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Temporal responses of coastal hypoxia to nutrient loading and physical controls

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Abstract. The incidence and intensity of hypoxic waters in coastal aquatic ecosystems has been expanding in recent decades coincident with eutrophication of the coastal zone. Worldwide, there is strong interest in reducing the size and duration of hypoxia in coastal waters, because hypoxia causes negative effects for many organisms and ecosystem processes. Although strategies to reduce hypoxia by decreasing nutrient loading are predicated on the assumption that this action would reverse eutrophication, recent analyses of historical data from European and North American coastal systems suggest little evidence for simple linear response trajectories. We review published parallel time-series data on hypoxia and loading rates for inorganic nutrients and labile organic matter to analyze trajectories of oxygen (O_2) response to nutrient loading. We also assess existing knowledge of physical and ecological factors regulating O_2 in coastal marine waters to facilitate analysis of hypoxia responses to reductions in nutrient (and/or organic matter) inputs. Of the 24 systems identified where concurrent time series of loading and O_2 were available, half displayed relatively clear and direct recoveries following remediation. We explored in detail 5 well-studied systems that have exhibited complex, non-linear responses to variations in loading, including apparent "regime shifts". A summary of these analyses suggests that O_2 conditions improved rapidly and linearly in systems where remediation focused on organic inputs from sewage treatment plants, which were the primary drivers of hypoxia. In larger more open systems where diffuse nutrient loads are more important in fueling O_2 depletion and where

climatic influences are pronounced, responses to remediation tended to follow non-linear trends that may include hysteresis and time-lags. Improved understanding of hypoxia remediation requires that future studies use comparative approaches and consider multiple regulating factors. These analyses should consider: (1) the dominant temporal scales of the hypoxia, (2) the relative contributions of inorganic and organic nutrients, (3) the influence of shifts in climatic and oceanographic processes, and (4) the roles of feedback interactions whereby O_2-sensitive biogeochemistry, trophic interactions, and habitat conditions influence the nutrient and algal dynamics that regulate O_2 levels.

1 Introduction

Depletion of dissolved oxygen from coastal waters is a widespread phenomenon that appears to be growing globally (Díaz and Rosenberg, 2008; Gilbert et al., 2009; Rabalais and Gilbert, 2009). There is considerable interest in this phenomenon because low oxygen causes physiological stress for most marine metazoans. Oxygen concentrations below approximately 30% saturation ("hypoxia"=$O_2 < 62.5\,\mu$M or $2\,\text{mg}\,\text{l}^{-1}$) interrupt normal metabolism and behavior of fish and invertebrates causing reduced growth and increased mortality (e.g., Díaz, 2001). Extended periods of hypoxia and relatively brief exposure to anoxia (zero O_2) tend to cause mortality for many marine animals (e.g., Vaquer-Sunyer and Duarte, 2008). Hypoxia may also affect predator-prey interactions and food web structures, with low O_2 zones providing more tolerant organisms extended habitat for foraging and refuge from predation (e.g., Nestlerode and Díaz, 1998; Decker et al., 2004). In addition, low O_2 levels

alter the oxidation-reduction balance in marine sediments and associated biogeochemical processes, including coupled nitrification-denitrification (e.g., Kemp et al., 1990) and inorganic phosphorus sorption to metal oxide-hydroxide complexes (Slomp and van Cappellen, 2007; Middelburg and Levin, 2009).

Oxygen depletion occurs at various time and space scales from an imbalance between biological and physical sources and sinks for O_2. In very shallow (1–5 m) tidal rivers and lagoons with well-mixed water columns that are enriched with inorganic nutrients, hypoxic conditions tend to appear and disappear on short (hours-days) time-scales (D'Avanzo and Kremer, 1994; Tyler et al., 2009). Slightly deeper (3–8 m) microtidal systems typically experience periodic stratification that may allow episodic hypoxia to occur on daily-to-weekly scales with changes in wind-driven mixing (Park et al., 2007). In deeper (10–50 m) estuaries and shelf systems with stratified water columns, hypoxia often occurs during much of the summer (2–4 mo) season (e.g., Kemp et al., 1992; Rabalais and Gilbert, 2008). In much deeper (>100 m) coastal seas and fjords, strongly stratified water columns result in virtually permanent hypoxia/anoxia, changing in size and position with decadal-scale variations in circulation (e.g., Zillén et al., 2008).

There is mounting evidence that eutrophication (i.e., anthropogenic nutrient and organic enrichment of waters) is contributing to the expansion of occurrence, intensity, and duration of hypoxic conditions in coastal waters worldwide (e.g., Díaz and Rosenberg, 2008; Gilbert et al., 2009; Rabalais and Gilbert, 2009). Nutrient additions tend to fertilize growth, sinking and decomposition of phytoplankton in bottom waters of estuaries, bays, and inland seas. For many coastal systems in the industrialized regions of the world, there have been major socio-economic commitments to remediate hypoxic zones by reducing nutrient loading from the adjacent catchment and overlying atmosphere (Boesch, 2002; Carstensen et al., 2006). Although reductions in anthropogenic nutrient inputs to coastal systems is the primary means that has been employed to remediate hypoxia associated with eutrophication, biomanipulation approaches have also been suggested, including re-establishment of diminished populations of benthic filter-feeding bivalves that consume phytoplankton directly (e.g., Cerco and Noel, 2007; Petersen et al., 2008). Engineering solutions (including enhanced vertical mixing, increased horizontal exchange, and mechanical air-bubbling) have also been discussed as options for mitigating human-induced coastal hypoxia (Stigebrandt and Gustafsson, 2007; Conley et al., 2009c). Although substantial socio-economic investments have been made to reduce hypoxia in many regions worldwide (e.g., Kronvang et al., 2005), recent analyses of historical data from European and North American coastal systems suggest little evidence for simple and straightforward responses of hypoxia to remediation actions (Duarte et al., 2009; Conley et al., 2009b).

The purpose of this paper is to review published concurrent time-series data (or proxies) on hypoxia and inputs of nutrients and labile organic matter to analyze trajectories of O_2 response to reductions in nutrient loading. Where available, we also review parallel time-series data on key physical and ecological processes that might also affect changes O_2 conditions in coastal marine waters. To minimize questions about data quality, we limited this review to information published in peer-reviewed literature. While most of the data series in case-studies reviewed here include extended periods (>10 yr) of declining nutrient inputs, a few were characterized more by strong interannual variations rather than long-term trends. The review is structured into seven sections: (1) introduction, (2) external drivers (3) internal processes (4) theoretical response trajectories, (5) hypoxia recovery, (6) complex responses, and (7) concluding comments. Sections 2 and 3 provide background information needed to interpret observed responses in terms of physical, biogeochemical and ecological controls. In Section 4 we describe theoretical trajectories along which hypoxia might be expected to respond to changes in nutrient loading. In the next two sections, we describe case studies of systems showing relatively clear responses to decreased nutrient loading (Sect. 5), and others where hypoxia has exhibited complex responses to fluctuations and changes in nutrient loading (Sect. 6). Section 7 provides conclusions and considers implications for remediating and managing low O_2 coastal waters.

2 External drivers

Although recent decades have seen widespread observations of hypoxia in diverse coastal systems (e.g., Díaz and Rosenberg, 2008), low O_2 conditions in different systems vary across a wide range of temporal (as well as spatial) scales. Here we provide a modified scheme for categorizing hypoxic systems according to scales of variability, and we discuss the major external drivers that regulate O_2 conditions by controlling physical transport and mixing as well as ecological production and consumption of organic matter.

2.1 Topology of coastal hypoxia

Drawing from previous hypoxia classification schemes based on duration and dominant time-scales of low O_2 (e.g., Díaz and Rosenberg, 2008), we define four broad categories of hypoxia: (1) permanent, (2) persistent seasonal, both stratified and vertically mixed, (3) episodic, and (4) diel. *Permanent* hypoxia occurs primarily in shelf regions, large fjords, and inland seas in which strong stratification isolates the bottom layer of deep water columns (>100 m), leading to bottom water hypoxia/anoxia (e.g., Helly and Levin, 2004; Gilbert et al., 2005) that tends to change only in size and position with annual-to-decadal scale variations in circulation (e.g., Helly and Levin, 2004; Zillén et al., 2008; Chen et al., 2007).

Persistent seasonal hypoxia occurs in many stratified temperate estuarine and shelf regions where the combination of spring river discharge and summer heat strengthen stratification, promote phytoplankton growth and stimulate respiration of sinking organic matter (e.g., Rabalais and Gilbert, 2009). Seasonal hypoxia may also occur throughout the water column in shallow well-mixed estuaries and tidal rivers that are heavily loaded with large inputs of labile organic material that are respired in warmer months (e.g., Soertaert et al., 2006). *Episodic* hypoxia tends to occur at irregular intervals (weeks to decades) in productive, shallow (5–15 m), weakly-stratified microtidal coastal systems that are generally subjected to wind mixing. These systems are susceptible to occasional hypoxic conditions that are terminated by wind events (e.g., Stanley and Nixon, 1992); however, they may be prolonged by extended warm calm weather (Møhlenberg, 1999) or exacerbated by major storm events that deliver large pulses of organic loading (Peierls et al., 2003). *Diel* hypoxia tends to occur in shallow productive lagoons and bays, when night-time respiration of organic matter produced during the day exceeds O_2 replenishment via air-sea exchange. Typically, daytime O_2 levels in these shallow systems are high (often supersaturated) because of strong photosynthetic O_2 production. Although this paper considers all types of hypoxia, it generally focuses on coastal systems with *seasonal* hypoxia (persistent or variable) because these systems tend to be well-studied and are often heavily influenced by anthropogenic nutrient enrichment. In contrast, systems with *diel* hypoxia are less studied, while systems with *permanent* hypoxia tend to be dominated by natural processes that are difficult or impossible to remediate.

2.2 Factors driving physical and ecological processes

In many coastal systems, density stratification is sufficient to create a bottom layer isolated from surface waters and impede downward mixing of O_2 from surface waters, thereby reducing physical replenishment and allowing depletion of bottom water O_2 through aerobic respiration of accumulated carbon (e.g., Kemp et al., 1992, 2005). Buoyancy of the upper layer is increased and stratification is strengthened by seasonal inputs of fresh water (Boicourt, 1992) and warming of surface waters (e.g., Welsh and Eller, 1991). Relatively weak stratification in systems such as the Neuse River estuary, Long Island Sound, and Mobile Bay can be disrupted by typical summer wind events (e.g., Turner et al., 1987; Stanley and Nixon, 1992; O'Donnell et al., 2008). In any given year, stronger stratification, created by larger freshwater input or warmer surface water, is more resistant to disruption by wind events (Lin et al., 2008). Ventilation of bottom-water hypoxia may involve relatively complex mechanisms, where for example wind stress induces the straining of density fields (e.g., Scully et al., 2005), lateral tilting of the pycnocline (Malone et al., 1986), alteration of far-field coastal circulation (e.g., Wiseman et al., 1997), or interaction with

spring-neap tidal cycles (Sharples et al., 1994). In stratified systems with estuarine circulation, bottom-water O_2 pools are also replenished by landward transport of O_2-rich water from downstream sources or offshore (e.g., Kuo et al., 1991; Kemp et al., 1992; Wiseman et al., 2004). Because hypoxia in stratified coastal systems is confined to the bottom layer, respiration must be fueled by labile organic matter, typically organic particles sinking from the upper water column (e.g., Hagy et al., 2005; Chen et al., 2007, 2009).

