Coastal Hypoxia Responses to Remediation

W. M. Kemp[1], J.M. Testa[1], D.J. Conley[2], D. Gilbert[3], J.D. Hagy[4]

[1]{University of Maryland, Center for Environmental Science, Horn Point Laboratory, Cambridge, MD 21673 USA}

[2]{GeoBiosphere Science Centre, Department of Geology, Lund University, Lund, Sweden}

[3]{Maurice-Lamontagne Institute, Department of Fisheries and Oceans, Mont-Joli, Québec, Canada, G5H 3Z4}

[4]{US Environmental Protection Agency, National Health and Environmental Effects Laboratory, Gulf Ecology Division, Gulf Breeze, FL, USA}

Correspondence to: W.M. Kemp (kemp@hpl.umces.edu)

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. Because of the negative effects hypoxia has on many organisms, extensive efforts have been made to reduce the size and duration of hypoxia in many coastal waters. Although it has been broadly assumed that reductions in nutrient loading rates would reverse eutrophication and consequently, hypoxia, recent analyses of historical data from European and North American coastal systems suggest little evidence for simple linear response trajectories. We review existing data, analyses, and models that relate variations in the extent and intensity of hypoxia to changes in loading rates for inorganic nutrients and labile organic matter. We also assess existing knowledge of physical and ecological factors regulating oxygen in coastal marine waters and examine a broad range of examples where hypoxia responses to reductions in nutrient (or organic matter) inputs have been documented. Of the 22 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 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 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 tend 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 including: (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, food-webs, and habitats 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 (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 20% saturation ("hypoxia" = $O_2 < 62.5$ µM) interrupt normal metabolism and behavior of fish and invertebrates causing reduced growth and increased mortality (e.g., Diaz 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 Diaz 1998; Decker et al. 2004). Low oxygen levels also alter the oxidation-reduction balance in marine sediments and associated biogeochemistry. For example, hypoxia and anoxia tend to reduce or eliminate 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).

Dissolved oxygen depletion results at various time and space scales from an imbalance between biological and physical sources and sinks for O_2. In shallow tidal rivers and lagoons with well-mixed water columns, the balance between ecosystem photosynthesis, respiration, and air-sea exchange generally controls O_2 concentrations (D'Avanzo and Kremer 1994. In deeper systems with stratified water columns, concentrations in bottom waters are usually set by the balance between O_2 respiration and physical O_2 replenishment from both vertical mixing across the pycnocline and horizontal transport from oxygenated seaward waters (e.g., Kemp et al. 1992). For stratified systems, O_2 concentrations are generally lower in the bottom layer, particularly in warmer months. In protected shallow coastal waters, O_2 generally varies markedly on hourly scales, with hypoxia often occurring at night when photosynthesis is zero (e.g., Tyler et al. 2008). In slightly deeper microtidal systems, periodic stratification may allow episodic hypoxia to occur on daily-to-weekly scales with wind-driven changes in vertical mixing (Park et al. 2007). In much deeper (>100 m) coastal seas and fjords, strongly stratified water columns result in virtually permanent hypoxia (or anoxia) that tends to change only in its size and position with decadal-scale variations in circulation (e.g., Zillén et al. 2008). Low O_2 waters in bottom layers of partially stratified estuaries and river-plume-shelf systems generally appear only in summer when stratification and respiration are strongest (e.g., Rabalais and Gilbert 2009).

There is mounting evidence that eutrophication (i.e., anthropogenic nutrient and organic enrichment of tidal waters) is contributing to the expansion of occurrence, intensity and duration of hypoxic conditions in coastal waters worldwide (e.g., Diaz and Rosenberg 2008; Rabalais and Gilbert 2009). Additional nutrients tend to fertilize growth, sinking and decomposition of phytoplankton in bottom waters of estuaries, bays, lagoons 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 reduction in anthropogenic nutrient loading to coastal systems is the primary means that has been employed for remediation of hypoxia associated with eutrophication, biomanipulation approaches have also been suggested. For example, there has been much discussion and analysis of potential impacts of re-establishing diminished populations of benthic filter-feeding bivalve populations as a means for reversing eutrophication and hypoxia by reducing phytoplankton biomass (e.g., Cerco and Noel 2007; Petersen et al. 2008). In addition, engineering solutions (including enhanced vertical mixing, increased horizontal exchange and mechanical air-bubbling) have been discussed as options for mitigating human-induced coastal hypoxia (Stigebrandt and Gustafsson 2007; Conley et al. 2009c). Although it has been broadly assumed that reductions in nutrient loading rates would reverse associated eutrophication, recent analyses of historical data from European and North American coastal systems suggest little evidence for simple linear response trajectories (Duarte et al. 2009; Conley et al. 2009b).

