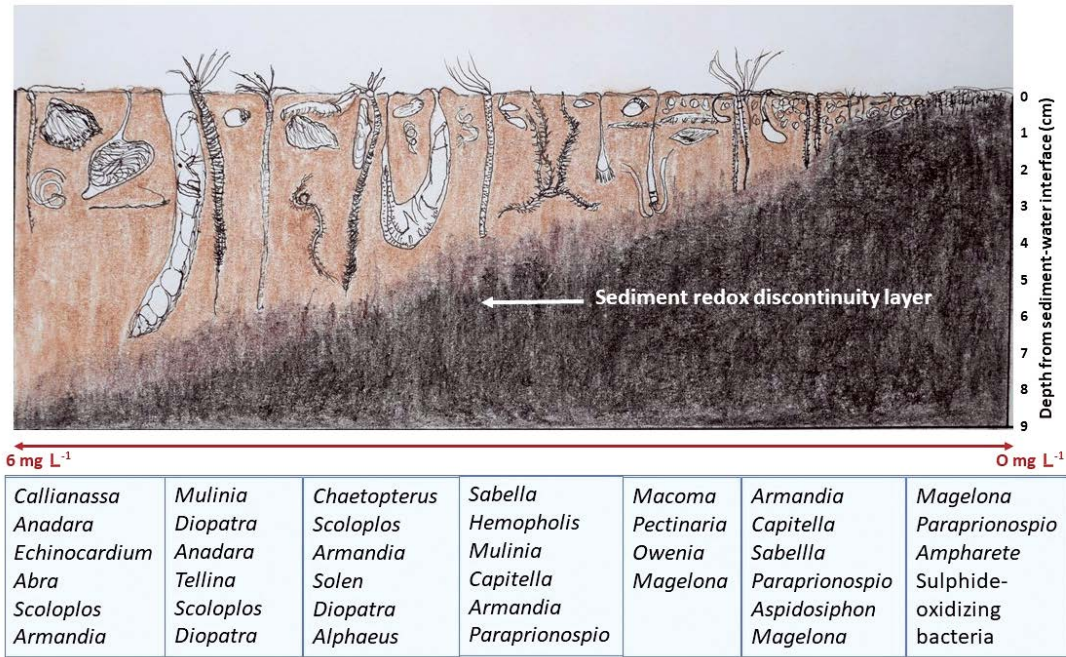


Figure 8.7.2 Diagram of changes in fauna and sediment structure including redox discontinuity layer from no oxygen on the right to well-oxygenated waters on the left. Source: N.N. Rabalais, based on benthic fauna in Rabalais et al. (2001b) and Baustian and Rabalais (2009) in a decline of dissolved oxygen similar to the organic pollution gradient originally in Pearson and Rosenberg (1976).

Benthic assemblages exposed to seasonally low dissolved oxygen over extended periods, i.e. weeks to months (Figure 8.7.1) become a less diverse species mixture, often shift species composition, experience decreased abundance of most organisms and, therefore, decreased biomass and secondary production, and shift from more mature, deeper burrowing groups of organisms to smaller forms associated with the upper few centimetres of the sediment.

This progression of benthic community responses along a gradient of decreasing oxygen concentration follows the classic model described by Pearson and Rosenberg (1978) resulting from organic loading of paper mill effluents (Figure 8.7.2). Advanced stage benthic communities with deep burrowing infauna and high diversity were replaced by less diverse communities of low oxygen-tolerant infauna or early successional communities of small-sized individuals. Following prolonged hypoxia over an area of several thousands of km², benthic communities in a Danish estuary transitioned from slower growing, burrowing species to fast-growing, surface-dwelling species (Conley et al., 2007). The gradient in the Pearson and Rosenberg (1978) model is distance from a polluting effluent; in the case of benthos affected by deoxygenation, the model follows a decline in oxygen levels. Recovery usually follows the opposite trend, but the recovered community is not necessarily the same as

the original community (Duarte et al., 2015; Rosenberg et al., 2002).

The following sections provide examples of how benthic assemblages change depending on how severe the deoxygenation becomes and for how long.

8.7.3.1 Migration from low oxygen

Benthic invertebrates, such as penaeid shrimp and nephropid lobsters, are well known for their ability to migrate away from oxygen-deficient waters, either laterally or vertically (Baden et al., 1990; Craig, 2012; Craig & Crowder, 2005; Rabalais et al., 2001a). Hypoxic conditions, occasionally observed in the Kattegat and the Adriatic can cause severe disruption of the natural emergence patterns and even mass mortality in Norwegian lobsters *Nephrops* populations (Hallbäck & Ulmestrand, 1990). At oxygen saturation levels <50% *Nephrops* are forced from their burrows, and at <25% oxygen saturation are dead within 24 h, particularly the juveniles that are more sensitive to low oxygen compared to adults. Emergence of *Nephrops* under low oxygen conditions may result in higher catches in bottom-dragging trawls and give a mistaken impression that stock density is increasing or sustainable (Hallbäck & Ulmestrand, 1990).

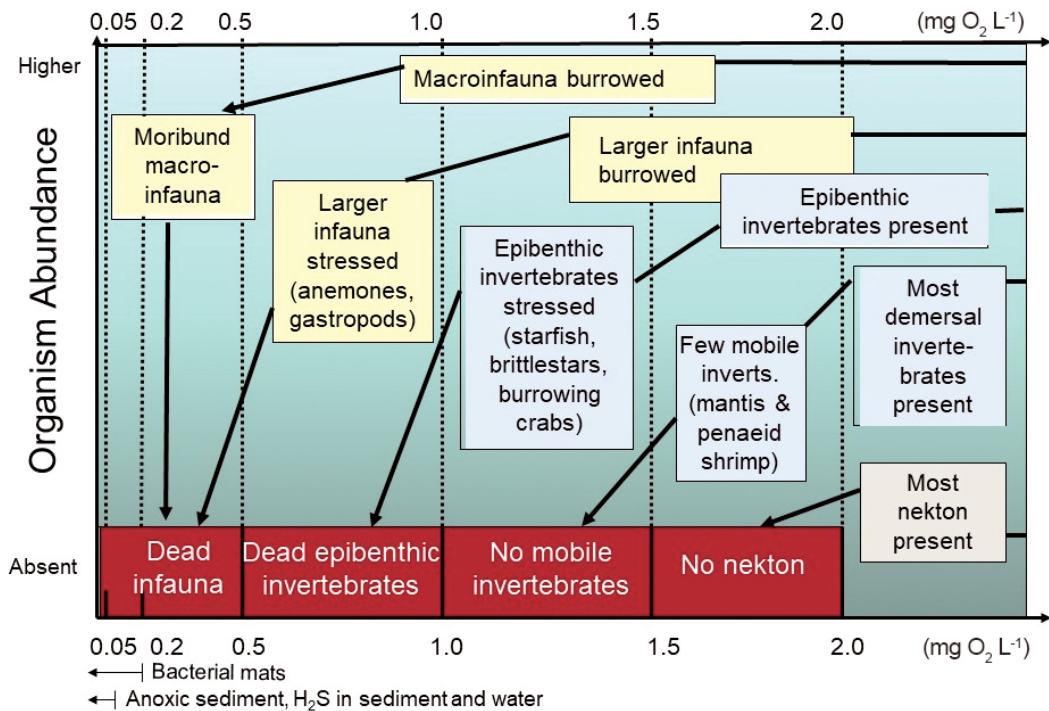


Figure 8.7.3 Progressive changes in fish and invertebrate fauna as oxygen concentration decreases from near 2 mg L⁻¹ to anoxia (0 mg L⁻¹). Source: generated from data and illustrations in Rabalais et al. (2001a).

Brown shrimp *Farfantepenaeus aztecus* catch per unit effort in trawls on the Louisiana continental shelf west of the Mississippi declined dramatically at a threshold of 1.3 ± 0.10 mg O₂ L⁻¹ (Craig, 2012), but Rabalais et al. (2001a) documented no brown shrimp in night-time remotely operated vehicle (ROV) videotapes at oxygen concentrations less than 2 mg O₂ L⁻¹ in the same area. The latter value is representative of the concentration of dissolved oxygen below which mobile fauna will move away from the area (Rabalais et al., 2001a; Renaud, 1986) (Figure 8.7.3).

The diagram begins just above 2 mg L⁻¹ dissolved oxygen on the right, because most demersal fish move out of the area before the oxygen becomes that low. Dead fish were not observed on the sediment surface and were not seen swimming in and out of the bottom area. Some penaeid shrimp and stomatopods (mantis shrimp) were observed at oxygen levels as low as 1.7 to 1.8 mg L⁻¹, but never below 1.5 mg L⁻¹. Stomatopods remaining in hypoxic waters down to 1.5 mg L⁻¹ is consistent with the results of Pihl et al. (1991) who indicated that the mantis shrimp *Squilla empusa* first adapted physiologically to hypoxia and then migrated as hypoxia became more severe, which is consistent with its more stationary and territorial behaviour. The blue crab *Callinectes sapidus* (Figure 8.7.4), however, in the York River (Pihl et al., 1991), migrated from hypoxic waters as soon as

the oxygen concentration fell below 2 mg L⁻¹ and then returned when conditions improved. Large aggregations of rock shrimp (*Sicyonia dorsalis* and *S. brevirostris*) and portunid crabs (*Portunus gibbesii*, *Callinectes sapidus*, and *C. similis*) were observed swimming at the surface above bottom waters on the Louisiana shelf that were severely oxygen depleted (0.1 to 0.2 mg L⁻¹) (N.N. Rabalais, personal observation).

8.7.3.2 Death of attached epibenthos

The northern Adriatic Sea is a shallow, semi-enclosed sea with a history of seasonal hypoxia and anoxia due to long-term eutrophication and increasing frequency, duration and severity of oxygen depletion since the mid-20th Century (Barmawidjaja et al., 1995; Danovaro, 2003; Justić, 1987). The epibenthic community there, specifically those organisms living attached to the sea bed usually on shells or shell hash amidst a fine-grained sediment surface, are subject to varying levels of low dissolved oxygen over extended time (Riedel et al., 2008; Stachowitsch et al., 2007). The foundations for these bioherms are typically sponges and ascidians (tunicates). Multiple brittlestars, anemones, living gastropods, hermit crabs in gastropod shells, amphipods, and crustaceans add levels of complexity. The eutrophication process of high carbon production in the form of phytoplankton begins the process of epibenthic habitat destruction and



Figure 8.7.4 Blue crab (*Callinectes sapidus*) © Mark Conlin / Alamy stock photo.

deoxygenation. The sinking senescent phytoplankton form a mucous-like detritus, called mucilage, that falls and settles on the sea bed and covers the bioherms (Figure 8.7.5). The subsequent decomposition of the mucilage results in oxygen depletion that causes further mortality in the sediment fauna that in turn decomposes reducing oxygen concentrations further.