Although water-column stratification is a key control on *persistent seasonal* hypoxia for many systems, other well-mixed coastal waters experience intermittent or persistent hypoxic conditions that are confined to the warm season. For example, vertically mixed shallow brackish tidal rivers and saline lagoons may experience relatively continuous summertime low O_2 concentrations if they are receiving heavy loads of labile organic wastes. In industrialized regions of the world prior to 1990, and even today in densely populated developing countries, large discharges of organic wastes can create high rates of O_2 demand that often lead to hypoxic conditions throughout the water column (e.g., Andrews and Rickard, 1980; Soetaert et al., 2006; Díaz and Rosenburg, 2008; Yin et al., 2008). If these systems are relatively turbid due to suspended sediment inputs and resuspension, photosynthesis and associated O_2 production would be severely light-limited. In this case, vertical mixing of the water column is typically induced by winds and/or tidal turbulence, and hypoxia results from a sink-source imbalance where community respiration exceeds the rate of O_2 replenishment via air-water exchange. In contrast, when shallow, clear-water coastal systems (e.g., lagoons) receive substantial inputs of inorganic nutrients, photosynthetic production (often dominated by benthic plants) represents an important O_2 source, leading to diel-scale cycling between supersaturated O_2 concentrations during the day and hypoxic conditions at night (e.g., MacPherson et al., 2007; Tyler et al., 2009). Although *diel hypoxia* is generally confined to the warmer summer months, its occurrence and intensity tends to vary on daily-to-weekly time-scales associated with periodic fluctuations in sunlight and tides, as well as rain and wind events (e.g., Shen et al., 2008). There are surprisingly few reports of diel-scale hypoxia in the scientific literature; however, recent evidence suggests that this phenomenon is widespread in shallow eutrophic waters (e.g., Wenner et al., 2004).

Key ecological controls on seasonal hypoxia in coastal waters involve the production and delivery of labile organic matter to the region of O_2 depletion. The origin of the organic matter that fuels respiratory O_2 sinks can either be from sources within the aquatic system or from external sources, including the adjacent watershed or ocean (Bianchi, 2007). Major external sources of organic material to coastal waters can be derived from runoff of terrestrial plant debris, phytoplankton biomass from adjacent river-borne or oceanic-upwelling sources, and anthropogenic inputs of particulate and dissolved organics, (e.g., sewage effluents; see Sect. 5).

For non-stratified coastal systems, respiration and hypoxia may be driven by inputs of dissolved organic matter (e.g., Andrews and Rickard, 1980; MacPherson et al., 2007). To fuel bottom respiration in stratified waters, however, organic matter must be in the form of particles capable of sinking to the bottom layer. Most bottom water hypoxia is fueled by sinking of living and detrital phytoplankton cells, whether they are transported from external sources or produced internally in overlying waters. The high rates of particulate organic input generally needed to support bottom-layer hypoxia, however, tend to be from algal production in overlying waters driven by inputs of inorganic nutrients from adjacent sources. Recent reviews of anthropogenic hypoxia suggest that O_2 depletion in stratified coastal waters is most often driven by nutrient-stimulated production of organic matter (e.g., Díaz and Rosenburg, 2008).

Long-term trends and decadal-scale cycles in climatic forcing can also exert control over O_2 concentrations in bottom waters via changes in temperature, salinity, freshwater inputs, and wind stress (Rabalais et al., 2009). For example, recent increases in water temperature (e.g., Nixon et al., 2004), which are expected to continue with increases in atmospheric CO_2 concentrations, will have direct and indirect consequences for hypoxia. The direct effects include decreased solubility of O_2 in water and enhanced respiration rates, while indirect effects include changes in food webs resulting from spatial and temporal shifts in species distribution and abundance (e.g., Najjar et al., 2000, 2009; Pyke et al., 2008). In addition, long-term increases in relative sea level occurring in many coastal regions worldwide (Holgate and Woodworth, 2004) may result in elevated bottom water salinities (Hilton et al., 2008), thus potentially enhancing stratification and reducing ventilation of deep waters. Long-term increases or decreases in freshwater input caused by global climate change will influence coastal hypoxia in many coastal systems by increasing or decreasing (respectively) the stratification strength and nutrient delivery rate (e.g., Justić et al., 2003; Arnell, 1999). Lastly, long-term trends and decadal-scale shifts in atmospheric pressure fields and circulation (e.g., Ogi et al., 2003) may alter the magnitude and direction of wind stress, causing changes in vertical mixing and oxygenation of O_2-depleted bottom waters in coastal systems (e.g., Wilson et al., 2008, Scully 2009; see Sect. 6).

3 Internal ecological processes

Although external forcing of physical and biological processes strongly influences coastal ecosystem dynamics and hypoxia development, internal ecosystem structure and associated processes are also important. For example, internal processes regulate key biogeochemical fluxes, including production and consumption of organic carbon and cycling of inorganic nutrients. These processes, which create positive and negative feedbacks within the ecological system, can in-

fluence O_2 dynamics in coastal water columns (e.g., Kemp et al., 2005). In this section we review key internal biogeochemical and ecological processes that interact with and regulate hypoxic conditions. This background information is essential for interpreting and predicting how zones of coastal hypoxia will respond to changes in external nutrient loading.

Oxygen depletion in most stratified coastal systems is ultimately supported by surface layer phytoplankton production and particulate sinking to the bottom layer. Herbivorous grazing in the upper water column tends to impede sinking of algal cells and detritus to the lower layer. However, most marine zooplankton are relatively less effective grazers compared to large-bodied cladocerans in lakes, which can strongly control phytoplankton biomass (e.g., Jeppesen et al., 2007). Marine zooplankton (primarily copepods) are less effective because of lower filtering efficiency and strong top-down control by planktivores (e.g., Roman and Gauzens, 1997; Stock and Dunne, 2009). On the other hand, marine suspension-feeding benthic bivalves can effectively control phytoplankton growth, especially in shallow coastal systems (e.g., Prins et al., 1998; Dame and Olenin, 2005), leading to the suggestion that mussels, oysters and other reef-forming benthic bivalves could potentially regulate phytoplankton sufficiently to reduce hypoxia in eutrophic coastal systems (e.g., Officer et al., 1982; Newell and Ott, 1999). A requirement for this to be effective is that benthic grazers must have access to upper mixed layer water where they can graze rapidly growing cells and retain organic matter in the shallow aerobic waters (e.g., Pomeroy et al., 2006; Newell et al., 2007). Although field-scale documentation of benthic grazing impacts mitigating coastal hypoxia is limited, several modeling studies have demonstrated potential effectiveness (e.g., Cerco and Noel, 2007; Banas et al., 2007). The observation that substantial reduction in nutrient loading to coastal waters can lead to food-limited conditions for benthic bivalves (e.g., Dame and Prins, 1998) suggests that benthic bivalve consumption of excess phytoplankton production might help retard development and maintenance of hypoxia. Variations in climatic conditions (e.g., increased temperature and rainfall, can initiate low O_2 events that weaken benthic filter-feeders, thereby reducing control on phytoplankton and further intensifying hypoxia (e.g., Fallesen et al., 2000; Petersen et al., 2008). Benthic bivalves thus represent potential negative feedback control on phytoplankton whereby hypoxia tends to increase with declines in bivalve populations (see Sect. 6, Chesapeake Bay).

Bottom water O_2 concentrations can influence the balance between decomposition and preservation of organic matter deposited on the seafloor through a variety of complex interactions (e.g., Middelburg and Levin, 2009). The fraction of sinking organic matter that is incorporated into the sediments tends to increase with deposition rate, possibly because high rates of organic input fuel O_2 depletion, which retards decomposition. This makes it challenging to resolve the relative importance of hypoxia, per se, as a control on

Table 1. Characteristic categories of coastal hypoxia defined by time-scales of variability and partially controlled by water column depth. See Zhang et al. (2009) for a broader classification.

Hypoxia Type	Dominant Time-Scale	Depth Range (m)	System Types	Key Controls	Example Systems*
(1) "Permanent"	Decades-Centuries	> 300 m	Silled Fjord, Inland Sea	Depth, mixing, Stratification Organic input flushing	Black Sea[1] Baltic Sea[2]
(2) "Persistent Seasonal" -Stratified	Months	~ 10-100 m	Estuary, Shelf plume	River flow, Temperature, Organic input	Chesapeake Bay[3] Pensacola Bay[4] Changjiang plume[5]
-Mixed	Months	~ 5-15 m	Tidal river	River flow, Tidal range, Organic input	Thames Estuary[6] Scheldt Estuary[7]
(3) "Episodic" (Intermittent)	Weeks-Years	~ 5-20 m	Lagoons, Bays	Wind & Tides, Storms, Organic input	Mobile Bay[8] Neuse Estuary[9]
(4) "Diel"	Hours-Days	~ 1-5 m	Lagoons, Bays	Wind, Light, Nutrient input, Organic input	DE Inland Bays[10] Waquoit Bay[11]

*References: [1] Mee (2006), [2] Conley et al. (2007), [3] Kemp et al. (1992), [4] Hagy and Murrell (2007), [5] Chen et al. (2007), [6] Andrews and Rickard (1980), [7] Soertaert et al. (2006), [8] Turner et al. (1987), [9] Borsuk et al. (2001), [10] Tyler et al. (2009), [11] D'Avanzo and Kremer (1994).

decomposition versus physical effects of rapid of burial (e.g., Hedges and Keil, 1995). Numerous experiments where natural organic matter is allowed to decompose under controlled conditions with and without O_2 have been generally inconclusive (e.g., Westrich and Berner, 1984); however, more recent laboratory and field investigations tend to support the idea that decomposition rates are retarded by absence of O_2 due to a range of mechanisms including loss of macrofauna activity and sulfide inhibition of microbial metabolism (e.g., Middelburg and Levin, 2009). Recent papers (see Sect. 6, northern Gulf of Mexico (NGOM) hypoxia) have speculated that relatively labile organic matter produced in one year could be buried and preserved under seasonally hypoxic conditions, until it is exposed by subsequent physical disturbance in the following year, when decomposition (and O_2 demand) would increase under aerobic conditions (e.g., Turner et al., 2008; Bianchi et al., 2008).

Sediment biogeochemical processes, porewater chemistry, and nutrient recycling are clearly influenced by low water column O_2 and associated sediment oxidation-reduction (redox) profiles. For both nitrogen (N) and phosphorus (P), benthic recycling efficiency (the fraction of inputs of organic N

and P to sediments that efflux back to overlying water) tends to increase with decreasing bottom water O_2 concentrations (e.g., Kemp et al., 2005). Particulate organic nitrogen delivered to bottom water and the sediment surface is decomposed via hydrolysis reactions using one of several available terminal electron acceptors (e.g., O_2, NO_3^-, Mn (III, IV), Fe (III), and SO_4^{2-}), generating inorganic ions of nitrogen (NH_4^+) and phosphorus (PO_4^{3-}) as end-products (Middelburg and Levin, 2009). In the presence of O_2, NH_4^+ tends to be oxidized completely to NO_3^- (or to NO_2^- and N_2O) by chemoautotrophic nitrifying bacteria, resulting in O_2 consumption. Although nitrification may be limited by NH_4^+ availability in sediments with low % organics, rates in eutrophic coastal systems are more often controlled by depth of O_2 penetration into NH_4^+-rich fine-grain organic sediments (e.g., Henriksen and Kemp, 1988). A substantial fraction of the NO_3^- generated in nitrification is generally reduced in surrounding anaerobic zones via denitrification to gaseous N_2 (or N_2O) – forms that are virtually unavailable for assimilation by plants (e.g., Seitzinger, 1988).