The purpose of this paper is to review existing data, analyses and models that relate variations in the extent and intensity of hypoxia to changes in nutrient and labile organic loading. We review existing knowledge on physical and ecological factors regulating oxygen conditions in coastal marine waters and examine a broad range of examples where hypoxia responses to nutrient (or organic matter) reduction have been documented. We also focus on five large, well-studied coastal marine ecosystems that have exhibited non-linear responses to changes in nutrient loading, and we discuss key mechanisms that have been suggested to explain the hypoxia

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response trajectories. We conclude with summary statements of implications for remediating and managing low O_2 waters.

2 External Factors Controlling Hypoxia

Although recent decades have seen widespread observations of hypoxic conditions in coastal marine waters worldwide (e.g., Diaz and Rosenberg 2008), the relative importance of specific physical and ecological conditions in regulating oxygen differs substantially among these diverse systems. Therefore, it is expected that responses of hypoxic coastal waters to remediation will also differ. We anticipate that those systems that are influenced most strongly by human activities will be most likely to respond to reductions in anthropogenic influence.

2.1 Typology of Coastal Hypoxia

Drawing from previous hypoxia classification schemes based on duration and dominant time-scales of low oxygen (e.g., Diaz 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 persistent bottom-water hypoxia/anoxia (e.g., Helly and Levin 2004; Gilbert et al. 2005) that tends to change only in its size and position with annual-to-decadal scale variations in circulation (e.g., Helly and Levin 2004; Zillén et al. 2008, Chan et al. 2008). *Persistent seasonal* hypoxia occurs in many stratified temperate estuarine and shelf regions where the combination of spring flow 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 in shallow well-mixed estuaries and tidal rivers that are heavily loaded with large inputs of labile organic material that is 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 frontal wind events (e.g., Stanley and Nixon 1991); however, they may be prolonged by extended warm calm weather (Møhlenberg 1999) or exacerbated following major storm events that deliver large pulsed 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 human activities. 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 (e.g., Kemp et al. 1992, 2005). Buoyancy of the upper layer is increased and stratification is strengthened by seasonal inputs of freshwater (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 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 (e.g., Kuo et al. 1991; Kemp et al. 1992). 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 2005; Chen et al. 2006, 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; Diaz 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. 2008). 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, adjacent phytoplankton biomass from river-borne or oceanic-upwelling sources, and

anthropogenic inputs of particulate and dissolved organics, (e.g., sewage effluents in non-industrialized nations). 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., Diaz 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. 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; 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. Justic 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.

3 Internal Processes Controlling Hypoxia

Although external forcing of physical and biological processes has a strong influence on coastal ecosystem dynamics, including the development of hypoxia, 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, strongly influence dynamics of dissolved oxygen in coastal water columns (e.g., Kemp et al. 2005). In this section we review important internal ecological processes that, on one hand, may be inhibited by eutrophication and hypoxia and, on the other, are capable themselves of reducing development and expansion of hypoxia.

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, in press). 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) shows the ability for benthic bivalves to consume excess phytoplankton production thereby retarding development and maintenance of hypoxia. Variations in climatic conditions, such as increased temperature and/or rainfall, can initiate hypoxic events that weaken benthic filter-feeders, leading to reduced control on phytoplankton, and resulting in further expansion or intensification of hypoxia (e.g., Fallesen et al. 2000; Petersen et al. 2008). Benthic bivalves thus represent a potential negative feedback control on phytoplankton whereby hypoxia distribution tends to increase with declines in bivalve populations.

Bottom water oxygen 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 organic matter deposited on the sediments tends to increase with organic matter deposition rate, possibly because high rates of organic input fuel oxygen depletion, which retards decomposition. This makes it challenging to resolve the relative importance of hypoxia, per se, as a control on 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, 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 activities (e.g., Middelburg and Levin 2009). Recent papers 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).