Similar to bioherms, coral reefs can be exposed to low oxygen events. A massive coral mortality event caused by deoxygenation affected corals and other reef-associated organisms such as sponges (Figure 8.7.6) in Bahía Almirante in the Bocas del Toro region of Panama (Altieri et al., 2017). In a well-oxygenated area only $3 \pm 2\%$ of corals were bleached, whereas $76 \pm 11\%$ of the corals were bleached in the severely deoxygenated area. The likelihood of coral reefs being exposed to deoxygenation in the future is high given the trends in resource use by developing countries in tropical regions.



Figure 8.7.5 Mucilage on bioherms of the Northern Adriatic Sea © Open source Google, Francesca Malfatti.

8.7.3.3 Seasonally severe hypoxia

8.7.3.3.1 Northern Gulf of Mexico continental shelf west of the Mississippi River delta

Low oxygen conditions that occur over weeks to months most often are exposed to shifts in sediment-water biogeochemical processes including the release of toxic hydrogen sulphide (H_2S) from sediments (Vaquer-Sunyer & Duarte, 2010; Villnäs et al., 2012). Gulf of Mexico hypoxic waters on the continental shelf off Louisiana and eastern Texas are most prevalent from late spring through late summer. Low oxygen waters occur from shallow depths near shore (4 to 5 m) to as deep as 60 m but more typically between 5 and 30 m. When the dissolved oxygen level falls below 2 mg L^{-1} , it often reaches less than 1 mg L^{-1} or severely depleted levels of less than 0.2 mg L^{-1} for periods of two to eight weeks (Rabalais et al., 2007).

The stages of this decline were documented with ROV showing severely hypoxic bottom sediments on the inner continental shelf of the northern Gulf of Mexico west of the Mississippi River (Rabalais et al., 2001a) (Figure 8.7.3). This area is hypoxic for extended periods in mid-summer recorded at a frequency of 75 to 100% during mid-summer shelf-wide hypoxia mapping cruises (Rabalais et al., 2018) (Figure 8.7.7).

As the oxygen level decreases from 1.5 to 1 mg L^{-1} , bottom-dwelling organisms exhibited stress behaviours. Crabs (*Libinia* sp. and *Persephona* sp.) and sea stars (*Astropecten* sp.) climbed on top of 'high' spots, such as burrow excavation mounds (Figure 8.7.8). Hermit crabs clustered on top of shells lying on the bottom. Brittlestars

emerged from the sediment and used their arms to raise their disks off the substrate. Burrowing shrimp (*Alpheus* sp.) emerged from their burrows (Rabalais et al., 2001a). Gastropods (*Oliva sayana*, *Terebra* sp., *Cantharus cancellarius* and *Distorsio clathrata*) moved through the surface sediments with their siphons extended directly upward. Large burrowing anemones (*Cerianthus* sp.) became partly or completely extended from their tubes and laid on the substrate, in a flaccid and non-responsive condition. Polychaete worms emerged from the substrate and laid motionless on the surface (e.g. *Chloea viridis* and *Lumbrineris* sp.). These behaviours were presumed to position the organisms in higher oxygen content waters, even though moving from the safety of the sediments exposed them to greater risk of predation. Jørgensen (1980) also found that many of the organisms seen lying on the bottom in hypoxic areas were moribund, not dead. The presence of large typically infaunal organisms on the sediment surface supported the idea that bottom-feeding fish were excluded from the hypoxic lower water column.

At oxygen levels of 1 to 0.5 mg L⁻¹, even the most tolerant burrowing organisms, principally polychaetes, emerged partially or completely from their burrows and lay moribund on the bottom. Below oxygen



Figure 8.7.6 Extremely low oxygen levels (<math><0.5 \text{ mg L}^{-1}</math>) near the bottom of a coral reef in Bahia Almirante, Panama killed the bottom half of erect sponges © Andrew Altieri / PNAS.

concentrations of 0.5 mg L⁻¹, there was a linear decline in species richness, abundance and biomass of benthic

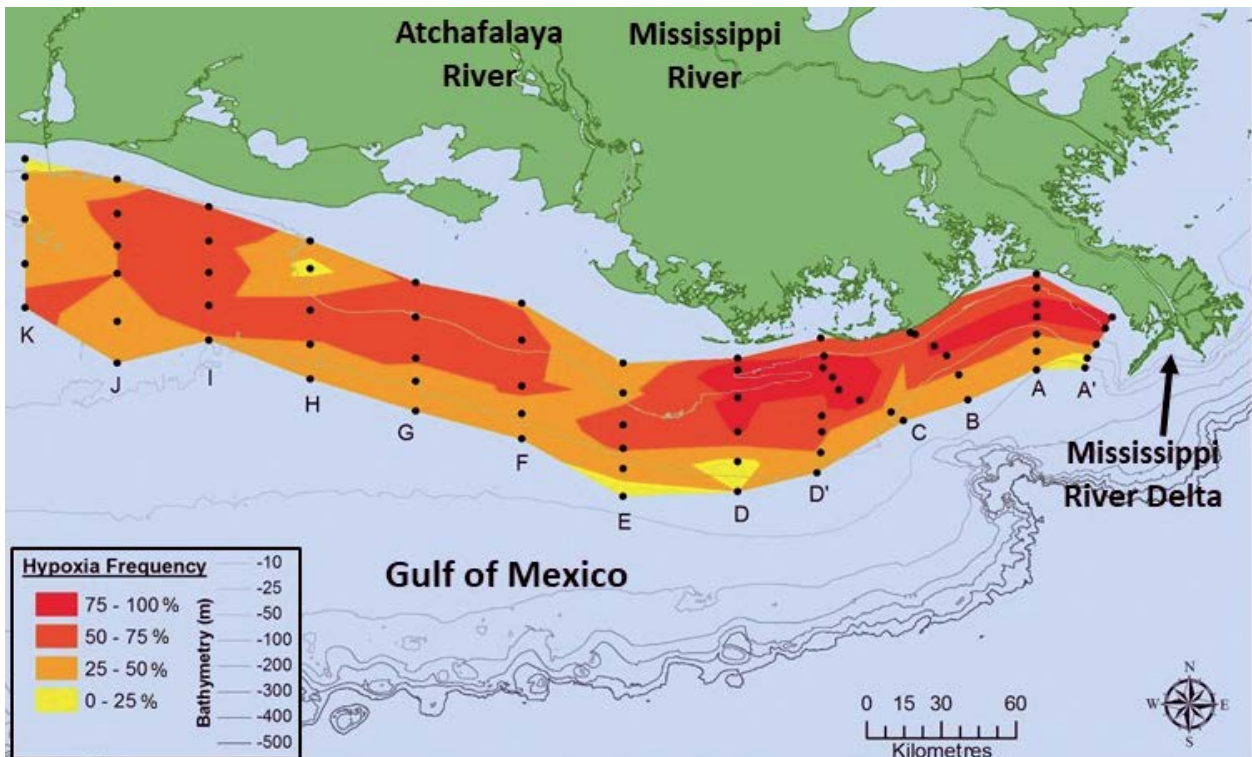


Figure 8.7.7 The frequency of bottom-water hypoxia occurrence from shelf wide hypoxia mapping from 1985 through 2014 (Rabalais et al., 2018) is shown in shades of yellow to red; frequency is determined from stations for which there are data for at least half of all cruises. Hypoxia frequency: Dark red >75%; Dark orange 50 – 75%; Orange 25 – 50%; Yellow <25%. Source: N.N. Rabalais.

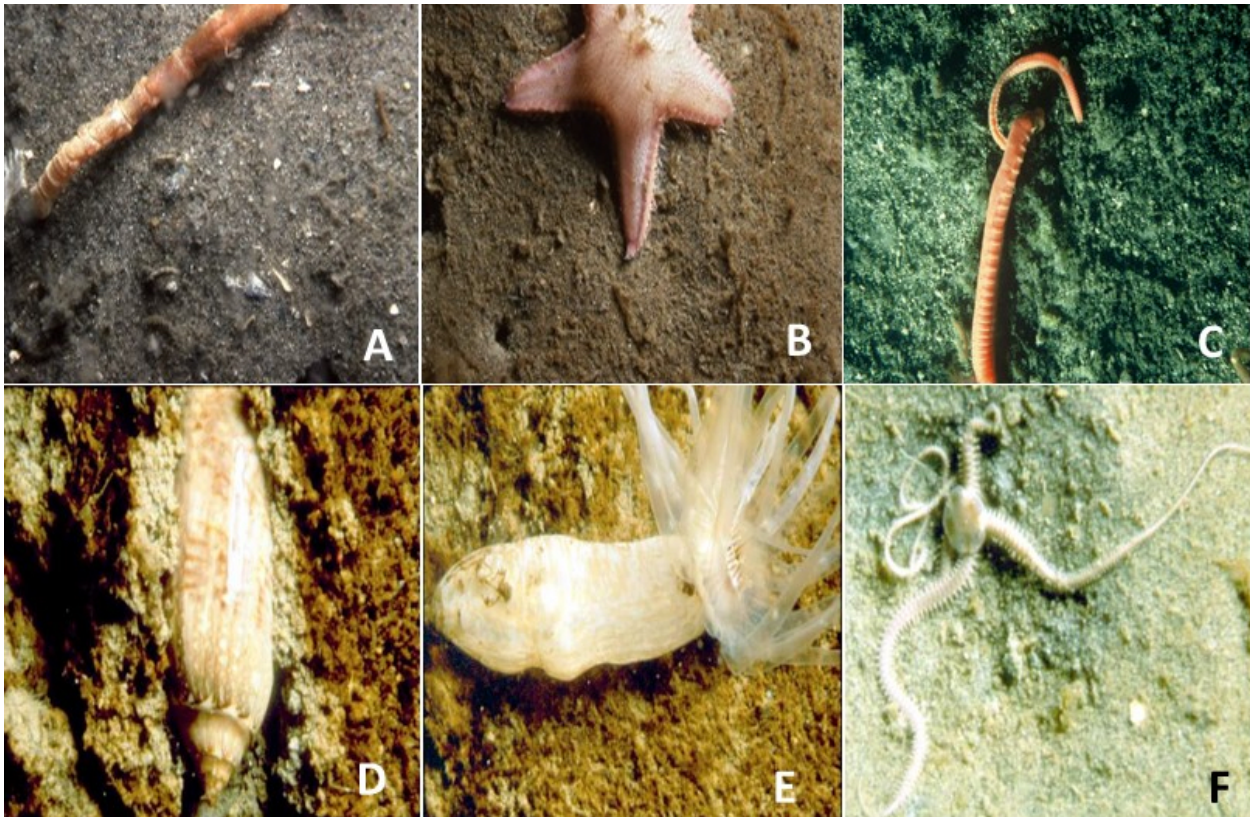


Figure 8.7.8 Living but stressed benthic infauna at the surface of the sediments. (A) polychaete *Owenia fusiformis*; (B) *Astropecten* starfish; (C) Terebellid polychaete; (D) gastropod *Oliva sayana*; (E) Cerianthid anemone; (F) brittlestar. © F. Viola & D.E. Harper, Jr.

macroinfauna (Rabalais et al., 2001b). Dead and decaying polychaetes and crustaceans were observed on the sediment surface at oxygen concentrations of less than 0.25 mg L^{-1} (Figure 8.7.9). Despite the anoxic appearance of sediments and detection of hydrogen sulphide in overlying waters, there usually remained some surviving fauna, typically polychaetes of the genera *Magelona*, *Paraprionospio* and *Sigambra* or sipunculans (Rabalais et al., 2001b) so that the sediments were not completely azoic. At oxygen values below 0.2 mg L^{-1} but above anoxia (0 mg L^{-1}) various-sized patches of “cottony” bacterial mats, *Beggiatoa* sp. covered the sediment surface (Figure 8.7.10).