Under conditions with hypoxic overlying water, sediments with low redox levels and high sulfide concentrations favor

dissimilatory reduction of NO_3^- back to NH_4^+ over denitrification (e.g., Tiedje, 1987) and strongly inhibit nitrification (e.g., Joye and Hollibaugh, 1995). Although anammox (anaerobic oxidation of NH_4^+ to N_2 with NO_2^-) may occur with anoxia, it is limited by availability of NO_2^-, and rates tend to be substantially lower than denitrification in most coastal sediments (Revsbech et al., 2006). Thus, hypoxic and anoxic bottom waters greatly suppress nitrification and coupled nitrification-denitrification rates, causing a higher % of total nitrogen to be recycled to overlying water as NH_4^+ (e.g., Kemp et al., 1990; see Sect. 6). Similar dynamics involving hypoxia and PO_4^{3-} recycling are attributable to totally different mechanisms. Under normoxic conditions, dissolved PO_4^{3-} binds to oxides and hydroxides of Fe and Mn, forming amorphous solid-phase substances that are retained in sediments (Froelich, 1988). In contrast, hypoxic conditions promote reduction of Fe and Mn to soluble states, thereby releasing bound PO_4^{3-} (Froelich et al., 1982). The presence of free sulfide, which has a very high affinity for binding sites on Fe and Mn, further promotes rapid release PO_4^{3-} and efflux to overlying waters (e.g., Caraco et al., 1989).

Many benthic invertebrate macrofauna (e.g., polychaetes, bivalves, amphipods) are highly susceptible to physiological stresses or mortality from bottom-water hypoxia and anoxia (e.g., Díaz and Rosenberg, 1995; Levin, 2003). Healthy benthic faunal communities can, however, exert strong influence on N and P cycling in coastal marine sediments (e.g., Aller, 1982). Although direct excretion by these organisms tends to increase nutrient recycling, activities of many species also retard recycling of NH_4^+ and PO_4^{3-} by enhanced O_2 advection into sediment porewaters. Macrofauna burrows, tunnels and tubes that penetrate (0.2–10 cm) into sediments are ventilated by natural circulation and by active animal pumping of overlying water (e.g., Aller, 1982). Macrofaunal ventilation tends to stimulate sediment nitrification and strengthen its coupling to denitrification by increasing the effective area of oxic-anoxic interfaces (e.g., Pelegri and Blackburn, 1995). Enhanced O_2 penetration into coastal sediments also retards dissolution of Fe-Mn-oxide-hydroxide complexes, promoting burial of PO_4^{3-} rather than release to overlying waters (e.g., Welsh, 2003; Middelburg and Levin, 2009). Feeding activities of other benthic fauna can dramatically alter sediment biogeochemistry by homogenizing or vertically transporting particles within the upper (0–30 cm) sediment column (e.g., Francois et al., 2001). Field observations and modeling studies suggest that vertical mixing of P-bound particles can reduce PO_4^{3-} release from sediments to overlying water in summer (e.g., DiToro, 2001). In summary, hypoxia and anoxia can further stimulate NH_4^+ and PO_4^{3-} recycling to overlying waters by reducing benthic macrofauna bioturbation.

Meadows of tidal marsh and seagrass plants effectively mitigate eutrophication and hypoxia along the coastal margins through dissolved nutrient uptake and particulate nutrient trapping (e.g., Kemp et al., 2005). Plant biomass accumulation in marshes and seagrass beds can store 10^3 more dry weight (dw) than phytoplankton, with plant stands sometimes exceeding $1000\,g\,dw\,m^{-2}$ (e.g., Valiela, 1995). Integrated nutrient pools contained in these macrophytes plant tissues and associated sediments can dominate coastal biotic nutrient budgets (e.g., Bricker and Stevenson, 1996; Kemp et al., 2005). These plants can respond to N and P enrichment by incorporating higher nutrient concentrations into their leaves (e.g., Duarte, 1990). In addition, denitrification rates in marsh and seagrass sediments are often much higher than those in nearby unvegetated sediments, because of enhanced nitrification associated with O_2 transported by roots into sediments and interception of nitrate-rich groundwater flux from watersheds (Bricker and Stevenson, 1996). The largest impact that these plants have on coastal N and P budgets is derived from their intense trapping of suspended nutrient-rich particles (e.g., Kemp et al., 2005; Boynton et al., 2008). As with benthic macrofauna, however, marsh and especially seagrass plants are also highly vulnerable to negative effects of coastal eutrophication, including reduced water clarity (e.g., Orth et al., 2006) and undermining of belowground tissue (Darby and Turner, 2008).

4 Theoretical response trajectories

To our knowledge, there are very few mechanistic models that have effectively predicted responses of eutrophication-induced coastal hypoxia to remediation, particularly reductions in nutrient loading. Numerical models, which are often used to provide quantitative guidance to the mitigation process, generally predict simple linear reductions in hypoxia in response to reduced nutrient loading (Arhonditsis and Brett, 2004) though recent data suggest that coastal ecosystem responses to nutrient reduction are often more complex (Duarte et al., 2009). Although relatively simple models have been used to hind-cast responses of shallow lakes to such remediation efforts (e.g., Scheffer and Jeppesen, 2007), few numerical forecasts have been documented for coastal systems (Soetaert and Middelburg, 2009). Detailed retrospective observations showing how hypoxia has changed with eutrophication abatement is limited to a few coastal systems (e.g., Díaz and Rosenburg, 2008).

A broad range of possible aquatic ecosystem responses to changes in nutrient loading (Fig. 1) have been defined from theory and observation (e.g., Scheffer et al., 2001; Zhang et al., 2009). In the simplest case, responses of hypoxia and other eutrophication effects might be relatively smooth, continuous and linear, where effects increase and decrease along the same pathway in lock-step with changes in nutrient inputs (Fig. 1a). Alternatively, hypoxia might exhibit little response to an initial increase or decrease in nutrients until the system approaches a "threshold" where relatively small changes in nutrient input cause an abrupt system change
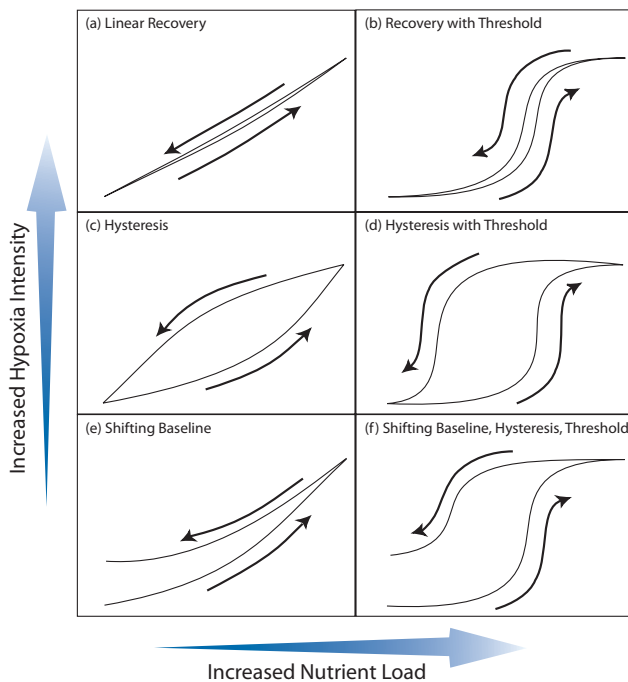
Fig. 1. Six hypothetical response trajectories of oxygen conditions in relation to changes in nutrient load. Trajectories include: **(a)** linear relationship of hypoxia to load with immediate responses, **(b)** direct threshold response to nutrient load, **(c)** delayed (hysteretic) response to nutrient load, **(d)** threshold response with hysteresis, **(e)** linear response with shifted baseline due to changes in other forcing variables, and **(f)** threshold response with hysteresis with a shifted baseline.

(Fig. 1b). In this case, hypoxia again follows the same basic pathway in response to nutrient increase (eutrophication) and nutrient decrease (oligotrophication). If, however, nutrient increases change the fundamental ecosystem character – including trophic structure, habitat conditions, and biogeochemical cycles – the system may follow a distinctly different trajectory and reach different endpoints in response to nutrient input declines (Fig. 1c, d, f). These altered ecosystems become resistant to a change in state, and relatively larger nutrient reductions and longer recovery times are required to induce a complete reversal of eutrophication-induced hypoxia and a return to the original state (Fig. 1, Lanthrop and Carpenter, 2008). Many coastal ecosystems are also experiencing disturbance from other factors (e.g., climate change, fishing harvest, species invasion) that can alter hypoxia responses to loading. Thus, these other factors may have caused the "baseline conditions" to change during long intervals between periods of nutrient increase and decrease. Such baseline shifts can lead to situations where complete recovery to pre-eutrophication conditions cannot be readily achieved simply with reduced nutrient loading (Fig. 1e, f), because of other important environmental changes (e.g., Duarte et al., 2009).

5 Hypoxia remediation with nutrient reduction

Perhaps the most important assumption of the hypothetical response trajectories presented above is that nutrient loading is the primary driver of hypoxia. Whereas several published cases report time series data documenting contemporaneous increases or interannual variations in hypoxia and nutrient loading (e.g., Hagy et al., 2004; Turner et al., 2006b; Kauppila et al., 2005), there are remarkably few examples with time series data that cover periods of both increasing and decreasing nutrient loads. For stratified coastal systems, strong experimental evidence links nutrient loading, phytoplankton productivity, organic particle sinking, and bottom water O_2 consumption (e.g., de Vries et al., 1998); however, the relative balance between this ecological pathway and bottom layer ventilation by vertical mixing is seldom well described. In contrast, the role of labile organic inputs to shallow well-mixed coastal systems in regulating hypoxia has been generally well described (Andrews and Rickard, 1980; Soetaert et al., 2006).

We compiled from the published literature a number of parallel time series of both hypoxia indices and nutrient (and organic matter) loading (or proxies) for several coastal systems to test theoretical expectations of system response to remediation. Available case studies include systems with hypoxia of varying duration (seasonal, episodic, diel), with different anthropogenic inputs fueling hypoxia (inorganic nitrogen or phosphorus, and labile organic matter), and in different system types (well-mixed tidal rivers and shallow lagoons, as well as stratified estuaries, inland seas, and continental shelves). Comparisons of observed responses with hypothetical trajectories described above are made where possible. In general, this analysis suggests that O_2 conditions improved rapidly and linearly in systems with large reductions in discharges of labile organic matter from point sources that had been sustaining O_2 consumption and hypoxia (Table 2). In larger stratified systems where diffuse input of inorganic nutrients was the primary driver of hypoxia through growth, sinking and decomposition of algal cells, the response to remediation tended to exhibit more complex non-linear behaviors (Table 2).