Many of the sediment biogeochemical processes that strongly influence porewater chemistry and associated nutrient recycling and retention in coastal sediments 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 (primarily 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. Although nitrification may be limited by NH_4^+ availability in sediments with low organic content, rates in eutrophic coastal systems rates 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). Lower redox conditions 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). Thus, hypoxia and anoxia greatly reduce nitrification and denitrification rates (e.g., Kemp et al. 1990). Although anammox (anaerobic oxidation of NH_4^+ to N_2 with NO_2^-) may occur in hypoxic environments, it is limited by availability of NO_2^-, and rates tend to be substantially lower than denitrification in coastal sediments (Revsbech et al. 2006). 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., Diaz 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 1988). 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; Darby and Turner 2008).

4   Theoretical Trajectories for Hypoxia Response to Remediation

Although low-oxygen zones are a natural part of many stratified coastal systems, anthropogenic increases in loading of inorganic nutrients and labile organic wastes have caused hypoxia to occur more widely, more frequently, and with greater severity in coastal regions throughout the world (Diaz and Rosenburg 2008). Coastal eutrophication results in a spectrum of ecological changes in addition to hypoxia, including algal blooms, reduced water clarity, loss of seagrasses, and changes in food-webs (e.g., Kemp et al. 2005). Many responses to eutrophication are undesirable because of associated degradation of habitat for demersal fish and benthic invertebrates (Breitburg 2002). Growing interest in these problems has motivated major socioeconomic commitments by regional, national and international authorities to reduce hypoxia and other environmental problems associated with coastal eutrophication. Consequently, expensive strategies are being devised to reduce watershed and atmospheric inputs of inorganic nutrients and organic wastes to coastal waters (Boesch et al. 2001; Rabalais et al. 2007). Numerical models are often used to provide quantitative guidance to this mitigation process. Although these models generally predict simple linear reductions in hypoxia in response to reduced nutrient loading (Arhonditsis and Brett 2004), recent data suggest that coastal ecosystem responses to nutrient reduction are often more complex (Duarte et al. 2009).

Scheffer et al. (2001) have illustrated a broader range of possible aquatic ecosystem response to changes in nutrient loading (Fig. 1). 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. 1, upper left panel). 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, upper right). 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 in response to nutrient input declines (Fig. 1, middle two panels). These altered ecosystems become resistant to a change in state: relatively larger nutrient reductions and longer recovery times are required to induce a reversal of

eutrophication effects (e.g., hypoxia) than the nutrient increases and degradation period that originally led to these effects. Because many coastal ecosystems are also experiencing perturbations from other factors (e.g., climate change, fishing harvest, species invasion) that can alter hypoxia responses, the "baseline conditions" may have changed during multi-decade time 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. 1, bottom two panels) due to multiple changes in factors that affect hypoxia (e.g., Duarte et al. 2009).

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. 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 remediation is limited to a few coastal systems (e.g., Diaz and Rosenburg 2008).