Benthic communities in seasonally severe hypoxic conditions on the Louisiana continental shelf are characterized by loss of longer-lived deeper burrowing infauna to shallow sediment dwellers, and decreases in species richness, abundance and biomass of organisms relative to similar habitats not suffering low oxygen levels (Rabalais et al., 2001b). These changes occur when the dissolved oxygen concentrations are well below 2 mg L^{-1} , close to anoxia, for an extended period of time. A spring through autumn continuous bottom-water dissolved oxygen record from a meter in

20 m depth about 100 km west of the Mississippi River delta illustrates these patterns. Water-column oxygen levels rose during mixing from cold fronts in spring and tropical storms in summer followed by respiration below the stratification that led to low bottom-water dissolved oxygen from the beginning of July through early October, when cold fronts began to occur more frequently (Figure 8.7.11). Bottom-water dissolved oxygen values of less than 2 mg L^{-1} occurred for 80% of the record and below 1 mg L^{-1} for 71% of the total record and were anoxic for more than 60% of the record (Rabalais et al., 1994).

Polychaetes comprised most of the species in the hypoxic area at 20 m depth 100 km west of the Mississippi River delta. Composition by other major taxonomic groups was high in the spring, and then reduced to four to six major taxa in July-October (Figure 8.7.12) (Table 8.7.1). The polychaetes *Ampharete* sp., *Paraprionospio pinnata* and *Mediomastus ambiseta* were common in spring and early summer of 1990, but as hypoxia worsened, the community was reduced to the small, surface feeding polychaetes *Ampharete* sp. and *Magelona* sp., and the sipunculan *Aspidosiphon* sp. Only *Magelona* sp. and *Aspidosiphon* sp. maintained any significant population levels in August 1990. There was evidence from

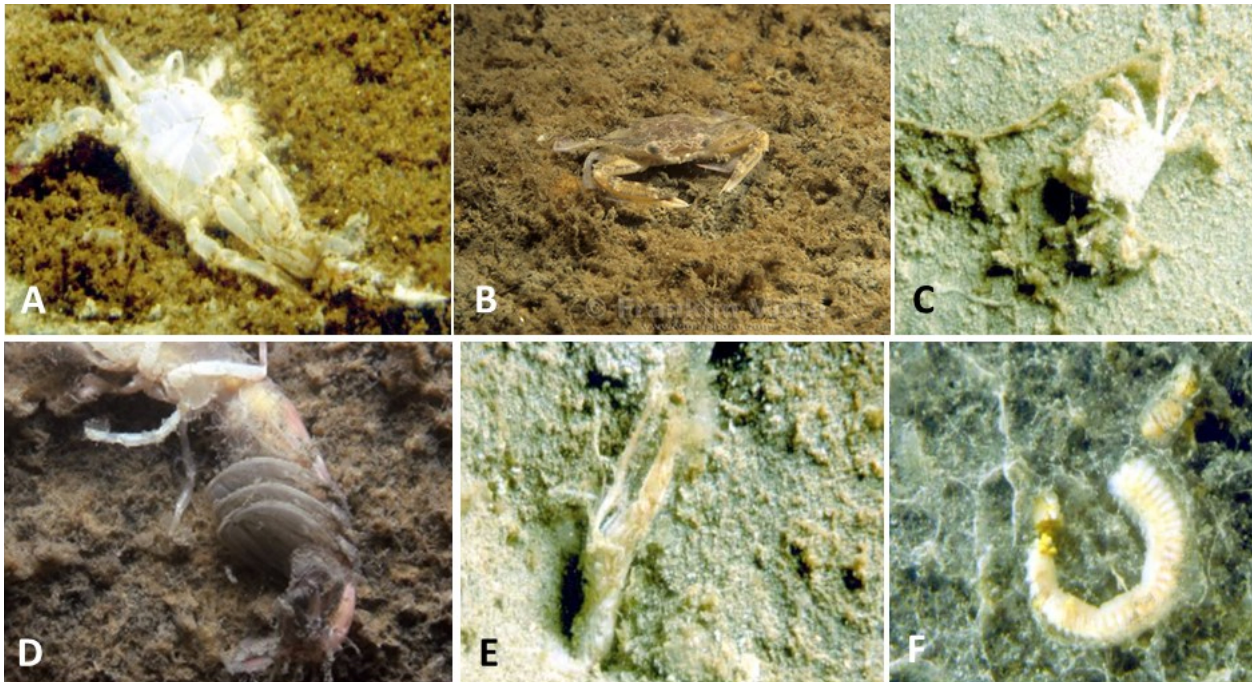


Figure 8.7.9 Dead and decomposing benthic infauna. (A) Portunid crab; (B) Portunid crab; (C) Goneplacid crab; (D) Thalassinid shrimp; (E) Alpheid shrimp; (F) Spionid polychaete. © F. Viola & D.E. Harper, Jr.

settlement traps deployed in the area of hypoxia that the polychaete *Paraprionospio pinnata* delayed settlement and remained in the water column until oxygen values returned to a level above 2.0 mg L^{-1} (Powers et al., 2001).

During September and October 1990, the overall increase in number of individuals was due primarily to the recruitment of *Paraprionospio pinnata* and *Armandia maculata* and sustained levels of *Magelona* sp. and *Aspidosiphon* sp. Species richness again increased during the spring of 1991, but polychaetes remained the dominant taxa (Figure 8.7.12). *Owenia fusiformis*, which had been a dominant member of the community in 1990,

was replaced by a population of *Sigambra tentaculata* in spring 1991.

The number of individuals and biomass of infaunal benthos decreased substantially from periods of normoxia to severely hypoxic conditions (Table 8.7.1). Abundance of individuals was high in April and June 1990 but dropped dramatically in July through September 1990. There was a slight recruitment of individuals in October 1990. Abundance increased somewhat in February–April 1991, then increased substantially in May 1991. A seasonal decrease began in June 1991 with a significant reduction in abundance in July and August. Abundance increased in September and October 1991 to about the same level

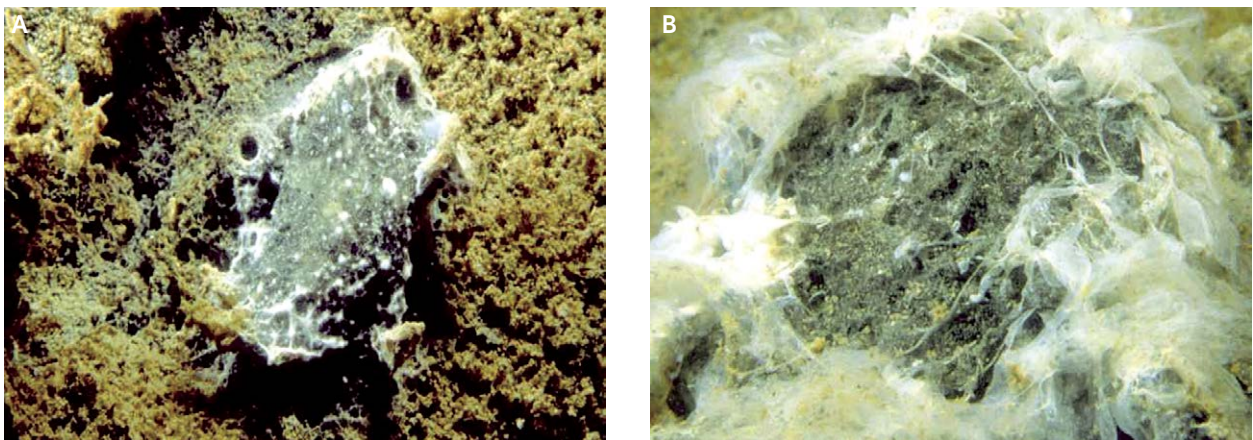


Figure 8.7.10 Sulphide oxidizing bacteria. (A) sulphide oxidizing bacteria on anoxic sediments; note tube opening is for the polychaete *Diopatra cuprea*, also the thick blanket of organic detritus on the sediment surface. (B) thicker mats of sulphide oxidizing bacteria on anoxic sediments. © F. Viola & D.E. Harper, Jr.

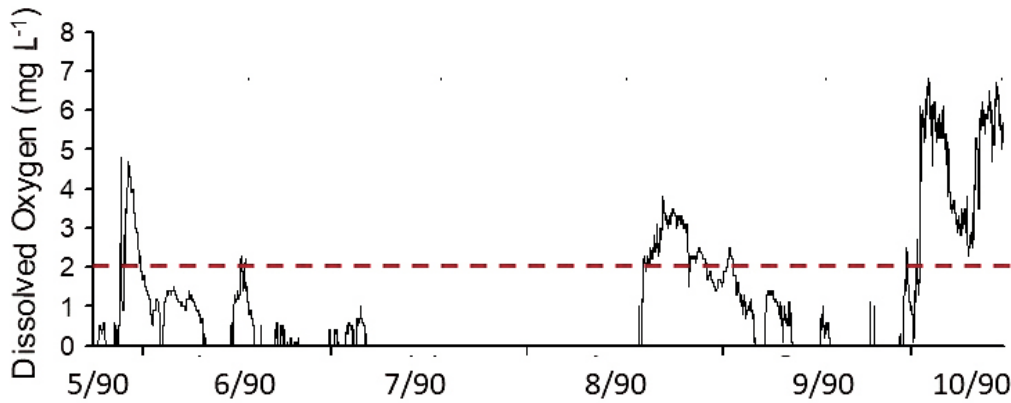


Figure 8.7.11 Time series plot of near-bottom dissolved oxygen concentration at a 20 m station 100 km west of the Mississippi River delta in 1990 (modified from Rabalais et al., 1994, 2001b). The horizontal dashed line defines hypoxia (from Rabalais et al., 2007).

as early spring 1991. Biomass generally followed the same pattern as number of individuals.

A similar cycle of more taxa and individuals in spring with a dramatic decline during deoxygenation in summer was described by Baustian and Rabalais (2009) for the same study area in May 2003 – October 2004. Similar organisms, primarily the polychaetes *Paraprionospio pinnata*, *Armandia maculata*, and *Magelona* sp., and nemertean remained as part of the benthic infaunal community during periods of low oxygen.