Improved and more widely applied secondary sewage treatment in the 1960s, 1970s, and 1980s led to major reductions in loads of dissolved and particulate labile organic material (or biochemical oxygen demand, BOD) to coastal waters (e.g., Smith et al., 1987). One striking example is the inner Thames estuary, which received high loads of nutrients and organic matter from two major London sewage treatment plants (STP) through the 1960s and 1970s, causing summer dissolved O_2 to remain well below saturation levels (e.g., Andrews and Rickard, 1980) for a stretch of river (>20 km) seaward of London Bridge (Tinsley, 1998). Installation of secondary treatment at the major STPs reduced BOD loads by 80% in the early 1970s, resulting in a return of non-hypoxic summer O_2 levels (Fig. 2), followed by a

Table 2. Summary of reported changes in dissolved oxygen for coastal ecosystems in the peer-reviewed literature, including the dominant loading source, target pollutant, and suggested trajectory of the response.

System	Hypoxia Type	Loading Source	Target[1]	Response[2]	Trajectory Type	Reference
Baltic Sea proper	Permanently Stratified	Diffuse/ Point	Nut.	No Red.	None	Conley et al., 2009a
Boston Harbor	Seasonal Stratified	Point	Nut./BOD	+	Unknown[3]	Díaz et al., 2008
Charlotte Harbor	Seasonal Stratified	Point	Nutrients	+	Unknown[3]	Turner et al., 2006a
Chesapeake Bay	Seasonal Stratified	Diffuse/ Point	Nut.	-	Reg. Shift[4]	Hagy et al., 2004
Danish Coastal Waters	Seasonal Stratified	Diffuse/Point	Nut.	None	Reg. Shift[4]	Conley et al., 2007
N. Gulf of Mexico	Seasonal Stratified	Diffuse	Nut.	No Red.	Reg. Shift[4]	Turner et al., 2008
Delaware estuary	Seasonal Mixed	Point	Nut./BOD	+	Linear[5]	Patrick, 1988
East River	Seasonal Mixed	Point	Nut./BOD	+	Linear[5]	Parker and O'Reily, 1991
Forth estuary	Seasonal Mixed	Point	Nut./BOD	+	Unknown[5]	Balls et al., 1996
Lajaalahti Bay	Seasonal Mixed	Point	Nut./BOD	+	Linear[5]	Kauppila et al., 2005
Los Angeles Harbor	Seasonal Mixed	Point	Nut./BOD	+	Unknown[3]	Reish, 2000
Lower Hudson	Seasonal Stratified	Point	Nut./BOD	+	Linear[5]	Brosnan and O'Shea, 1996
Lower Patuxent estuary	Seasonal Stratified	Point	Nut.	-	Unknown[3]	Testa et al., 2008
Mersey estuary	Seasonal Mixed	Point	BOD	+	Unknown[3]	Jones, 2006
New River estuary	Seasonal Stratified	Point	Nut.	+	Unknown[3]	Mallin et al., 2006
New York Harbor	Seasonal Stratified	Point	Nut./BOD	+	Linear[5]	Parker and O'Reily, 1991
Nervión estuary	Seasonal Stratified	Point	Nut./BOD	+	Unknown[3]	Borja et al., 2006
NW Shelf Black Sea	Seasonal Stratified	Diffuse/ Point	Nut.	+	Hysteresis	Mee, 2006
Raritan Bay	Seasonal Mixed	Point	Nut./BOD	+	Linear[5]	Parker and O'Reily, 1991
Scheldt estuary	Seasonal Mixed	Diffuse/ Point	Nut./BOD	+	Linear[5]	Soetaert et al., 2006
Thames estuary	Seasonal Mixed	Point	BOD	+	Threshold	Andrews and Rickard, 1980
Upper Patuxent estuary	Seasonal Stratified	Point	Nut.	+	Linear[5]	This study
Upper Potomac estuary	Seasonal Stratified	Point	Nut	+	Linear[5]	Kemp et al., 2005
Western LIS	Seasonal Stratified	Point	Nut./BOD	-	Hysteresis	Wilson et al., 2008

[1] Nut. = Nutrients, BOD = biochemical oxygen demand.
[2] + = improvement, − = degradation, None = no response, No Red. = No reduction in load.
[3] Unknown = data too limited to reveal both degradation and recovery trajectory.
[4] See Conley et al., 2009b for regime shift analysis.
[5] Relationship of O_2 and nutrient loading was significantly and linearly related or publication cited a rapid response to remediation.

recovery of fish, benthic macroinvertebrates, and benthic algal communities (Andrews and Rickard, 1980). Although no data were available to describe the time course of degradation (hypoxia development), the remediation response of O_2 (% saturation) versus BOD load suggests threshold behavior, where O_2 conditions improved slowly until ∼70% of the load was removed, followed by rapid response to the final 30% of BOD removal (Fig. 2). The explanation for this threshold is unclear; however, it may reflect that community respiration had been saturated with respect to organic loading, where O_2 levels began to increase only after loading decreased sufficiently for respiration to become substrate-limited. Alternatively, a decline in turbidity following waste load reductions may have been sufficient to allow net photosynthesis by benthic algae, which would augment O_2 replenishment during summer (Andrews and Rickard, 1980). A final possibility is that BOD loading from other, upstream STPs remained high (and kept O_2 low) during the initial phase of
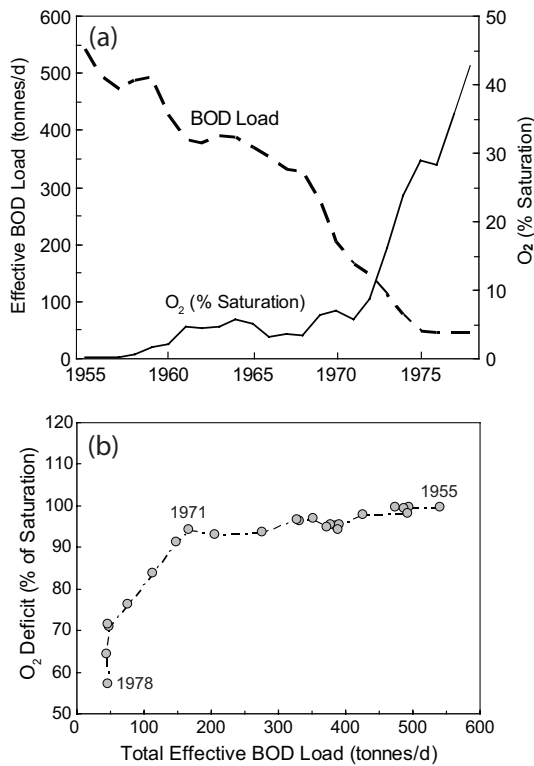
Fig. 2. Time series (1955–1980) of observations in the upper Thames River estuary (England) for **(a)** BOD load from major sewage treatment plants and summer O_2 % saturation, and **(b)** relationship of O_2 % saturation deficit (concentration units below mean saturation) to BOD load showing threshold response of O_2 to reduced BOD load. Data are from Andrews and Rickard (1980).
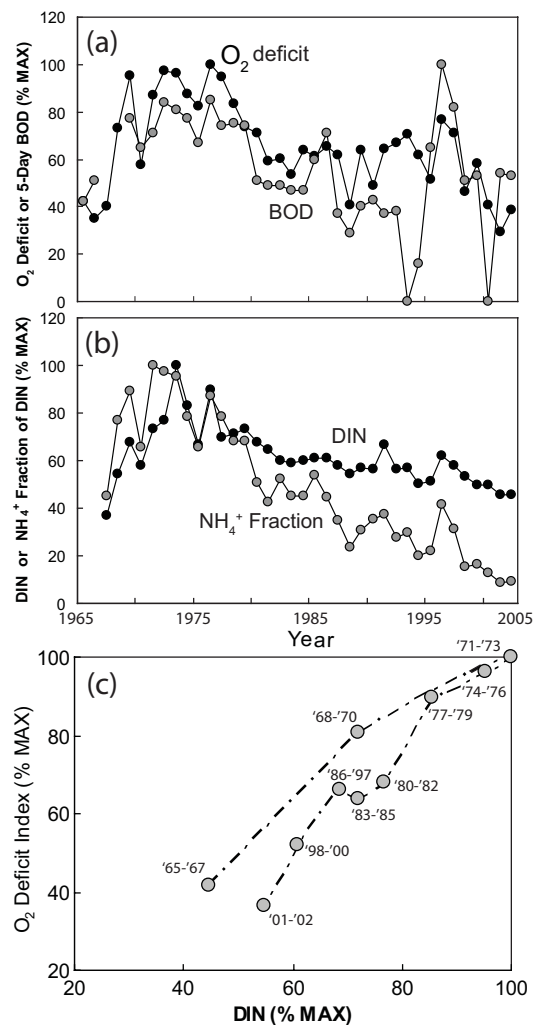

Fig. 3. Time series (1965–2002) of observations at a brackish water station near the Dutch-Belgian border in the Scheldt River estuary (Netherlands) for **(a)** BOD and O_2 % saturation deficit and for **(b)** DIN concentrations and fraction of DIN as NH_4^+ and **(c)** relationship of O_2 deficit index to DIN concentration, showing a favorable linear shifting baseline response of O_2 to reduced DIN and BOD loads. Data are from Soetaert et al. (2006).

the remediation. Several other recently published time series data from shallow well-mixed estuaries have also documented hypoxia responses to increases and decreases in BOD loading from STPs (Table 2). These case studies, including the Delaware River estuary (Patrick, 1988), the lower Hudson River and adjacent estuaries (Brosnan and O'Shea, 1996; O'Shea and Brosnan, 2000), and the Mersey estuary (Jones, 2006), have generally reported relatively positive and rapid responses to reduced BOD inputs.

The Scheldt estuary is another example of a shallow, turbid, and eutrophic upper estuarine system that responded strongly to changes in both nutrient and organic matter loading (Soetaert et al., 2006). The tidal Scheldt is a macrotidal, relatively shallow (∼10–12 m) estuary that received increasing nutrient and organic loads through the 1970s. Declining O_2 levels during this period were linearly related to loading and associated both with oxidation of NH_4^+ (nitrification) and respiration of organic matter (Fig. 3). It appears that nutrient-stimulated algal production was not an important source of organic matter to fuel O_2 depletion in this system because of high turbidity and associated light limitation. When improved sewage treatment reduced BOD loads in the

mid-1970s, O_2 returned to pre-load levels (Fig. 3) over a 20-year period. We explored relationships between O_2 deficits and DIN concentrations (proxy for nutrient loading) in the upper Scheldt to examine the response trajectory of O_2 to nutrient loading (Fig. 3). Although data on N loading were not available (Soetaert et al., 2006), both DIN and phytoplankton chlorophyll-a declined in the upper Scheldt during the period of reported nutrient load reduction. Plots of O_2 deficit versus DIN concentration revealed that the slope of O_2 increase with DIN reduction was flatter than the slope of O_2 decline during increasing DIN (Fig. 3). This trajectory reveals a "favorable" shifted baseline scenario that appears to be related, in part, to a declining ratio of NH_4^+ to NO_3^- loading and concomitant BOD loading reductions (Fig. 3) during this period

(Soetaert et al., 2006). A direct but more complex response to nutrient load reduction has also been reported for the tidal fresh region of the Scheldt (Cox et al., 2009). This success of remediation in the Scheldt despite complicating changes in nutrient ratios, biogeochemistry, and climate (Soetaert et al., 2006) underscores the ability to control low O_2 conditions in shallow tidal estuaries dominated by point source inputs of nutrients and labile organics.