5 Observed Hypoxia Responses to Remediation

Perhaps the most important assumption of the hypothetical response trajectories presented above is that nutrient loading is the primary driver of hypoxia. Much of the evidence suggesting nutrient loading reduction as an approach for hypoxia remediation is derived from retrospective observation of parallel increasing trends of nutrient loading and hypoxia (e.g., Turner et al. 2005; Hagy et al. 2004; Kauppila et al. 2005; Conley et al. 2009a). However, there is also strong theoretical and experimental evidence linking nutrient loading, algal productivity, organic particle sinking, and bottom water O_2 consumption, providing a mechanistic expectation for the responses that have been observed and evidence that nutrients are likely the primary driver. A possible exception is vertically mixed systems with significant inputs of sewage effluents rich in both dissolved inorganic nutrients and labile organics, where the organics may sustain respiration and hypoxia directly (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 for several coastal systems to test theoretical expectations of system response to remediation. Our analysis includes systems with hypoxia of varying duration (seasonal, episodic, diel), with different anthropogenic inputs fueling hypoxia (nutrients, 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 realized response trajectories to the hypothetical trajectories described above are made where relevant. 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 sewage treatment plants 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 hysteresis and other non-linear behavior (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. Where BOD from sewage treatment plants was the major source of oxygen demand, the situation usually involved large municipal plants discharging into the often shallow upper reaches of estuaries. One example is the inner Thames estuary, which received high loads of nutrients and organic matter from two major London sewage treatment plants 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 sewage treatment plants reduced BOD loads by 80% in the early1970s and quickly returned summer O_2 levels to near-saturation (Fig. 3), followed by a recovery of fish, benthic macroinvertebrates, and benthic algal communities (Andrews and Rickard 1980). The remediation trajectory of the BOD load versus % O_2 saturation indicates threshold behavior, where O_2 conditions improved slowly until ~70% of the load was removed, followed by rapid improvement during the final 30% of BOD removal (Fig. 3). Although no clear explanation exists for this response in the literature, the threshold may represent a synergy of biological and physical conditions. Up to the point where oxygen recovered, respiration, particularly in sediments, may have been saturated with respect to organic loading, such that reduced oxygen demand occurred only when availability of organic substrates became limiting. Interacting with this biological-physical threshold is the possibility that turbidity declined following wasteload reductions sufficiently to allow O_2 production by benthic algae (Andrews and Rickard 1980). Improvements in other sewage treatment plants in the area in the late 1970s may also have contributed to rapidly improving O_2 conditions (Tinsley 1998). Most other shallow well-mixed estuaries receiving high sewage loads have exhibited positive linear responses (rather than threshold responses) to reduced BOD loads in recent decades. These include 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).

The Scheldt estuary is another example of a shallow, turbid, and eutrophic upper estuarine system that responded strongly to changes in nutrient and organic matter loading (Soetaert et al. 2006). The tidal Scheldt, whose densely populated catchment includes parts of France, Belgium, and the Netherlands, is macrotidal with a mean depth of 10-12 meters. Nutrient and organic loads to the Scheldt increased through the 1970s and were linearly related to an O_2 decline resulting from respiration of organic matter and oxidation of NH_4^+ (Fig. 4). Because the upper Scheldt is turbid and is characterized by high nutrient levels, light limitation of phytoplankton generally prevailed and nutrient loads did not contribute to O_2 depletion via production of algal biomass. When improved sewage treatment reduced BOD loads in the mid-1970s, O_2 returned to pre-load levels (Fig. 4) over a 20-year period. In using DIN concentration as a proxy for N loading to the Scheldt, we observed that the slope of O_2 increase following DIN reduction was flatter than the slope of O_2 decline during increasing DIN (Fig. 4). This favorable shifting baseline scenario may be related to the fact that the fraction of DIN in a form that could be oxidized (NH_4^+/DIN) declined steeply (Fig. 4) during this period (Soetaert et al. 2006). This success of remediation in the Scheldt despite complicating changes in nutrient ratios, nitrogen biogeochemistry, and climate (Soetaert et al. 2006) underscores the dominance of point sources in controlling O_2 in some shallow tidal estuaries.

Laajalahti Bay is another example of a simple linear response of low O_2 to loading. This shallow (mean depth = 2.4 m), well-mixed, and semi-enclosed estuary is located west of Helsinki and is 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 during the peak of eutrophication in this estuary, O_2 percent saturation was frequently below 30% during the period of highest nutrient and BOD loads in the mid 1960s (Fig. 5). In response to the realization that Laajalahti Bay was one of the most polluted coastal waters near Helsinki, improvements in sewage treatment in the late 1960s led to a steep decline in nutrient and BOD loading to the estuary. O_2 concentrations increased linearly following a decline in BOD loading, but subsequently stabilized in the early 1980s (Fig. 5). Further remediation occurred when Helsinki wastewaters were diverted to the outer archipelago in the mid-1980s, resulting in a second increase in O_2 to near saturation levels (Fig. 5). This second O_2 increase was significantly and linearly correlated with a decline in chlorophyll-*a*, which was related to decreased TN loading; however, O_2 was likely also affected by removal of all wastewater BOD loads following the diversion (Kauppila et al 2005). Thus, both phases of remediation in Laajalahti Bay caused a linear increase in O_2, one via reduced BOD input and a second linked to reduced inputs of inorganic nutrients (and BOD). As in all the examples presented above, shallow and well-mixed waters appear to respond positively and rapidly to nutrient and organic matter load reductions. Such systems are good targets for remediation because they do not have naturally occurring low O_2 conditions, and hypoxia can be readily controlled via improved sewage-treatment.