Murrell and Fleeger (1989) surveyed the meiofaunal assemblages at three stations (8 – 13 m) over an annual cycle of decreasing dissolved oxygen in the same area of severe and persistent low oxygen in the northern Gulf of Mexico. Total meiofaunal abundances were high in spring ranging from 800 to 3800 individuals 10 cm^{-2} before a hypoxic event. During severely low dissolved oxygen concentrations there were pronounced declines in abundance and diversity of major meiofauna taxa (Murrell & Fleeger, 1989). Harpacticoid copepods were least tolerant to low oxygen, while nematodes and kinorhynchans were less affected. Copepods declined from

high values of 100 – 410 to 0 individuals 10 cm^{-2} when hypoxia developed. Nematode abundance ranged from 600 to 3100 individuals 10 cm^{-2} before hypoxia and from 500 to 1100 individuals 10 cm^{-2} after hypoxia. There was evidence from settlement traps deployed in the area that nematodes migrated into the water column away from hypoxic sediments and resettled on the sediments with the return of normoxic conditions (Wetzel et al., 2001).

8.7.3.3.2 Chesapeake Bay and tributaries

Moderate hypoxia (dissolved oxygen of 2 mg L^{-1}) to anoxia (no oxygen) affects much to all of the sub-pycnocline waters in the central one-third of Chesapeake Bay for most or all of the summer (Hagy et al., 2004). Chesapeake Bay is a large estuary on the east coast of the United State (Figure 8.7.13) stretching 320 km from the Susquehanna River in the north to where it connects with the Atlantic Ocean at its seaward end. Deoxygenation has been a feature of the Chesapeake Bay since at least 1600 and seasonally since 1900 (Zimmerman & Canuel, 2002). Seasonal hypoxia has increased in extent, duration and intensity since the 1950s (Brush, 2009; Hagy et al., 2004).

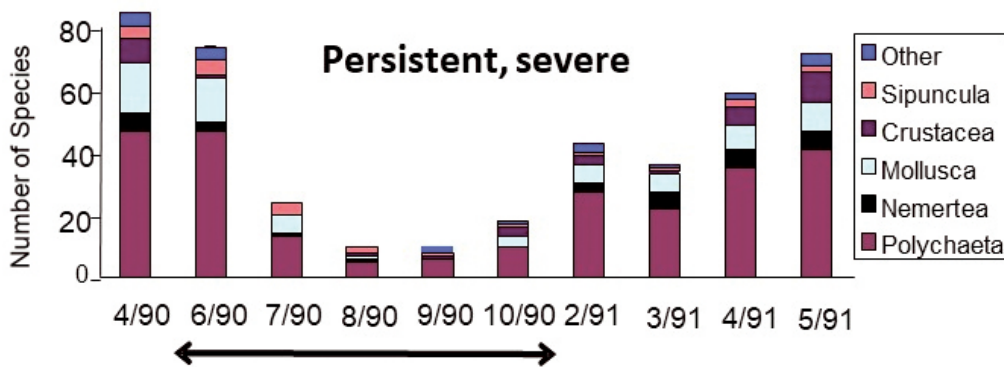


Figure 8.7.12 Number of species within taxonomic groups (total for $n = 10 \times 0.02\text{ m}^2$ cores) at a 'persistent, severe' site for months indicated in 1990 and 1991 (from Rabalais et al., 2001b). The arrow corresponds to the duration of the bottom-water dissolved oxygen levels illustrated in Figure 8.7.11.

Table 8.7.1 Comparisons of benthic community parameters in areas with seasonally persistent and severe hypoxia and seasonal but intermittent hypoxia. Data for the northern Gulf of Mexico are from Rabalais et al. (2001b) and for the Chesapeake Bay are from Dauer et al. (1992). There were also sedimentary and salinity differences among the sites that explained some differences in fauna.

	<i>Periodicity</i>	<i>Oxygen Level</i>	<i>Density (no. m⁻²)</i>	<i>Species Richness (no. 0.02-m⁻²)</i>	<i>Biomass (g AFDW m⁻²)</i>
Northern Gulf of Mexico					
Silty mud, Apr 1990, <i>n</i> = 10	Intermittent	Normoxic	8,637	22	2.59
Silty mud, Sep 1990, <i>n</i> = 10	Intermittent	Hypoxic	1,431	12	0.45
Sandy mud Apr 1990, <i>n</i> = 10	Persistent	Normoxic	18,437	51	2.92
Sandy mud Sep 1990, <i>n</i> = 10	Persistent	Hypoxic	730	4	0.23
Sandy mud, Feb-May, <i>n</i> = 10	Persistent	Normoxic	6,486	22	1.55
Sandy mud, Jul-Aug, <i>n</i> = 10	Persistent	Hypoxic	1,346	8	0.46
Chesapeake Bay					
Mainstem, polyhaline mud, spring, <i>n</i> = 4	Persistent	Normoxic	1,978	10	9.9
Mainstem, polyhaline mud, summer, <i>n</i> = 4	Persistent	Hypoxic	1,723	6	1.7
Tributaries, mesohaline mud, spring, <i>n</i> = 4	Persistent	Normoxic	3,065	9	2.5
Tributaries, mesohaline mud, summer, <i>n</i> = 4	Persistent	Hypoxic	902	4	1.1
Intermittent, varying levels of dissolved oxygen over the annual cycle, even in summer					
Persistent, seasonal cycle with severely low dissolved oxygen for extended periods in summer					

There is compression of suitable habitat for fishes and mobile crustaceans, such as blue crabs *Callinectes sapidus*, and potentially reduced access to food or overall food availability (Officer et al., 1984). However, demersal fishes may feed on moribund benthos at the sediment-water interface during hypoxia in the York River tributary to Chesapeake Bay (Pihl et al., 1992). The demise of benthic species and assemblages has been well documented in Chesapeake Bay and its tributaries with reduced species diversity (50% lower), lower biomass (70% lower), loss of deep-dwelling, long-lived species and dominance of shallow-dwelling, short-lived opportunistic species (Dauer et al., 1992), similar to persistent deoxygenation on the northern Gulf of Mexico (Table 8.7.1).

8.7.3.4 Intermittent hypoxia

8.7.3.4.1 Northern Gulf of Mexico continental shelf west of the Mississippi River delta

Intermittent exposure to low oxygen conditions occurs at depths on the periphery of more severely hypoxic waters. In the case of a 20 m depth site 50 km west of the Mississippi River delta on the Louisiana continental shelf, the cycle of mixing with reoxygenation and decrease in oxygen concentrations from respiration are similar to Figure 8.7.11, with the exception of a strong tidal advection component (Rabalais et al., 1994) (Figure 8.7.14). Bottom-water dissolved oxygen values less than 2 mg L⁻¹ occurred for 50% of the record from (June 15

– October 16) with many incursions below and above 2 mg L⁻¹.

Species richness at the intermittently hypoxic station was 2-fold lower in summer hypoxia than either spring period compared to a 13-fold decrease in species richness at the ‘persistent, severe’ station from spring through summer (Table 8.7.1). Polychaete species comprised about half of all benthic species at the ‘intermittent’ site but increased in relative proportion during the summer (Figure 8.7.15) as less tolerant infauna taxa decreased. The benthic community at the ‘intermittent’ station was diverse, with a complement of pericaridean crustaceans, bivalves, gastropods and other taxa, but the dominant species were small, surface-feeding polychaetes.

Dominant species for most months were *Paraprionospio pinnata* and *Mediomastus ambiseta* (Rabalais et al., 2001b). The abundance of *Armandia maculata* increased in August 1990. Changes in several dominant species through 1990 were evident, with *Prionospio cristata*, *Nephtys incisa*, *Magelona* spp., *Ampharete* sp., and *Owenia fusiformis*. *Armandia maculata*, *Ampharete* sp., and *Magelona* sp., replaced in spring 1991 by *Sigambra tentaculata* and *Cossura soyeri*.

8.7.3.4.2 Chesapeake Bay and tributaries

The washing of water from the main Chesapeake Bay onto the adjacent shores via a combination of winds and tides generates similar intermittent episodes of

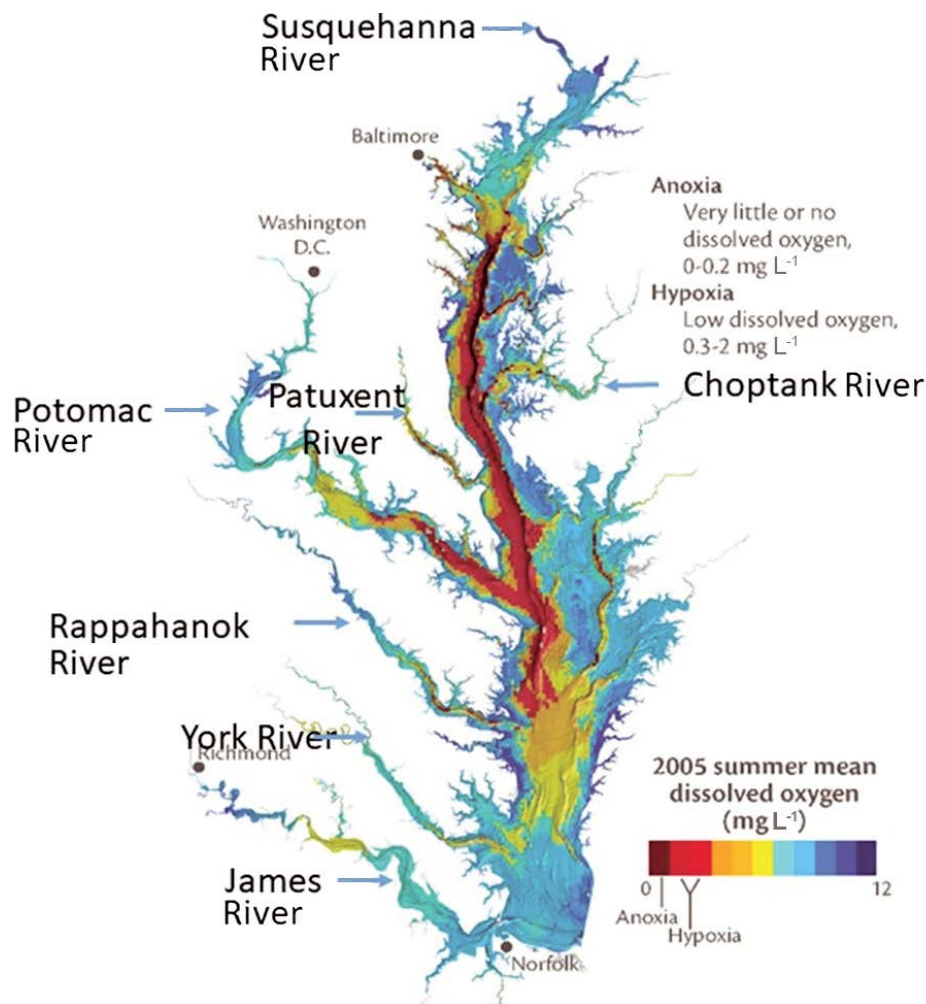


Figure 8.7.13 Map of bottom-water dissolved oxygen concentrations in Chesapeake Bay and its tributaries in the summer of 2005 that are detrimental to benthic and demersal assemblages (from Chesapeake Bay Program, http://www.eco-check.org/pdfs/do_letter.pdf, accessed 1-8-18).

severe hypoxia in summer (Breitburg, 1990). Collection of continuous bottom-water oxygen concentrations at a 4 m deep station on the western shore of Chesapeake Bay recorded about 40% of the days during the instrument deployment that fell below 2 mg L^{-1} , similar to the 50% of time on the Louisiana shelf (Rabalais et al., 1994). Oxygen fell below 1 mg L^{-1} 10% of the time during the same Chesapeake Bay deployment. Yet, the temporary nature of the intrusions allowed water of sufficient dissolved oxygen to support most estuarine organisms during part of the day.