Laajalahti Bay is a shallow ($\sim$2.4 m), well-mixed, semi-enclosed estuary adjacent to Helsinki and connected to the Gulf of Finland by a series of straits and sounds (Kauppila et al., 2005). Although the well-mixed nature of the estuary generally prevented anoxia from occurring in this estuary, hypoxic conditions were relatively common during the mid 1960s when nutrient and BOD loads were highest (Fig. 4). Improved sewage treatment in the late 1960s led to a steep decline in nutrient and BOD loading to the estuary, and O_2 levels increased linearly following a decline in BOD loading then stabilized in the early 1980s (Fig. 4). Further remediation occurred when STP effluents were diverted to the outer archipelago in the mid-1980s, resulting in a second increase in O_2 to near saturation levels (Fig. 4). This second O_2 increase was significantly and linearly correlated with a decline in chlorophyll-a, which was in turn related to decreased TN loading. Improvements in O_2 were, however, likely also affected by removal of the remaining BOD loads following the diversion (Kauppila et al., 2005). Both phases of remediation in Laajalahti Bay caused a linear increase in O_2, one via reduced BOD input and a second linked primarily to reduced inputs of inorganic nutrients (but also BOD). These examples suggest that low O_2 conditions in shallow and well-mixed coastal systems respond positively and rapidly to reductions in both inorganic nutrients and labile organic matter.

In coastal systems where only nutrient loads were reduced, few examples exist where data show that hypoxia decreased markedly with decreased nutrient loading. Where positive O_2 responses have been documented (e.g., Mallin et al., 2005), increases were relatively small despite significant declines in nutrient concentrations. To improve O_2 conditions, reductions in nutrient loading must first cause decreases in the phytoplankton biomass and production that fuels O_2 consumption. Although non-linear responses of phytoplankton biomass to nutrient loading reduction have been reported for many coastal systems (e.g., Duarte et al., 2009), there is a growing number of examples where reductions in algal biomass have been linearly correlated with decreasing nutrient loading (e.g., Henriksen, 2009; van Beusekom et al., 2009). In many large stratified coastal systems, physical processes (e.g., wind stress, river flow, and tidal mixing) play key roles in O_2 depletion, where variations in ventilation of bottom waters may dominate the O_2 balance and control hypoxia formation. Thus, climate-induced changes in circulation and mixing at decadal or longer scales might mask hypoxia responses to decreases nutrient loading, even if organic production and ecosystem respiration decline significantly.

6 Complex responses of hypoxia to nutrients

Recent studies have revealed complex, dynamic relationships between hypoxia, nutrient loading, food webs, and climate for a number of well-studied coastal systems including Chesapeake Bay and its tributaries (e.g., Hagy et al., 2004; Testa et al., 2008), the northern Gulf of Mexico (Turner et al., 2009), the Black Sea (Oguz and Gilbert, 2007), the Baltic Sea (Conley et al., 2009a), Long Island Sound (Wilson et al., 2008), the Danish Coastal straits (Conley et al., 2007), and the shelf region off the northwestern United States (Chan et al., 2008). In several cases, the complexity of responses was manifested in terms of the extent of hypoxia water generated per unit nitrogen loading. For example, the Patuxent River estuary, Chesapeake Bay, and the northern Gulf of Mexico have all exhibited relatively abrupt increases (by more than 2-fold) in hypoxia per N-loading occurring between 1983 and 1993 (Fig. 5). Although these increases may be caused by different factors in different systems, the changing hypoxia-loading relationship underscores the importance of interactions among multiple ecological and physical factors in regulating coastal hypoxia. In this section, we review and analyze selected case studies toward improved understanding of hypoxia responses to remediation in large coastal ecosystems.

6.1 Patuxent River estuary

The Patuxent River estuary, which is a tributary system of Chesapeake Bay, is characterized by two-layered circulation (seaward-flowing surface layer and landward-flowing bottom layer) during most of the year. The mesohaline region has broad shoals ($<$6 m) flanking a deep channel ($>$10 m) with bottom waters that experience hypoxia each year in summer (May–September). Large interannual variations in hypoxia volume and duration are driven largely by changes in freshwater flow and associated nutrient loading and stratification (Testa et al., 2008). Although episodic low-O_2 bottom water has been reported since 1940s (Newcombe et al., 1939), large persistent bottom water hypoxic zones have been evident for the last 5 decades following increased urbanization in the upper watershed (D'Elia et al., 2003).

In an effort to decrease hypoxia and other eutrophication effects, upgrades to sewage treatment reduced loads of TN (via Biological Nitrogen Removal, or BNR) and TP (via chemical precipitation) from point sources, thereby reducing total N and P inputs to the estuary by 25–30% in the mid 1980s for P and early 1990s for N (Fig. 6). Associated with nutrient loading reductions, there have been significant decreases in DIN and DIP concentrations throughout the estuary, as well as declines in phytoplankton chlorophyll-a (chl-a) and light-saturated carbon fixation for the upper estuary (Testa et al., 2008). Bottom water O_2 in the upper estuary increased rapidly following the nutrient load reductions, where hypoxia now rarely occurs during summer (Fig. 6). Despite the improvements in the upper estuary and reduced transport
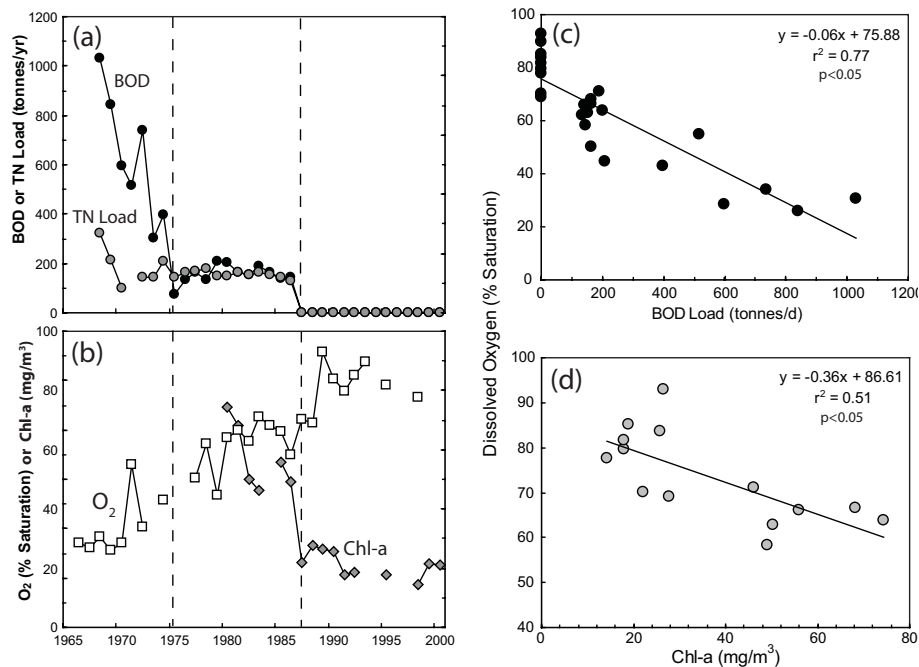
Fig. 4. Time series (1965–2000) observations in Laajalahti Bay (Finland) of **(a)** BOD and TN loads and of **(b)** O_2 % saturation and chlorophyll-*a*. Relationship of **(c)** O_2 % saturation to BOD Load and **(d)** O_2 % saturation to chlorophyll-*a*. Data are from Kauppila et al. (2005).

of N and P to the lower estuary, the total hypoxic volume in the estuary has not changed (Fig. 6).

Analysis of time series data revealed two separate, but positive correlations between NO_3^- load from the watershed and volume of bottom water hypoxia when data were parsed into pre- and post-BNR years, with more hypoxic volume per unit NO_3^- load after BNR was initiated (1990; Testa et al., 2008). Elevated hypoxia per unit N load (Fig. 5) corresponded to increases in summer chl-*a*, turbidity, and surface-layer net O_2 production in the lower estuary since 1990 (Fig. 6). This degradation of water quality and persistence of high hypoxic volume in the lower estuary appears to be linked to three unexpected changes in external and internal factors driving hypoxia. First, after 1990 annual input of DIN to the Patuxent estuary via bottom-layer transport from the nutrient-rich Chesapeake Bay began to increase at a mean rate sufficient to offset the reduced loading from upstream (Fig. 6). Secondly, several consecutive years with above-average river flow and associated watershed nutrient loading in the mid-1990s contributed to strong stratification and elevated watershed N-loading (Testa et al., 2008). Lastly, an abrupt increase in populations of the planktivorous ctenophore, *Mnemiopsis leidyi* (Purcell and Decker, 2005) significantly reduced summer abundance (and potential phytoplankton grazing) of the calanoid copepod, *Acartia tonsa*, from 1990 to 2002 (Fig. 6). Thus, to relieve hypoxia in estuaries like the Patuxent, which are tidally connected to nutrient-rich downstream waters, nutrient inputs must be managed from both

landward and seaward sources where possible (Jordan et al., 1991; de Jonge, 1997), while potential effects of trophic interactions must also be considered in evaluating hypoxia responses to remediation.

6.2 Northwestern shelf of the Black Sea

The Black Sea, which is the largest enclosed sea in the world, receives freshwater, nutrient, and sediment loads from Europe and Asia via the Danube and other rivers (Lancelot et al., 2002). Centuries of human impact have affected the Black Sea, but large ecosystem changes over the past 50 years dramatically affected nutrient and O_2 levels, biogeochemical processes, and trophic relations (Oguz and Gilbert, 2007). A deep and permanently anoxic basin exists in the central part of the Black Sea, but seasonal (summer) hypoxia has occurred on the Sea's northwestern (NW) shelf, which is directly influenced by the Danube River discharge. Although areas of hypoxic bottom-water on the NW shelf have been observed to varying extents since the early 1970s (Mee, 2006), recent reports indicate that this shelf hypoxic zone has nearly disappeared with dramatic reductions in agriculturally-based nutrient loading in the late 1980s (Mee, 2006; Rabalais et al., 2009).