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. 2008), 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. Under these conditions, 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. 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 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), and the Baltic Sea (Conley et al. 2009a). In the following section, we review and analyze these case studies toward improved understanding of hypoxia responses to remediation in large coastal ecosystems.

6 Complex Relationships between Nutrient Loading and Hypoxia

6.1 Patuxent River estuary

The Patuxent River estuary is a tributary system of Chesapeake Bay whose watershed straddles two major metropolitan areas. Two-layered circulation occurs for most of the year in the estuary, with a generally seaward-flowing surface layer and landward-flowing bottom layer. The mesohaline region of the Patuxent estuary has a deep channel (>10m) that is flanked by broad shoals (<6m) on each side. Bottom waters of the Patuxent River estuary develop hypoxia between May and September each year, with high interannual variation driven to a large extent by changes in freshwater inputs and associated nutrient loading and stratification (Testa et al. 2008). Although low-O_2 bottom water has been reported occasionally in the estuary since at least the 1940s (Newcombe et al. 1939), signs of eutrophication 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, upgraded sewage treatment reduced loads of TN (via Biological Nitrogen Removal, or BNR) and TP (via chemical precipitation) from point sources (which comprised 45% of the total N and P inputs to the estuary) by 40-60% in the mid 1980s for P and early 1990s for N (Fig. 7). 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 upper regions of the estuary (Testa et al. 2008). Bottom water O_2 concentrations in the upper estuary increased rapidly following the nutrient load reductions, where hypoxia now rarely occurs during summer (Fig.7). Despite the improvements in the upper estuary and reduced transport of N and P to the lower estuary, the total estuarine hypoxic volume did not change (Fig. 7).

In fact, we found two separate positive correlations between NO_3^- load from the watershed and hypoxic volume when data were parsed into pre- and post-BNR years, with more hypoxic volume per unit NO_3^- load after BNR was initiated (after 1990) than before (Testa et al. 2008). Elevated hypoxia per unit N load (Fig. 6) corresponded to increases in summer chl-*a*, turbidity, and surface-layer net O_2 production in the lower estuary in years following BNR (Fig. 7). This degradation of water quality in the lower estuary and maintenance of high hypoxic volume 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 River estuary (via estuarine circulation) from the nutrient-rich Chesapeake Bay bottom layer began to increase at a mean rate sufficient to offset the reduced loading from upstream (Fig. 7). Secondly, several consecutive years with above-average river flow and associated watershed nutrient loading in the mid-1990s contributed to stratification and elevated N-loading from non-point sources (Testa et al. 2008). Lastly, an abrupt increase in populations of the planktivorous ctenophore, *Mnemiopsis leidyi* (Purcell and Decker 2005) significantly reduced summer zooplankton abundance (and potential phytoplankton grazing) for the calanoid copepod, *Acartia tonsa*, from 1990 to 2002 (Fig. 7). Thus, to relieve hypoxia in estuaries like the Patuxent, which are tidally connected to nutrient-rich down-stream waters, nutrient inputs must be managed from both landward and seaward sources, while potential effects of trophic interactions must also be considered in the course of 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 a large fraction of Europe and from some regions of 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 caused more dramatic changes in nutrient and O_2 levels, as well as ecological changes at all trophic levels (Oguz and Gilbert 2007). A deep and permanently anoxic basin exists in the central part of the Black Sea, but seasonal hypoxia (i.e., during warm months) has occurred on the northwestern shelf of the sea, which is directly influenced by the Danube River discharge. Areas of hypoxic bottom-water have been observed to varying extents since the early 1970s (Mee 2006). The development, variability, and ultimate removal of the hypoxic zone in the northwestern shelf is an example of how the extent of hypoxia can respond to changes in nutrient loads, as mediated by climatic variability and food web shifts resulting from over-fishing.

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. 8, Mee 2006). The extent of hypoxia on the northwestern shelf has been linked to elevated phytoplankton biomass, which increased from the early 1970s to a peak in the 1980s with increased nitrogen fertilizer use and N loads from the Danube River (Mee 2006; Oguz and Gilbert 2007). 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 N fertilizer use and animal agriculture. The resulting large decrease in Danube River N loads (Fig. 8, Mee 2006; Oguz and Gilbert 2007) was quickly followed by the disappearance of the associated hypoxic area by 1993. A small area of hypoxic water has returned in only one year since 1993 (Mee 2006).