The Patuxent River, a tributary of Chesapeake Bay (Figure 8.7.13), has deoxygenated waters in its lower reaches that are well below 2 mg L^{-1} and often anoxic. Benthic invertebrates that recruit to these deeper waters likely suffer extensive mortality during the summer as oxygen levels approach 0.5 to 0.1 mg L^{-1} . Samples of the benthic community in 3 to 16 m water depth show declining biomass, and below 8 m is essentially zero.

The assumption drawn by Breitburg et al. (2003) was that extremely low oxygen values were the probable cause for the decline of benthic invertebrates.

8.7.3.4.3 Baltic Sea coastal

The Baltic Sea is a brackish, permanently stratified, semi-enclosed sea with a geologic history of deoxygenation through the Holocene (Zillén et al., 2008). Severely low oxygen, often anoxia, occurs below the halocline at 80 - 100 m over as much as $60,000 \text{ km}^2$. In addition to salinity stratification and physical processes, human-caused nutrient-driven eutrophication has led to a 10-fold increase in deoxygenation in the Baltic Sea since 1900 (Carstensen et al., 2014). Deeper anoxic seas such as the Baltic Sea and Black Sea are not part of this review, but the Baltic Sea coastal areas are increasingly experiencing low levels of dissolved oxygen (Conley et al., 2011) (Figure 8.7.16). Most of these areas experience intermittent low oxygen.

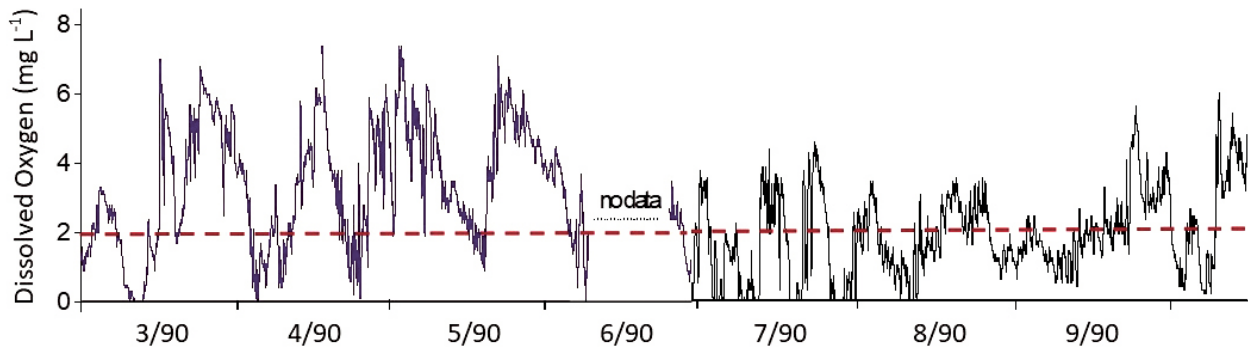


Figure 8.7.14 Continuous bottom-water dissolved oxygen in 20 m depth on the continental shelf (50 km west of the Mississippi River) (March – October 1990) (modified from Rabalais et al., 1994, 2001b). The horizontal dashed line defines hypoxia (from Rabalais et al., 2007).

Many studies of benthic communities have been conducted in the Baltic Sea in a continuum of depths of a few metres to 400 m and along a longitudinal salinity gradient, but this section focuses on depths less than 60 to 100 m. The brackish Baltic Sea typically supports low species richness because of salinity inhibitions (Villnäs & Norkko, 2011). Above the halocline, benthic macrofauna abundances increased with eutrophication (Elmgren, 1989; Karlson et al., 2002) with more recent declines in benthic macrofauna related to declines in oxygen concentration. Where species diversity is low, such as in the Baltic Sea and where diversity further decreases under deoxygenation, the relative abundance of a few species, may be more important in modifying ecosystem function than higher diversity, multi-functional group assemblages in the Baltic Sea (Törnroos & Bonsdorff, 2012).

A study by Josefson et al. (2012) on bioturbation and burial of phytoplankton debris provided the opportunity to examine abundance of benthos in a gradient of dissolved oxygen concentrations in depths of 45 to 290 m from north to south in the Baltic Sea coastal

areas. Most continental shelf studies of deoxygenation are restricted to 70 m and less. Thus, relationships of dissolved oxygen concentrations, abundance of individuals of a few species, and bioturbation potential (BPI) were examined for depths of ≤ 70 m from a gradient to 290 m coastal areas of the Baltic – Gulf of Finland, Eastern Gotland Basin, and Southern Baltic. The relationships were strong – the number of organisms increased with increasing oxygen levels and the bioturbation potential increased with the number of organisms.

8.7.3.5 Diel exposure

Changes in dissolved oxygen levels on a diel (day/night) or tidal cycle (Perez-Dominguez et al., 2006) are natural, but human activities that constrict or eliminate flow into and out of a tidal lagoon (Kauffman et al., 2018; Tweedley et al., 2016; Vignes et al., 2009,) or enhanced primary production can aggravate or worsen low oxygen conditions (Beck et al., 2001; Beck & Bruland, 2000; Ringwood & Keppler, 2002). The oxygen dynamics are most pronounced in summer warming as

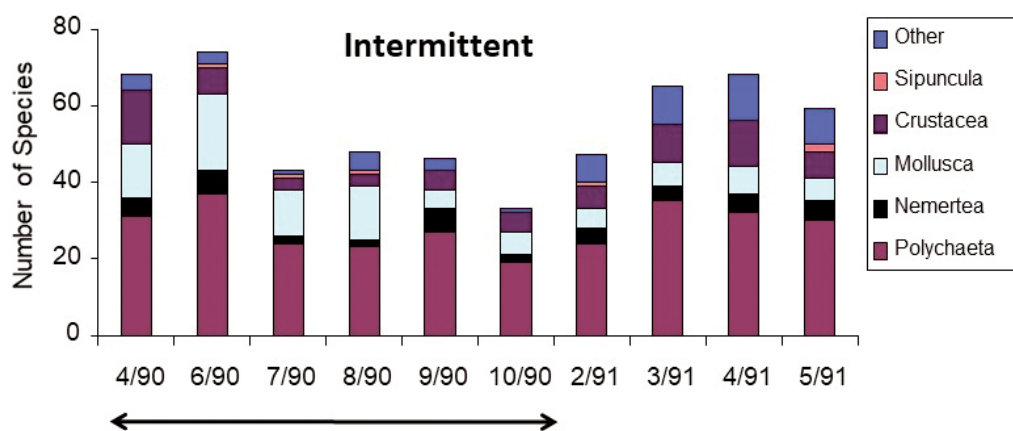


Figure 8.7.15 Number of species within taxonomic groups (total for $n = 10 \times 0.02 \text{ m}^2$ cores) at intermittently hypoxic sites for months indicated in 1990 and 1991. The arrow corresponds to the duration of the bottom-water continuous dissolved oxygen levels in Figure 8.7.11. Source: Rabalais et al. (2001b).

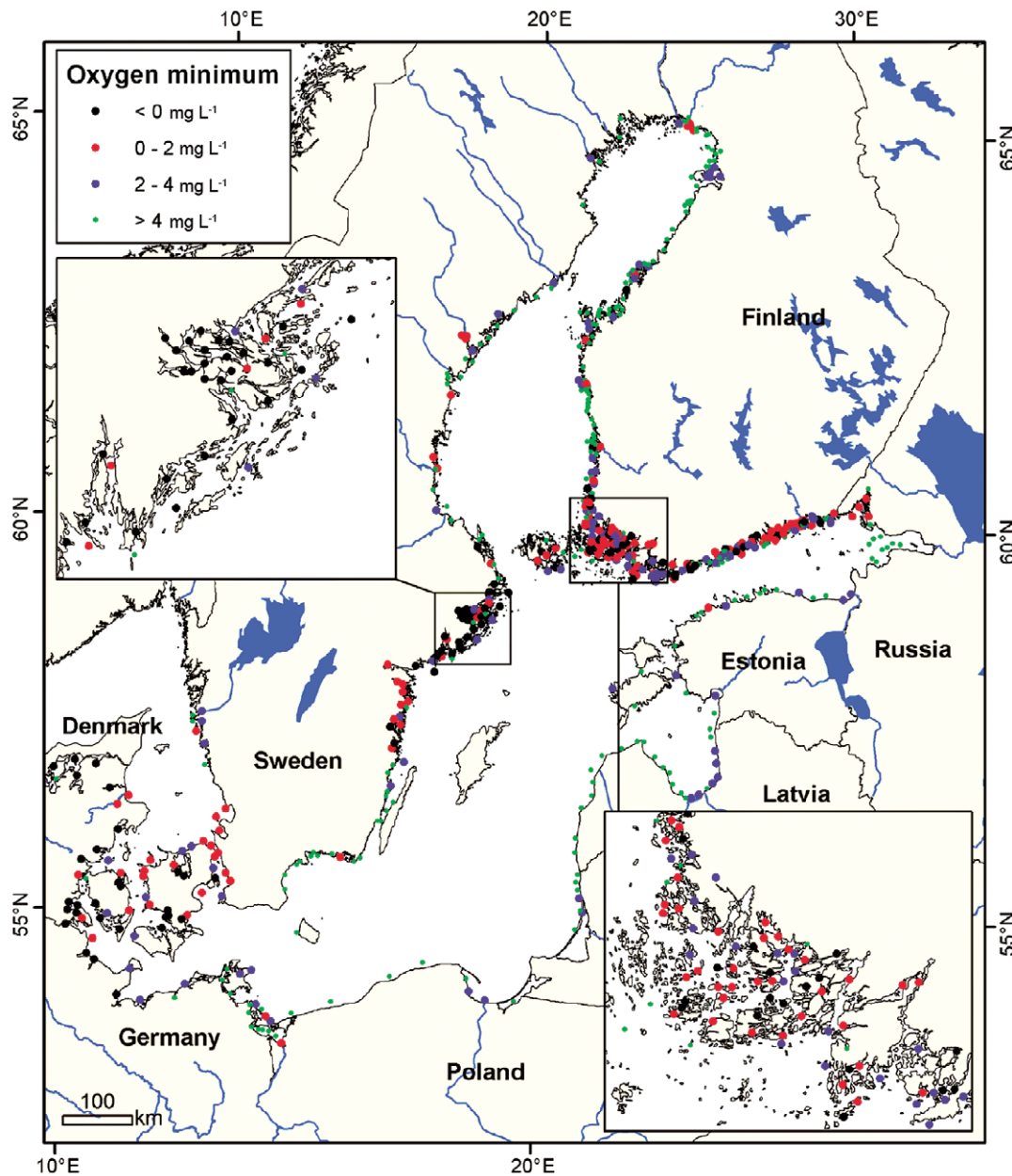


Figure 8.7.16 Lowest recorded oxygen concentration at all monitoring locations through the period (1955-2009) in the coastal areas of the Baltic Sea with insets for the Stockholm Archipelago (upper left) and the Finnish Archipelago Sea (lower right) (from Conley et al., 2011). Oxygen concentrations in bottom waters are (< 0 mg L⁻¹, anoxic; 0-2 mg L⁻¹, hypoxic; 2-4 mg L⁻¹, oxygen stressed; > 4 mg L⁻¹, adequate oxygen).

higher temperatures reduce dissolved oxygen solubility and increase rates of oxygen consumption by aerobic bacterial decomposition.