Hypoxic waters, which were first observed on the northwest shelf in the summer of 1973, occurred annually until 1993, with substantial inter-annual variability (Fig. 7, Mee, 2006). The extent of hypoxia on the northwestern shelf has
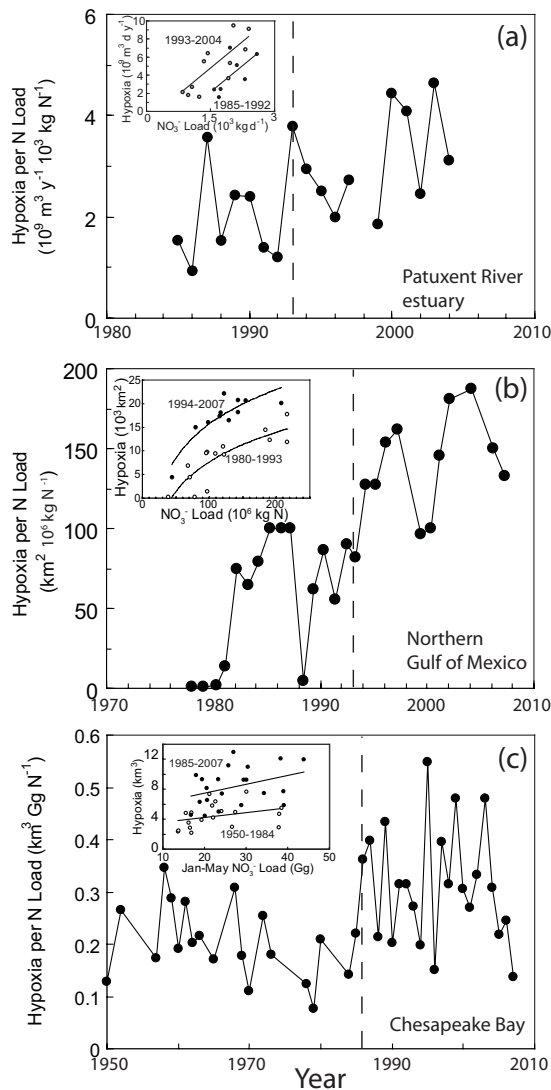
Fig. 5. Multi-decadal time series data for hypoxia per unit nitrogen load in the **(a)** Patuxent River estuary, USA, **(b)** northern Gulf of Mexico, USA, and **(c)** Chesapeake Bay, USA. Inset figures are relationships between N load and hypoxia for each system during periods before and after statistically significant change points (vertical dashed lines) in time-series of hypoxia per unit N load. Patuxent data are from Testa et al. (2008), Gulf of Mexico data are from Turner et al. (2008), and Chesapeake data are from Hagy et al. (2004).

been linked to elevated phytoplankton biomass, which increased from the early 1970s to a peak in the 1980s with increased nitrogen and phosphorus fertilizer use and loads from the Danube River (Fig. 7, Mee, 2006). Following the collapse of the former Soviet Union and Warsaw Pact governments in Eastern Europe in the late 1980s, agricultural subsidies were greatly reduced, causing abrupt and substantial declines in fertilizer use and animal agriculture. The resulting large decrease in Danube watershed's N and P fertil-

izer use was quickly followed by the virtual disappearance of the associated hypoxic area by 1993 (Fig. 7, Mee, 2006; Oguz and Gilbert, 2007). Parallel time-series of hypoxia and both N and P fertilizer application (proxies for nutrient loading) suggest a threshold response of hypoxia to increasing nutrient input, where nutrient loads increased for more than a decade before hypoxia appeared (Fig. 7). While the explanation for this threshold is unclear, Danube River nutrient loading, as well as chl-a in the open Black Sea (Oguz and Gilbert, 2007), have generally followed trends in fertilizer use (Behrendt et al., 2005).

As fertilizer use began to decline in the late 1980s, hypoxic areas were still observed for ∼5 years (1989–1993). This brief hysteretic time-lag may be linked multiple factors: First, a period of sustained phytoplankton production on the northwestern shelf occurred in concert with depressed zooplankton grazing and enhanced upward mixing of nutrient-rich deep water into the photic zone in the adjacent, open Black Sea (Oguz and Gilbert, 2007). Secondly, the observed shift in the N:P ratio in the loading may have caused a shift from N- to P-limitation for phytoplankton growth on the shelf (Fig. 7; T. Oguz, personal communication, 2009). Finally, sustained N and P loading may have occurred despite reduced fertilizer application, due to residual nutrient (especially NO_3^-) pools in groundwater and soils (Behrendt et al., 2005). By the mid-1990s, continued nutrient loading reductions, recovered zooplankton and benthic communities, and reduced wintertime mixing appear to have helped decrease the extent of hypoxia (Mee, 2006; Oguz and Gilbert, 2007). Although physical and ecological factors modulated the effects of nutrient loading on hypoxia in the Black Sea NW shelf, this system represents a relatively rare example of how a major reduction in diffuse nutrient loading can dramatically reduce or eliminate hypoxia.

6.3 Baltic Sea

The Baltic Sea is a large and permanently stratified estuary in northern Europe that receives freshwater inflow from an expansive watershed and salt water inflow with North Sea intrusions via the Kattegat, Skagerrak, and Danish straits. Hypoxia has been present in the Baltic Sea to varying degrees since the Holocene, when the previously freshwater lake was connected to the adjacent ocean, and brackish conditions were established (Zillén et al., 2008). Evidence suggests that the extent of hypoxic water in the Baltic has, however, increased since 1950 (Jonsson et al., 1990). Expanding hypoxic areas appear to have accompanied increased nutrient loads derived from the large and populous Baltic watershed, which includes parts of Scandinavia and Eastern Europe (Conley et al., 2009a). Concerted international efforts to reduce eutrophication and hypoxia in the Baltic Sea have been unsuccessful thus far. Below we explore the factors responsible for controlling the extent of hypoxia in this ecosystem.
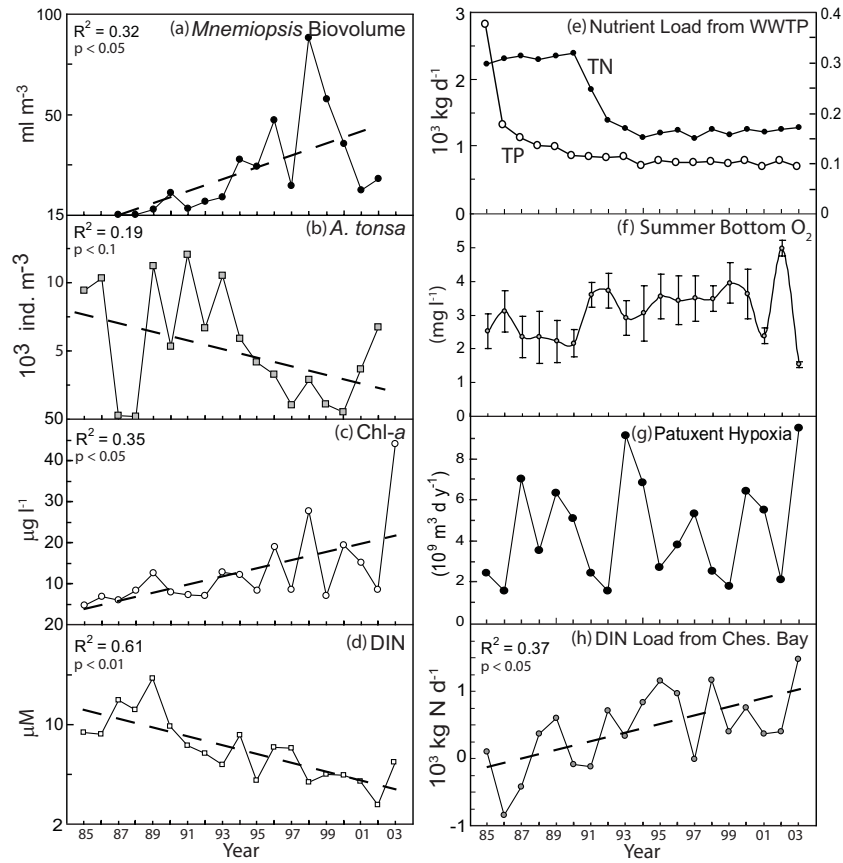
Fig. 6. Time series and trend lines (1985 to 2003) of annual mean June-August concentrations **(a)** *Mnemiopsis* sp. biovolume, **(b)** *Acartia tonsa* abundance, **(c)** chlorophyll-*a*, and **(d)** DIN, and **(e)** mean annual TN (left axis) and TP (right axis) loads from upstream sewage plants, **(f)** upper Patuxent summer (June–August) mean concentrations of bottom water O_2, **(g)** hypoxic volume days in the entire Patuxent River estuary, and **(h)** mean annual DIN inputs from Chesapeake Bay to the Patuxent River estuary. Data are from Testa et al. (2008).

The time-series data describing Baltic Sea hypoxia span from 1960 to the present (Fig. 8, Conley et al., 2009a). A steady decline in the extent of hypoxia from 1970 through 1993 is easily apparent against a small background of inter-annual variability (Fig. 8). The latter decade of the decline (1985–1995) is associated with a decrease in total phosphorus (TP) load and concentration (Fig. 8), which upon first inspection would suggest that nutrient load remediation efforts were successful. However, a steady increase in hypoxic area and dissolved inorganic phosphorus (DIP) occurred from 1993 to 2000, despite no apparent increase in TP load (Fig. 8). Increased DIP levels appear to be attributable both to sustained external P inputs and to increased internal P loading, where iron-bound P was presumably released from sediments in larger quantities during the expansion of hypoxic bottom area from the mid-1990s to early 2000s (Conley et al., 2002; see Sect. 3).

Shifts in climate and physical circulation appear also to have been involved in both the decrease in hypoxic area prior to 1993, and the subsequent hypoxia increase (Fig. 8). The Baltic Sea proper is permanently stratified and has fairly lim-

ited exchange with adjacent oceanic waters. Thus, mechanisms replenishing O_2 to bottom waters via both vertical cross-pycnocline mixing and water renewal via the Danish straits are highly restricted. These processes, which are controlled by physical circulation, may set an upper limit on Baltic hypoxia (Conley et al., 2009a). The 1993 hypoxia minimum followed a 10-year period of low salt water inflows through the Danish straits (Fig. 8). This served to reduce stratification and enhance downward mixing of O_2 (Conley et al., 2009a), as inferred by a steady decline in deep water (200 m) salinity in the Gotland Deep through the 1980s to a minimum in 1992 (Fonselius and Valderrama, 2003). A return of inflowing salt water, documented in the early 1990s, probably continued and caused increasing deep water salinity from 1992–2000 (Fig. 8). This would be expected to increase stratification strength (Fonselius and Valderrama, 2003), contributing to an expanding hypoxic area (Fig. 8). It appears that changes in water renewal rate and stratification combined with increasing temperature (Fonselius and Valderrama, 2003; Omstedt et al., 2004), persistently high nutrient loads (Fig. 8), and enhanced P release from
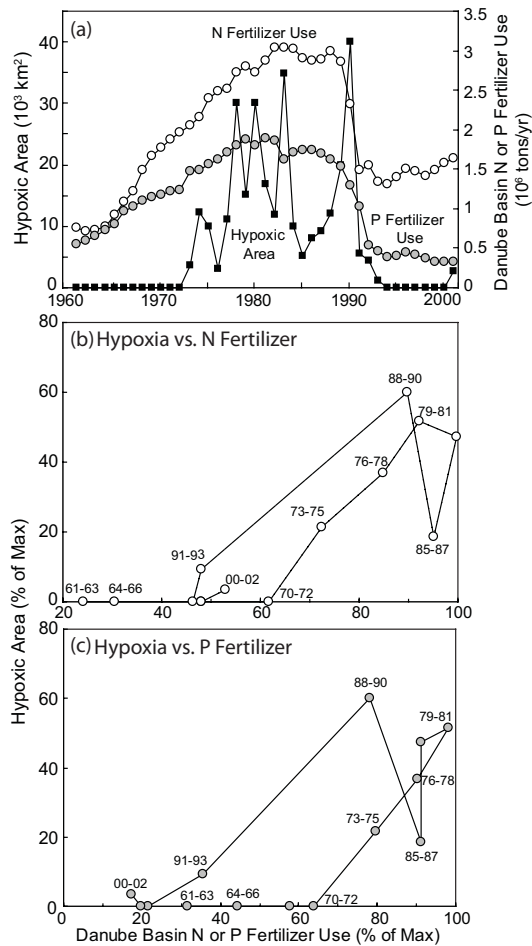
Fig. 7. (a) Time series (1960–2001) of Danube River watershed nitrogen and phosphorus fertilizer use and summer hypoxic area in the northwest shelf of the Black Sea and response trajectory of hypoxic area on the northwest shelf of the Black Sea to interannual changes in (b) nitrogen and (c) phosphorus fertilizer use derived from time series data. Data are from Mee (2006).