Mortality is usually minimal if the exposure to lower oxygen levels is over a short period but sublethal effects on juvenile clam growth were identified by Ringwood and Keppler (2002). Juvenile clams, *Mercenaria mercenaria*, were deployed with co-occurring oxygen meters for 7 day periods in tidal creeks near Charleston, South Carolina, USA. The primary effect related to lower

growth rate was the pH, intermediate was the dissolved oxygen, and minimal was salinity.

The invasive Eurasian milfoil *Myriophyllum spicatum* is now the dominant aquatic vegetation in the Mobile-Tensaw Delta, Alabama, USA, in protected waters north of a human-made obstruction to flow in the form of a causeway that significantly reduced wave action. The more quiescent waters north of the causeway resulted in lower dissolved oxygen values, and associated nektonic and benthic fauna were less abundant (a five-fold reduction in faunal abundance) during night

compared to the fauna collected during the day in the *Vallisneria americana* beds, the dominant native vegetation, to the south of the causeway. This nocturnal decrease in dissolved oxygen was accompanied by reductions in invertebrates such as *Gammarus* amphipods, *Neritina* snails, and blue crabs *Callinectes sapidus*, leaving behind mostly *Gammarus* amphipods and insects at much lower abundance. In contrast, faunal communities in *V. americana*, although distinct from *M. spicatum*, exhibited little spatial or temporal (diel) difference.

8.7.4 Ecosystem consequences

The community structure of benthos exposed to deoxygenation, because they are relatively immobile, varies by the severity of oxygen deficiency, the duration of exposure to low levels of dissolved oxygen concentrations, their susceptibility to low oxygen, and their functional group (Solan et al., 2004). Typical responses of benthic communities to oxygen stress are a loss of diversity and a change in faunal composition. Abundance of organisms decreases along with a reduction in overall biomass. Large longer-lived, deep burrowing species are replaced by small opportunistic species that live within the upper few cm of sediments. The loss of deeper burrowing species reduces the bio-irrigation and bioturbation of the sediments (Solan et al., 2004), resulting in a shift of the redox potential discontinuity layer towards the sediment-water interface and a compression of suitable benthic habitat. On the other hand, some deep burrowing species are responsible for transporting organic matter deeper into the sediments and increasing the biological oxygen demand and eventually deoxygenation (e.g. the invasive polychaete *Marenzelleria* spp. in the Baltic Sea (Josefson et al., 2012).

The types of benthos and their shifts with deoxygenation influence nutrient cycling of both nitrogen and phosphorus in the sediments and overlying water. Bottom water hypoxia typically leads to enhanced regeneration of phosphate and ammonium from deoxygenated sediments (Gammal et al., 2017) with a positive feedback in enhanced productivity in the surface waters and a negative feedback of an increased flux of organic matter to the sediments and continued deoxygenation (Conley et al., 2002). Elevated levels of ammonium and ortho-phosphate are typical in severely deoxygenated waters overlying reduced

sediments (Rabalais et al., 2014). Phosphorus returns to the sediments during oxic conditions. Savchuk (2005) estimated the net sediment burial of P for 1991-1999 to be ca. 20 kt P y⁻¹, far exceeding the P received from external sources. The nitrogen cycle is highly dependent on oxygen concentrations. Nitrogen removal through nitrification/denitrification is dependent on oxic conditions. Nitrification/denitrification rates decrease as dissolved oxygen concentrations decrease but can recover as oxic conditions return; recovery is curtailed following long periods of highly reduced sediments (Karlson et al., 2005).

8.7.5 Societal consequences

Benthic organisms and their productivity in areas of nutrient-enhanced eutrophication support high yield demersal fisheries, such as the commercially important shrimping industry in the northern Gulf of Mexico (Figure 8.7.17). Loss of secondary production where deoxygenation is widespread is assumed to curtail fisheries yields, but this is not always the case (Chesney et al., 2000; Rose et al., 2018). Sturdivant et al. (2013) estimated benthic community production in the lower Rappahannock River, a tributary of the Chesapeake Bay, over four months coupled with continuous dissolved oxygen concentrations at selected sites for discrete periods. They estimated that hypoxic sites had as much as 85% lower macrobenthic production compared to normoxic sites. Diaz and Rosenberg (2008) projected lost secondary production in terms of carbon biomass and loss of energy transfer to higher trophic levels. Area estimates of missing biomass for about a third of the world's oxygen-depleted coastal areas indicated that as much as 343,000 to 734,000 metric tons of carbon are displaced over a total area of 245,000 km² as a result of deoxygenation.

Relating an economic model with secondary production loss of a fishery exposed to low oxygen conditions has been elusive (Diaz & Solow, 1999). Huang et al. (2010) estimated that hypoxia might have resulted in a 12.9% annual decrease in the North Carolina brown shrimp harvest during the period 1999–2005, and a monetary value of US\$8,645,167 for Pamlico Sound. Smith et al. (2017) tackled the economic side of the Louisiana brown shrimp fishery on market prices for small and large shrimp based on the disruptive expanse of a severely depleted dissolved oxygen area across the Louisiana inner shelf in summer. The presence of areas



Figure 8.7.17 Shrimp boat on the Gulf of Mexico coast © Ruth Burke / Alamy stock photo.

of dissolved oxygen below 2 mg L^{-1} cause migration of shrimp to the nearshore coastal zone or farther offshore of the low oxygen water mass in deeper waters with no trawlable shrimp populations in between (Craig & Crowder, 2005; Zimmerman & Nance, 2001). This results in reduced suitable habitat, impaired growth of individuals exposed to low oxygen, 'herding' of smaller individuals closer to shore where they are easily captured in high abundance, inability of smaller shrimp to migrate offshore as part of their natural annual cycle to increase in size and thus attract better market prices, and decisions of trawlers to not target the farther offshore population because of increased distance and fuel costs. What Smith et al. (2017) were able to show was that hypoxia decreased the quantity of large shrimp relative to small shrimp and increased the price of large shrimp relative to small shrimp. Smaller shrimp were a larger proportion of the inshore population and the higher abundance of small shrimp drove down their market price. Fewer, larger shrimp further offshore drove up their market price. Imports of larger non-native shrimp were cheaper than the native shrimp to the detriment of local trawler incomes. These economic data were the first to demonstrate negative economic impacts on a valuable commercial fishery of the Louisiana shelf.

8.7.6 Conclusions / Recommendations

Increasing deoxygenation is occurring more and more in estuaries and coasts. In these productive systems, members of the benthic communities are critical as food resources for higher trophic levels and for the healthy functioning of a coastal ecosystem. When these assemblages are exposed to low oxygen conditions, there is a standard response of mobile species evacuation from the area, loss of deeper burrowing community members, and reduced diversity, abundance, and replacement by individuals that are mostly opportunistic species with limited burrowing ability. Living resources are disrupted and even lost, including commercially important demersal species. In the case of limited examples of economic costs of deoxygenation on benthic communities and commercial resources, results point to loss of secondary production and less desirable market prices and monetary losses. Economic considerations of coastal resources should be coupled into models of economic costs and benefits of nutrient mitigation to reduce deoxygenation in coastal waters and their watersheds. There are additional disruptive effects on coastal ecosystems, such as habitat alteration, chemical pollutants, altered hydrology,

overfishing and sea-level rise, which may mask or compound the effects due to deoxygenation.

Recovery pathways for eutrophied and deoxygenated benthic communities are not the same among the limited examples where steps have been taken to reduce nutrient inputs to estuarine and coastal waters (Carstensen et al., 2014; Kemp et al., 2009; Riemann et al., 2016). Long-lived species, especially deep-burrowing ones require longer periods for recovery to the extent that they can affect positive feedbacks (Norkko et al., 2010, 2013). Recovery of benthic assemblages may take years to decades following long-term exposure to long-lasting deoxygenation. Furthermore, return to normoxic conditions is not immediate or even after a few years (Riemann et al., 2016). An integrated coastal ecosystem understanding of recovery (e.g. phytoplankton, rooted or attached vegetation, food webs, invasive species, species interactions, and shifts in biogeochemical processes) is the larger context into which oxygen condition recovery and improved benthic communities should be placed. This is not to deter nutrient mitigation, but to place it within the larger context of ecosystem recovery so that nutrient mitigation efforts are not abandoned but continue.

8.7.7 References

- Altieri, A.H., Harrison, S.B., Seemann, J., Collin, R., Diaz, R.J., & Knowlton, N. (2017). Tropical dead zones and mass mortalities on coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 3660–3665. <https://doi.org/10.1073/pnas.1621517114>
- Baden, S.P., Pihl, L., & Rosenberg, R. (1990). Effects of oxygen depletion on the ecology, blood physiology and fishery of the Norway lobster *Nephrops norvegicus*. *Marine Ecology Progress Series*, 67, 141–155. <https://doi.org/10.3354/meps067141>
- Barmawidjaja, D.M., van der Zwaan, G.J., Jorissen, F.J., & Puscaric, S. (1995). 150 years of eutrophication in the northern Adriatic Sea: evidence from a benthic foraminiferal record. *Marine Geology*, 122, 367–384. [https://doi.org/10.1016/0025-3227\(94\)00121-Z](https://doi.org/10.1016/0025-3227(94)00121-Z)
- Baustian, M.M., & Rabalais, N.N. (2009). Seasonal composition of benthic macroinfauna exposed to hypoxia in the northern Gulf of Mexico. *Estuaries and Coasts*, 32, 975–983. <https://doi.org/10.1007/s12237-009-9187-3>
- Beck, N.G., & Bruland, K.W. (2000). Diel biogeochemical cycling in a hyperventilating shallow estuarine environment. *Estuaries*, 23, 177–187. <https://doi.org/10.2307/1352825>
- Beck, N.G., Fisher, A.T., & Bruland, K.W. (2001). Modeling water, heat, and oxygen budgets in a tidally dominated estuarine pond. *Marine Ecology Progress Series*, 217, 43–58. <https://doi.org/10.3354/meps217043>
- Breitburg, D.L. (1990). Near-shore hypoxia in the Chesapeake Bay: Patterns and relationships among physical factors. *Estuarine, Coastal and Shelf Science*, 30, 593–609. [https://doi.org/10.1016/0272-7714\(90\)90095-9](https://doi.org/10.1016/0272-7714(90)90095-9)
- Breitburg, D. (2002). Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries*, 25, 767–781. <https://doi.org/10.1007/BF02804904>
- Breitburg, D.L., Adamack, A., Rose, K.A., Kolsar, S., Decker, M.B., Purcell, J.E., ... Cowan Jr., J.H. (2003). The pattern and influence of low dissolved oxygen in the Patuxent River, a seasonally hypoxic estuary. *Estuaries*, 26, 280–297. <https://doi.org/10.1007/BF02695967>
- Brush, G.S. (2009). Historical land use, nitrogen, and coastal eutrophication: A paleoecological perspective. *Estuaries and Coasts*, 32, 18–28. <https://doi.org/10.1007/s12237-008-9106-z>
- Caddy, J.F. (1993). Towards a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. *Reviews in Fisheries Science*, 1, 57–95. <https://doi.org/10.1080/10641269309388535>
- Carstensen, J., Andersen, H.H., Gustafsson, B.G., & Conley, D.J. (2014). Deoxygenation of the Baltic Sea during the last century. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 5628–5633. <https://doi.org/10.1073/pnas.1323156111>
- Chesney, E.J., Baltz, D.M., & Thomas, R.G. (2000). Louisiana estuarine and coastal fisheries and habitats: Perspectives from a fish's eye view. *Ecological Applications*, 10, 350–366. [https://doi.org/10.1890/1051-0761\(2000\)010\[0350:LEACFA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0350:LEACFA]2.0.CO;2)
- Conley, D.J., Homburg, C., Lars, R., Savchuk, O.P., & Wulff, F. (2002). Hypoxia in the Baltic Sea and basin-scale changes in phosphorus biogeochemistry. *Environmental Science and Technology*, 36, 5315–5320. <https://doi.org/10.1021/es025763w>
- Conley, D.J., Carstensen, J., Ærtebjerg, G., Christensen, P.B., Dalsgaard, T.J., Hansen, L.S., & Josefson, A.B. (2007). Long-term changes and impacts of hypoxia in Danish coastal waters. *Ecological Applications*, 17, S165–S184. <https://doi.org/10.1890/05-0766.1>
- Conley, D.J., Carstensen, J., Aigars, J., Axe, P., Bonsdorff, E., Eremina, T., ... Zillén, L. (2011). Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environmental Science and Technology*, 45, 6777–6783. <https://doi.org/10.1021/es201212r>
- Craig, K. (2012). Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the northern Gulf of Mexico. *Marine Ecology Progress Series*, 445, 75–95. <https://doi.org/10.3354/meps09437>
- Craig, J.K., & Crowder, L.B. (2005). Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. *Marine Ecology Progress Series*, 294, 79–94. <https://doi.org/10.3354/meps294079>
- Danovaro, R. (2003). Pollution threats in the Mediterranean Sea: an overview. *Chemistry and Ecology*, 19, 15–32. <https://doi.org/10.1080/0275754031000081467>
- Dauer, D.M., Rodi Jr., A.J., & Ranasinghe, J.A. (1992). Effects of low dissolved oxygen events on the macrobenthos of the lower Chesapeake Bay. *Estuaries*, 15, 384–391. <https://doi.org/10.2307/1352785>

- Díaz, R.J., & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science*, 321, 926-929. <https://doi.org/10.1126/science.1156401>
- Díaz, R.J., & Solow, A. (1999). Ecological and Economic Consequences of Hypoxia. Topic 2 Report for the Integrated Assessment on Hypoxia in the Gulf of Mexico. NOAA Decision Analysis Series No. 16. National Oceanic and Atmospheric Administration, National Ocean Service, Coastal Ocean Program, 46 pp.
- Duarte, C.M., Borja, A., Carstensen, J., Elliott, M., Krause-Jensen, D., & Marbà, N. (2015). Paradigms in the recovery of estuarine and coastal ecosystems. *Estuaries and Coasts*, 38, 1202-1212. <https://doi.org/10.1007/s12237-013-9750-9>
- Elmgren, R. (1989). Man's impact on the ecosystem of the Baltic Sea: energy flows today and at the turn of the century. *Ambio*, 18, 326-332.
- Gammal, J., Norkko, J., Pilditch, C.A., & Norkko, A. (2017). Coastal hypoxia and the importance of benthic macrofauna communities for ecosystem functioning. *Estuaries and Coasts*, 40, 457-46. <https://doi.org/10.1007/s12237-016-0152-7>
- Gooday, A.J., Jorissen, F., Levin, L.A., Middelburg, J.J., Naqvi, W., Rabalais, N.N., ... Zhang, J. (2009). Historical records of coastal eutrophication and hypoxia. *Biogeosciences*, 6, 1707-1745. <https://doi.org/10.5194/bg-6-1707-2009>
- Gray, J.S., Wu, R.S.-S., & Or, W.Y. (2002). Effects of hypoxia and organic enrichment in the coastal marine environment. *Marine Ecology Progress Series*, 238, 249-279. <https://doi.org/10.3354/meps238249>
- Hagerman, L., Josefson, A.B., & Jensen, N. (1996). Benthic macrofauna and demersal fish. In B.B. Jørgensen & K. Richardson, (Eds.), *Eutrophication in Coastal Marine Ecosystems*. Coastal and Estuarine Studies 52, pp.155-178, American Geophysical Union, Washington, D.C. <https://doi.org/10.1029/CE052p0155>
- Hagy, J.D., Boynton, W.R., Keefe, C.W., & Wood, K.V. (2004). Hypoxia in Chesapeake Bay, 1950–2001: Long-term change in relation to nutrient loading and river flow. *Estuaries*, 27, 634-638. <https://doi.org/10.1007/BF02907650>
- Hallböck, H., & Ulmestrand, M. (1990). Havskräfta i Kattegat. *Fauna Flora*, 85, 186-192.
- Hofmann, A.F., Peltzer, E.T., Walz, P.M., & Brewer, P.G. (2011). Hypoxia by degrees: Establishing definitions for a changing ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, 58, 1212-1226. <https://doi.org/10.1016/j.dsr.2011.09.004>
- Huang, L., Smith, M.D., & Craig, J.K. (2010). Quantifying the economic effects of hypoxia on a fishery for brown shrimp *Farfantepenaeus aztecus*. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 2, 232-248. <https://doi.org/10.1577/C09-048.1>
- Jørgensen, B.B. (1980). Seasonal oxygen depletion in the bottom water of a Danish fjord and its effect on the benthic community. *Oikos*, 34, 68-76. <https://doi.org/10.2307/3544551>
- Josefson, A.B., Norkko, J., & Norkko, A. (2012). Burial and decomposition of plant pigments in surface sediments of the Baltic Sea—role of oxygen and benthic fauna. *Marine Ecology Progress Series*, 455, 33-49. <https://doi.org/10.3354/meps09661>
- Justić, D. (1987). Long-term eutrophication of the Northern Adriatic Sea. *Marine Pollution Bulletin*, 18, 281-284. [https://doi.org/10.1016/0025-326X\(87\)90505-4](https://doi.org/10.1016/0025-326X(87)90505-4)
- Karlson, K., Rosenberg, R., & Bonsdorff, E. (2002). Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic waters - a review. *Oceanography and Marine Biology: An Annual Review*, 40, 427-489. <https://doi.org/10.1201/9780203180594.ch8>
- Karlson, K., Hulth, S., Ringdahl, K., & Rosenberg, R. (2005). Experimental recolonization of Baltic Sea reduced sediments: survival of benthic macrofauna and effects on nutrient cycling. *Marine Ecology Progress Series*, 294, 35-49. <https://doi.org/10.3354/meps294035>
- Kauffman, T.C., Martin, C.W., & Valentine, J.F. (2018). Hydrological alteration exacerbates the negative impacts of invasive Eurasian milfoil *Myriophyllum spicatum* by creating hypoxic conditions in a northern Gulf of Mexico estuary. *Marine Ecology Progress Series*, 592, 97-108. <https://doi.org/10.3354/meps12517>
- Kemp, W.M., Testa, J.M., Conley, D.J., Gilbert, D., & Hagy, J. (2009). Temporal responses of coastal hypoxia to nutrient loading and physical controls. *Biogeosciences*, 6, 2985-3008. <https://doi.org/10.5194/bg-6-2985-2009>
- LeKieffre, C., Spangenberg, J.E., Mabileau, G., Escrig, S., Meibom, A., & Geslin, E. (2017). Surviving anoxia in marine sediments: The metabolic response of ubiquitous benthic foraminifera (*Ammonia tepida*). *PLoS ONE*, 12, e0177604. <https://doi.org/10.1371/journal.pone.0177604>
- Levin, L.A., Ekau, W., Gooday, A., Jorissen, F., Middelburg, J., Naqvi, W., ... Zhang, J. (2009). Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences*, 6, 2063-2098. <https://doi.org/10.5194/bg-6-2063-2009>
- Murrell, M.C., & Fleeger, J.W. (1989). Meiofauna abundance on the Gulf of Mexico continental shelf affected by hypoxia. *Continental Shelf Research*, 9, 1049-1062. [https://doi.org/10.1016/0278-4343\(89\)90057-5](https://doi.org/10.1016/0278-4343(89)90057-5)
- Norkko, J., Norkko, A., Thrush, S.F., Valanko, S., & Suurkuukka, H. (2010). Conditional responses to increasing scales of disturbance, and potential implications for threshold dynamics in soft sediment communities. *Marine Ecology Progress Series*, 413, 253-266. <https://doi.org/10.3354/meps08745>
- Norkko, A., Villnäs, A., Norkko, J., Valanko, S., & Pilditch, C. (2013). Size matters: Implications of the loss of large individuals for ecosystem function. *Scientific Reports*, 3, article no. 2646. <https://doi.org/10.1038/srep02646>
- Officer, C.B., Biggs, R.B., Taft, J.L., Cronin, L.E., Tyler, M.A., & Boynton, W.R. (1984). Chesapeake Bay anoxia: origin, development, and significance. *Science*, 223, 22-27. <https://doi.org/10.1126/science.223.4631.22>
- Pearson, T.H., & Rosenberg, R. (1976). A comparative study of the effects on the marine environment of wastes from cellulose industries in Scotland and Sweden. *Ambio*, 5, 77-79.
- Pearson, T.H., & Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution in the marine environment. *Oceanography and Marine Biology: An Annual Review*, 16, 229-311.