Fig. 8. Time-series (1970 to 2000) of (a) annual TP loads to the Baltic Sea (Conley et al., 2002), (b) annual concentration of DIP (solid circles) and DIN (open circles) in the Baltic Proper for depths <100 m (Fonselius and Valderrama, 2003), (c) index of water inflow to the Baltic (solid bars, Schinke and Matthäus, 1998) and deep water (200 m) salinity (grey circles, Fonselius and Valderrama, 2003) in the Gotland Deep, and (d) hypoxic area in the Baltic Proper, Gulf of Riga, and Gulf of Finland from 1970 to 2000 (Conley et al., 2002).

sediments (Conley et al., 2002, 2009a) have all contributed to stable but generally increasing hypoxic zones in this system. Despite the importance of abiotic controls on current hypoxia in the Baltic, modeling studies indicate that effective watershed nutrient management will help to reduce eutrophication and hypoxia (Wulff et al., 2007). The water volume and complex physical circulation of the Baltic suggest, however, that such a recovery would follow hysteretic pathways with long time-lags.

6.4 Chesapeake Bay

Chesapeake Bay is a large estuary in the United States and receives freshwater, nutrient, and organic matter inputs from several rivers, the largest of which is the Susquehanna. Dramatic ecological changes have occurred in Chesapeake Bay during the past century as a result of nutrient enrichment
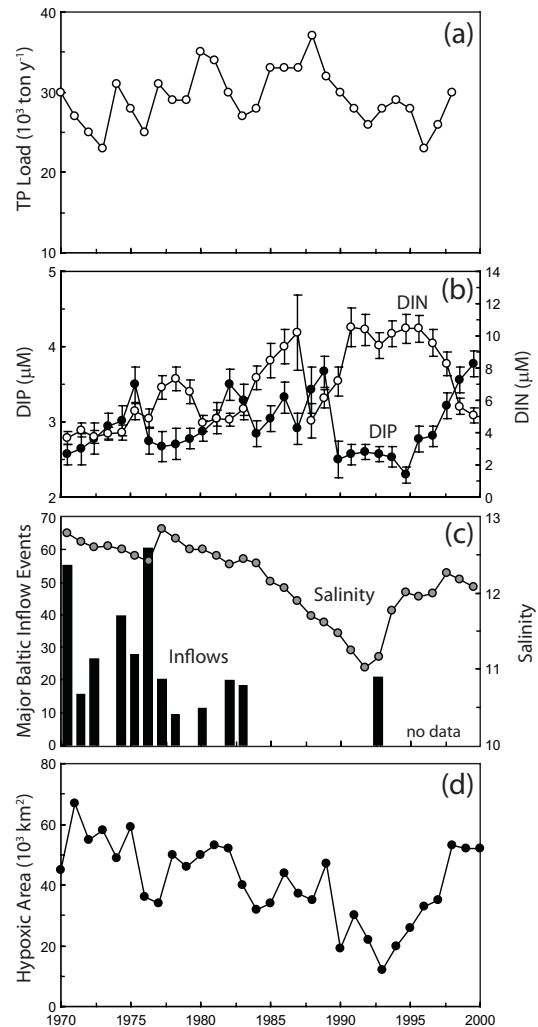
driven by human population growth and land-use changes in its watershed (Kemp et al., 2005). Effects of Bay eutrophication have been compounded by extensive loss of key habitats, including tidal marshes, seagrass beds, and reefs of the filter-feeding eastern oyster, which harbor diverse animal populations and act as sinks for suspended particles and dissolved nutrients. One of the most important ecologically damaging effects of nutrient enrichment in Chesapeake Bay has been a long-term increase in the duration and volume of seasonal bottom-water hypoxia (Hagy et al., 2004).

Because Chesapeake Bay has a large ratio of watershed-to-estuary area, a deep channel isolated from the atmosphere during summer stratification, and a long water-residence-time, it is particularly susceptible to hypoxia and related effects of eutrophication (Kemp et al., 2005). Although incidents of hypoxia were reported as early as the 1930s (Newcombe and Horne, 1938), direct measurements and geochemical indicators suggest that intense and recurrent hypoxia and anoxia were uncommon before a rapid increase in nutrient loading starting in the 1950s (Hagy et al., 2004). Extensive efforts to curb nutrient enrichment of Chesapeake Bay are reflected in the stabilization and slight decline in spring nitrogen loading from the Susquehanna River since $\sim$1990 (Fig. 9). Here we focus on N-loading because it is viewed as the primary limiting nutrient for phytoplankton production (e.g., Fisher et al., 1992, 1999). During this period of declining N loading, however, hypoxia volume has continued to rise (Hagy et al., 2004), resulting in an abrupt doubling of the hypoxia volume per unit spring N load (Fig. 5).

The cause for this unexpected shift in hypoxia volume per N-loading is uncertain. However, it generally coincided with notable changes in several key factors that may have contributed to the hypoxia increase, including a sharp increase in water temperature, a potential decrease in nutrient retention in the upper Bay, and a rapid decrease in oyster abundance (indexed to harvest) and associated filtration capacity (Fig. 9). The rapid increase in surface water temperatures ($\sim$0.7 °C) that occurred over two decades around 1985 (Kaushal et al., in press) would be sufficient to reduce O_2 saturation level by $\sim$0.20 mg l^{-1} and possibly increase respiration by $\sim$5–10% (Sampou and Kemp, 1994). The relative abundance and filtering capacity of the eastern oyster (*Crassostera virginica*) in Chesapeake Bay have declined by almost 100-fold over the past 150 years due to over-fishing and two disease outbreaks (Newell, 1988; Newell and Ott, 1999; Newell et al., 2007). The drought-induced final decline in oyster harvest during the 10–15 yr around 1985 was $\sim$10% of this overall drop between 1900 and the present (Fig. 9, Kimmel and Newell, 2007). Recent modeling (Cerco and Noel, 2007) studies have concluded that 10-fold increases in oyster filtration (equivalent to reversing the decline in the 1980s) would induce a 0.3 mg l^{-1} increase in average mid-Bay bottom water O_2 concentration. The absence of any signal of increased phytoplankton corresponding to the oyster decline, however, raises some doubt about this explanation for the hypoxia shift. Other large changes in the Bay, including losses of marshes and seagrass beds, were important for Bay nutrient budgets (Kemp et al., 2005); however, they are out of phase with this abrupt increase in hypoxia.

While many of these changes in the ecosystem may have contributed to increased hypoxia in Chesapeake Bay, none appear to be sufficiently large and synchronous with hypoxia trends to have caused this hypoxia regime shift. The sub-pycnocline recycling of nitrogen is a key biogeochemical process that has, however, exhibited a time-course of change that parallels the hypoxia regime shift trajectory. Previous studies have suggested that as O_2 decreases, a larger fraction of the total nitrogen load is recycled from sediments as NH_4^+ and mixed vertically into the euphotic zone where it can stimulate further algal growth (see Sect. 3). This increase in NH_4^+ recycling arises because coupled nitrification-denitrification is restricted under hypoxic conditions (Kemp et al., 1990), especially with anoxia-induced loss of benthic macrofauna (Kemp et al., 2005), which otherwise increase O_2 penetration into sediments though ventilation of their tube and burrow habitats (e.g., Mayer et al., 1995). Preliminary analyses of time-series data from mid-Chesapeake Bay suggest an abrupt increase in mean summer bottom water NH_4^+ concentration per unit spring TN loading that closely follows the trend in hypoxia per N loading. While this analysis suggests the potential for hypoxia enhancement via benthic N recycling, this signal is restricted to a small area of the bay and thus it is difficult to imagine how this mechanism could have driven the observed regime shift in hypoxia per unit N loading.

On the other hand, abrupt changes in atmospheric forcing or continental shelf circulation might be strong enough to alter vertical or horizontal replenishment of bottom water O_2 in the Bay. For example, recent modeling and data analysis suggest that sea level rise tends to cause increases in salt flux and bottom-layer salinity in Chesapeake Bay (Hilton et al., 2008), which could have increased stratification. Other evidence suggests an increase in the latitude of the north wall of the Gulf Stream since the 1980s (Taylor and Stephens, 1998) that may have reinforced the trend associated with sea level rise by causing an increase in salinity at the Bay mouth (Lee and Lwiza, 2008). A shift from negative to positive values for the winter North Atlantic Oscillation (NAO) index in the late 1970s (http://www.cgd.ucar.edu/cas/jhurrell/indices.html, Fig. 9) may be related to the change in the Gulf Stream position (Taylor and Stephens, 1998). Such a shift in NAO might also lead to changes in the prevailing wind direction and intensity during summer (Ogi et al., 2003; Scully, 2009), which could affect the strength of stratification and associated ventilation of hypoxic bottom waters in summer (e.g., Malone et al., 1986; Scully et al., 2005). Although many of the ecological and biogeochemical factors discussed here may have contributed to the initiation and resilience of this hypoxia regime shift, we conclude that physical factors are likely involved in the initiation of this change in hypoxia per N loading.