- Perez-Dominguez, R., Holt, S.A., & Holt, G.J. (2006). Environmental variability in seagrass meadows: effects of nursery environment cycles on growth and survival in larval red drum *Sciaenops ocellatus*. *Marine Ecology Progress Series*, 321, 41-53. <https://doi.org/10.3354/meps321041>
- Pihl, L., Baden, S.P., & Diaz, R.J. (1991). Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Marine Biology*, 108, 349-360. <https://doi.org/10.1007/BF01313644>
- Pihl, L., Baden, S.P., Diaz, R.J., & Schaffner, L.C. (1992). Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea. *Marine Biology*, 112, 349-361. <https://doi.org/10.1007/BF00356279>
- Powers, S.P., Harper Jr., D.E., & Rabalais, N.N. (2001). Effects of hypoxia/anoxia on the supply and settlement of benthic invertebrate larvae. In N.N. Rabalais & R.E. Turner (Eds.), *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*. Coastal and Estuarine Studies 58, pp. 185-210, American Geophysical Union, Washington, D.C. <https://doi.org/10.1029/CE058p0185>
- Rabalais, N.N., Wiseman Jr., W.J., & Turner, R.E. (1994). Comparison of continuous records of near-bottom dissolved oxygen from the hypoxia zone along the Louisiana coast. *Estuaries*, 17, 850-861. <https://doi.org/10.2307/1352753>
- Rabalais, N.N., Harper Jr., D.E., & Turner, R.E. (2001a). Responses of nekton and demersal and benthic fauna to decreasing oxygen concentrations. In N.N. Rabalais & R.E. Turner (Eds.), *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*. Coastal and Estuarine Studies 58, pp. 115-128, American Geophysical Union, Washington, D.C. <https://doi.org/10.1029/CE058p0115>
- Rabalais, N.N., Smith, L.E., Harper Jr., D.E., & Justić, D. (2001b). Effects of seasonal hypoxia on continental shelf benthos. In N.N. Rabalais & R.E. Turner (Eds.), *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*. Coastal and Estuarine Studies 58, pp. 211-240, American Geophysical Union, Washington, D.C. <https://doi.org/10.1029/CE058p0211>
- Rabalais, N.N., Turner, R.E., Sen Gupta, B.K., Boesch, D.F., Chapman, P., & Murrell, M.C. (2007). Characterization and long-term trends of hypoxia in the northern Gulf of Mexico: Does the science support the Action Plan? *Estuaries and Coasts*, 30, 753-772. <https://doi.org/10.1007/BF02841332>
- Rabalais, N.N., Díaz, R.J., Levin, L.A., Turner, R.E., Gilbert, D., & Zhang, J. (2010). Dynamics and distribution of natural and human-caused coastal hypoxia. *Biogeosciences*, 7, 585-619. <https://doi.org/10.5194/bg-7-585-2010>
- Rabalais, N.N., Cai, W.-J., Carstensen, J., Conley, D.J., Fry, B., Quiñones-Rivera, Z., ... Zhang, J. (2014). Eutrophication-driven deoxygenation in the coastal ocean. *Oceanography*, 70, 123-133. <https://doi.org/10.5670/oceanog.2014.21>
- Rabalais, N.N., Smith, L.M., & Turner, R.E. (2018). The Deepwater Horizon oil spill and Gulf of Mexico shelf hypoxia. *Continental Shelf Research*, 152, 98-107. <https://doi.org/10.1016/j.csr.2017.11.007>
- Renaud, M. (1986). Hypoxia in Louisiana coastal waters during 1983 Implications for fisheries. *Fishery Bulletin*, 84, 19-26.
- Riedel, R., Stachowitsch, M., & Zuschin, M. (2008). Sea anemones and brittle stars: unexpected predatory interactions during induced in situ oxygen crises. *Marine Biology*, 153, 1075-1085. <https://doi.org/10.1007/s00227-007-0880-0>
- Riemann, B., Carstensen, J., Dahl, K., Fossing, H., Hansen, J.W., Jakobsen, H.H., ... Andersen, J.H. (2016). Recovery of Danish coastal ecosystems after reductions in nutrient loading: A holistic ecosystem approach. *Estuaries and Coasts*, 39, 82-97. <https://doi.org/10.1007/s12237-015-9980-0>
- Ringwood, A.H., & Keppler, C.J. (2002). Water quality variation and clam growth: Is pH really a non-issue in estuaries? *Estuaries*, 25, 901-907. <https://doi.org/10.1007/BF02691338>
- Rose, K.A., Creekmore, S., Justić, D., Thomas, P., Craig, J.K., Neilan, R.M., ... Kidwell, D. (2018). Modeling the population effects of hypoxia on Atlantic croaker (*Micropogonias undulatus*) in the northwestern Gulf of Mexico: Part 2—Realistic hypoxia and eutrophication. *Estuaries and Coasts*, 41, 255-279. <https://doi.org/10.1007/s12237-017-0267-5>
- Rosenberg, R., Agrenius, S., Hellman, B., Nilsson, H.C., & Norling, K. (2002). Recovery of marine benthic habitats and fauna in a Swedish fjord following improved oxygen conditions. *Marine Ecology Progress Series*, 234, 43-53. <https://doi.org/10.3354/meps234043>
- Savchuk, O.P. (2005). Resolving the Baltic Sea into seven sub-basins: N and P budgets for 1991-1999. *Journal of Marine Systems*, 56, 1-15. <https://doi.org/10.1016/j.jmarsys.2004.08.005>
- Seibel, B.A. (2011). Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *The Journal of Experimental Biology*, 214, 326-336. <https://doi.org/10.1242/jeb.049171>
- Smith, M.D., Oglend, A., Kirkpatrick, A.J., Aschec, F., Benneara, L.S., Kevin Craig, J.K., & Nance, J.M. (2017). Seafood prices reveal impacts of a major ecological disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 1512-1517. <https://doi.org/10.1073/pnas.1617948114>
- Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., & Srivastava, D.S. (2004). Extinction and ecosystem function in marine benthos. *Science*, 306, 1177-1180. <https://doi.org/10.1126/science.1103960>
- Stachowitsch, M., Riedel, B., Zuschin, M., & Machan, R. (2007). Oxygen depletion and benthic mortalities: the first in situ experimental approach to documenting an elusive phenomenon. *Limnology and Oceanography: Methods*, 5, 344-352. <https://doi.org/10.4319/lom.2007.5.344>
- Sturdivant, S.K., Seitz, R.D., & Diaz, R.J. (2013). Effects of seasonal hypoxia on microbenthic production and function in the Rappahannock River, Virginia, USA. *Marine Ecology Progress Series*, 490, 53-68. <https://doi.org/10.3354/meps10470>
- Törnroos, A.M., & Bonsdorff, E. (2012). Developing the multitrait concept for functional diversity: Lessons from a system rich in functions but poor in species. *Ecological Applications*, 22, 2221-2236. <https://doi.org/10.1890/11-2042.1>
- Turner, R.E., Qureshi, N., Rabalais, N.N., Dortch, Q., Justić, D., Shaw, R.F., & Cope, J. (1998). Fluctuating silicate:nitrate ratios and coastal plankton food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 13048-13051. <https://doi.org/10.1073/pnas.95.22.13048>
- Tweedley, J.R., Warwick, R.M., & Potter, I.C. (2015). Can biotic indicators distinguish between natural and anthropogenic

- environmental stress in estuaries? *Journal of Sea Research*, 102, 10-21. <https://doi.org/10.1016/j.seares.2015.04.001>
- Tweedley, J.R., Warwick, R.M., & Potter, I.C. (2016). The contrasting ecology of temperate macrotidal and microtidal estuaries. *Oceanography and Marine Biology: An Annual Review*, 54, 73-171. <https://doi.org/10.1201/9781315368597-3>
- Tyler, R.M., Brady, D.C., & Targett, T. (2009). Temporal and spatial dynamics of diel-cycling hypoxia in estuarine tributaries. *Estuaries and Coasts*, 32, 123-145. <https://doi.org/10.1007/s12237-008-9108-x>
- Vaquer-Sunyer, R., & Duarte, C.M. (2008). Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 15452-15457. <https://doi.org/10.1073/pnas.0803833105>
- Vaquer-Sunyer, R., & Duarte, C.M. (2010). Sulfide exposure accelerates hypoxia-driven mortality. *Limnology and Oceanography*, 55, 1075-1082. <https://doi.org/10.4319/lo.2010.55.3.1075>
- Vignes, F., Barbone, E., Breber, P., D'Adamo, R., Leonilde, R., Ungaro, N., ... Basset, A. (2009). Spatial and temporal description of the dystrophic crisis in Lesina lagoon during summer 2008. *Transitional Waters Bulletin*, 3, 47-62.
- Villnäs, A., & Norkko, A. (2011). Benthic diversity gradients and shifting baselines: Implications for assessing environmental status. *Ecological Applications*, 21, 2172-2186. <https://doi.org/10.1890/10-1473.1>
- Villnäs, A., Norkko, J., Lukhari, K., Hewitt, J., & Norkko, A. (2012). Consequences of increasing hypoxic disturbance on benthic communities and ecosystem functioning. *PLoS ONE*, 7, e44920. <https://doi.org/10.1371/journal.pone.0044920>
- Warwick, R.M., Tweedley, J.R., & Potter, I.C. (2018). Microtidal estuaries warrant special management measures that recognize their critical vulnerability to pollution and climate change. *Marine Pollution Bulletin*, 135, 41-46. <https://doi.org/10.1016/j.marpolbul.2018.06.062>
- Wetzel, M.A., Fleeger, J.W., & Powers, S.P. (2001). Effects of hypoxia and anoxia on meiofauna: A review with new data from the Gulf of Mexico. In N.N. Rabalais & R.E. Turner, (Eds.), *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*. Coastal and Estuarine Studies 58, pp. 165-184, American Geophysical Union, Washington, D.C. <https://doi.org/10.1029/CE058p0165>
- Zillén, L., Conley, D.J., Andrén, T., Andrén, E., & Björck, S. (2008). Past occurrences of hypoxia in the Baltic Sea and the role of climate variability, environmental change and human impact. *Earth Science Reviews*, 91, 77-92. <https://doi.org/10.1016/j.earscirev.2008.10.001>
- Zimmerman, A.R., & Canuel, E.A. (2002). Sediment geochemical records of eutrophication in the mesohaline Chesapeake Bay. *Limnology and Oceanography*, 47, 1084-1093. <https://doi.org/10.4319/lo.2002.47.4.1084>
- Zimmerman, R.J., & Nance, J.M. (2001). Effects of hypoxia on the shrimp fishery of Louisiana and Texas. In N.N. Rabalais & R.E. Turner, (Eds.), *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*. Coastal and Estuarine Studies 58, pp. 293-310, American Geophysical Union, Washington, D.C. <https://doi.org/10.1029/CE058p0293>