6.5 Northern Gulf of Mexico

A large region of the Gulf of Mexico's northwest continental shelf is highly influenced by outflow of the Mississippi and Atchafalaya Rivers, with associated buoyancy causing stratification and river-borne nutrient loads supporting rich phytoplankton productivity (e.g., Bianchi et al., 2008). Under present conditions, bottom-water hypoxia occurs during summer months in this northern Gulf of Mexico (NGOM)
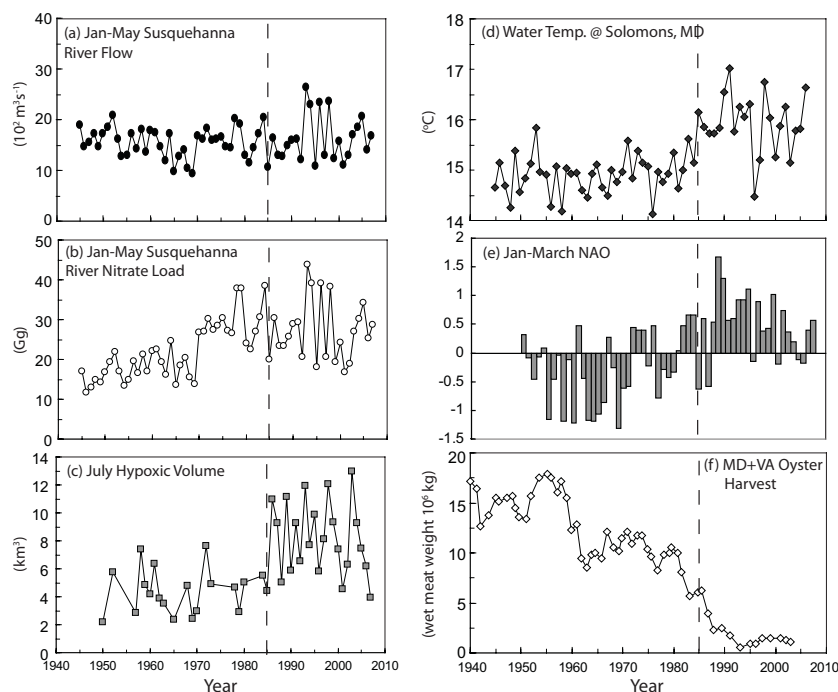
Fig. 9. Time-series (1945–2007) of **(a)** Susquehanna River Flow at Conowingo, MD, **(b)** January–May NO_3^- loads to Chesapeake Bay, **(c)** July hypoxic volume in Chesapeake Bay, **(d)** mean annual water temperature at Solomons, MD, **(e)** January to March North Atlantic Oscillation, and **(f)** annual Maryland (MD) and Virginia (VA) oyster harvest. All data are from Kemp et al. (2005), except temperature data (Kaushal et al., 2009) and NAO data (http://www.cgd.ucar.edu/cas/jhurrell/indices.html).

region. This low-O_2 zone, which was first noted in the early 1970s, has been mapped annually since the mid-1980s (e.g., Rabalais et al., 2007). Fossil records of low-oxygen-tolerant foraminifera and modeling studies, however, suggest that infrequent hypoxia probably occurred back into the 1950s (Osterman et al., 2005; Greene et al., 2009), but that large-scale hypoxic zones likely did not occur prior to the 1970s (Scavia et al., 2003; Justić et al., 2005; Turner et al., 2006b; Greene et al., 2009). A significant trend of increasing areal extent of NGOM hypoxia corresponds strongly with a parallel trend of increasing nitrogen (N) loads from the Mississippi River (Turner et al., 2005), driven largely by the growth of intensive agricultural production in the Midwest region of the USA (Alexander et al., 2008). Since the mid-1980s, the July hypoxic zone has ranged in size from 40 to 22 000 km² and has been correlated with May TN and NO_3^- loading from the Mississippi River (Scavia et al., 2004; Turner et al., 2008). A small (17%) decrease in TN loading between 1997 and 2005 (Turner et al., 2007), however, produced no significant decrease in the extent of July hypoxia (Rabalais et al., 2007). Recent analyses have shown that, much like the situation in Chesapeake Bay, the extent of hypoxia increased substantially in 1993 and thereafter, while N loading has changed very little, resulting in an increase in the area of hypoxia observed per unit of N loading (Turner et al., 2008; Greene et al., 2009).

Although there is no clear explanation for this change in hypoxia per unit N loading, a range of physical and biological factors may have contributed to this hypoxia "regime shift" (Rabalais et al., 2007). Turner et al. (2008) suggested that increased sediment oxygen demand (SOD) could have caused the observed rapid increase in hypoxia. They hypothesized that intensified SOD in recent years was derived from organic matter produced in previous years but preserved and stored in sediments. They further suggested that this stored organic matter would be exposed (e.g., through resuspension events) in subsequent years to fuel enhanced respiration, thereby causing larger than expected hypoxic regions per unit N loading in a given year. Empirical support for this hypothesis (e.g., long-term records of SOD) is limited, and previous observations from warm marine systems suggest that the vast majority of labile organic matter produced in any year is generally respired within months (e.g., Burdige, 1991). A related hypothesis is that there has been a recent increase in organic matter inputs from sources other than the Mississippi-Atchafalaya River System (Bianchi et al., 2008). The primary postulated source for this increased organic matter input is cross-shelf transport of material from Louisiana's eroding coastal wetlands (e.g., Barras et al., 2008). Although the general magnitude of eroding wetland organic matter fluxes have been estimated, they have not been directly linked to Gulf hypoxia (Dagg et al., 2007). While

hypoxia per N loading has been increasing, the rate of coastal land loss has been relatively constant (apart from hurricane-driven increases in 2005) for the last several decades (Barras et al., 2008). Others have emphasized the role of phosphorus (P) inputs in regulating NGOM hypoxia (e.g., Sylvan et al., 2006; Dagg et al., 2007). Although statistical analysis reveals that N loading was by far the best hypoxia predictor, inclusion of winter P levels in a multiple regression model did improve summer hypoxia predictions (e.g., Greene et al., 2009). However, the absence of long-term trends in P loading (Sylvan et al., 2006) indicates that it is not likely responsible for the observed hypoxia shift.

The general open nature of the NGOM system, with unrestricted boundaries to the south along the Gulf and to the west across the broad continental shelf, makes hypoxia development and control highly sensitive to physical circulation processes. Key physical controls on NGOM hypoxia include freshwater inflow, local meteorological forcing, and interactions with the open Gulf circulation. Of these, only the impact of freshwater flow has been considered in analyses of changes and long-term trends in the extent of hypoxia (e.g., Justić et al., 2003; Turner et al., 2005; Greene et al., 2009). One way that a change in other physical factors could impact the extent of hypoxia (and its ratio to N loading), is by modulating the flux of freshwater and nutrients between the shelf and open Gulf (e.g., Bianchi et al., 2006). Current estimates indicate that only 43% of the Mississippi River flow and associated nutrients enters the western shelf, whereas the remainder is directed eastward or otherwise lost to the open Gulf (Etter et al., 2004). Any change in water or nutrient transport at the shelf margin (e.g., Bianchi et al., 2006) would likely impact the extent of hypoxia independently from the riverine N loading rate. Summer winds are also important in regulating NGOM hypoxia, where up-coast (southwesterly) winds favor retention of freshwater (plus nutrients and plankton) on the Louisiana-Texas shelf and enhance stratification and hypoxia, until September when down-coast winds (northeasterly) promote vertical mixing and Gulf-shelf exchange (Cochrane and Kelly, 1986). Although the extent of hypoxia can be reduced quickly when frontal wind events reduce stratification (Rabalais and Turner, 2006), such events are relatively rare in summer. Clearly, changes in these physical forces are important in controlling NGOM hypoxia; however, there is no evidence to suggest decadal scale changes needed to explain the observed shift in hypoxia per unit N loading.

In summary, a long-term increase in the areal extent of hypoxia in the northern Gulf of Mexico since the early 1980s is linked principally to increases in N loading from the Mississippi-Atchafalaya River System. Since 1993, observed hypoxic areas have been larger than expected from spring N loading alone, suggesting changes in other ecological or physical drivers of hypoxia. While many alternative explanations have been suggested, no empirical evidence and/or modeling analyses have been presented to support these hypotheses. Prior to 1993, the statistical relationship between hypoxia and N-inputs might suggest a relatively linear response to proposed reductions in Mississippi River N-loading. However, the recently described and yet unexplained shift in this hypoxia versus N relationship now indicates that more complex response trajectories with hysteresis, shifting baselines, and time-lags might be anticipated.

7 Concluding comments

In response to the recently documented worldwide increase in eutrophication-induced cases of coastal hypoxia, we conducted this review of published case studies, focusing on temporal trajectories of hypoxia responses to changes in nutrient loading for a range of coastal systems. The purpose of this effort was to expand the knowledge-base toward improved (1) understanding of factors controlling hypoxia, (2) simulation modeling of observed hypoxia response trajectories, and (3) strategies for nutrient management to remediate coastal hypoxia. For 24 case studies published in the scientific literature, we compared observed trajectories of hypoxia response to nutrient loading to diverse patterns derived from ecological theory. Although our sample of hypoxic systems with published time series data on hypoxia, nutrients and other factors provides a rich and diverse set of examples, it appears that appropriate temporal data series may also exist (in unpublished monitoring reports) for other hypoxic coastal systems.

In general, we found that shallow well-mixed coastal systems tended to be more responsive to changes in inorganic and organic nutrient loading compared to deeper stratified estuaries and shelf regions. Most of the clearest examples of hypoxia response to loading reductions are from systems where nutrient and organic matter inputs were dominated by point sources (e.g., from sewage treatment plants). Hypoxia in vertically well-mixed coastal systems has generally responded strongly along linear or threshold trajectories to large reductions in loading of labile dissolved organic matter (BOD). Other shallow well-mixed systems have also exhibited declines in hypoxia following decreased loading of inorganic nutrients; however, responses were sometimes delayed by 5–10 years. Even for shallow well-mixed systems, there are few published cases demonstrating hypoxia responses to reduced nutrient loading from watersheds with predominantly diffuse sources.

For deep stratified estuaries, seas or shelf systems, there are surprisingly few examples in the published literature documenting temporal responses of hypoxia to nutrient remediation. The Black Sea is the one case that is most often cited to demonstrate that large rapid reductions in nutrient loading can elicit rapid dramatic decreases in bottom-water hypoxia. Unfortunately, however, response trajectories for this example are based on proxies for N and P loading and relatively sparse measurements of O_2 profiles in a very large

system. Other deep, stratified systems, where hypoxia responses to reduced nutrient loading have been monitored generally suggest recalcitrance with respect to hypoxia improvement. Many of the best documented time series for hypoxia and nutrient loading for these stratified systems have revealed unexpected complex non-linear relationships between hypoxia extent and nutrient loading. These responses are often characterized by abrupt increases in hypoxia per unit nutrient loading that have been speculatively attributed to a range of altered internal ecosystem processes. In many instances, however, evidence is presented suggesting that changes in climatic and/or hydrodynamic conditions coincided with the observed increase in hypoxia and that these physical changes may have altered ventilation of hypoxic bottom waters or transport of nutrients to the overlying euphotic zone.

Lessons learned from this comparative analysis of hypoxia responses to changes in nutrient loading will be useful for coastal researchers and managers alike. Improved understanding of the dominant physical and biological processes is needed to characterize the natural susceptibility of specific coastal systems to hypoxia. Further information is needed concerning interactions among climatic trends and cycles, hydrodynamic circulation and mixing, biogeochemical cycles, and food-web relationships. Analyses should involve application of sophisticated statistical methods and diagnostic studies using biophysical numerical models. Remediation in smaller well-mixed systems dominated by point sources of nutrients are more likely to yield clear and immediate results compared to larger stratified systems with predominantly diffuse nutrient sources. In any case, managers will need to adopt realistic expectations regarding the speed, extent, and nature of hypoxia responses to remediation. What appears to be unsuccessful remediation may simply result from time-lags in ecological response to nutrient input reductions. Successful remediation may require combinations of nutrient loading reductions, restoration of key ecological habitats, and hydrologic engineering solutions (e.g., river flow controls). Effective sustained hypoxia remediation may require open communication among researchers, managers and stakeholders.

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