Parallel time-series of hypoxia and N fertilizer application (a proxy for N loading) suggest a threshold response of hypoxia to increasing nutrient input, where N loads increased for more than a decade before hypoxia appeared (Fig. 8). An explanation for this threshold is not clear, but Danube River loading (and chl-*a* in the open Black Sea) did not begin to increase until 1970 (Oguz and Gilbert 2007), suggesting that increased fertilizer use did not translate into increased loads until this time. 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 to a period of increased phytoplankton production on the northwestern shelf associated with depressed zooplankton grazing in the open Black Sea, and with enhanced upward mixing of nutrient-rich deep water into the photic zone (Oguz and Gilbert 2007). By the mid-1990s, sustained low nutrient loads, recovered zooplankton and benthic communities, and milder climatic conditions, all helped to sustain the absence of hypoxic events (Mee 2006; Oguz and Gilbert 2007). Although the interaction of "top down" effects and other external conditions appears to have modulated the effect of N loading on hypoxia in the Black Sea, this system provides a relatively rare example of how a major reduction in 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, Skaggerak, 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 Sweden, Finland, Denmark, Germany, Poland, Russia, and several smaller countries (Conley et al. 2009a). Concerted efforts by these countries 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.

The time-series data describing Baltic Sea hypoxia span 1960 to the present (Fig. 9, Conley et al. 2009a). A steady decline in the extent of hypoxia from 1970 through 1993 is easily apparent against a small background of interannual variability (Fig. 9). The latter decade of the decline (1985-1995) is associated with a decrease in total phosphorus (TP) load and concentration (Fig. 9), 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. 9). The increase in 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).

Shifts in climate and physical circulation appear also to have been involved in the decrease in hypoxic area prior to 1993, as well as the subsequent hypoxia increase (Fig. 9). The Baltic Sea proper is permanently stratified and has fairly limited 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 are controlled by physical circulation, and associated stratification strength 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. 9), which served to reduce stratification and enhance downward vertical 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 one year in the early 1990s, probably continued and caused increasing salinity in the Gotland Deep from 1992-2000 (Fig. 9). This would be expected to increase stratification strength (Fonselius and Valderrama 2003), contributing to expanding hypoxic area (Fig 9). 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. 9), and enhanced P release from sediments (Conley et al. 2002, 2009a) have caused stable and increasing hypoxic areas in this system. Despite the importance of abiotic controls on current hypoxia in the Baltic,

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modeling studies indicate that effective nutrient management in the Baltic watershed will help to reduce eutrophication and hypoxia (Wulff et al. 2007).

6.4 Chesapeake Bay

Chesapeake Bay is the largest estuary in the United States and receives freshwater, nutrient, and organic matter inputs from several rivers, the largest of which is the Susquehanna River. Dramatic ecological changes have occurred in Chesapeake Bay during the past century as a result of nutrient enrichment associated with human population growth and watershed land-use changes (Kemp et al. 2005). Effects of Bay eutrophication have been compounded by extensive loss of key habitats, including meadow- and canopy-forming beds of submersed aquatic plants and reefs of the filter-feeding eastern oyster, both of which form habitats for diverse animal populations and 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 bottom-water hypoxia during the warm months of the year (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 the mid 1950s following the large post-WWII increase in nitrogen loading (Hagy et al. 2004). Extensive efforts to curb nutrient (both N and P) enrichment of Chesapeake Bay have led to a stabilization and slight decline in spring nitrogen loading from the Susquehanna River since ~1990 (Fig. 10). 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 same time period, however, the volume of hypoxia has continued to rise, resulting in an abrupt doubling of the hypoxia volume per unit spring N load (Hagy et al. 2004). This "regime shift" with respect to N effects on hypoxia (Kemp et al. 2005) appears to have been initiated in 1986 (Conley et al. 2009b).

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 could 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. 10). Monitoring data indicate that surface water temperatures have been generally increasing in the middle region of Chesapeake Bay since 1945, but a relatively rapid rise (~1.0^{o}C) occurred in the period 1980-1990 (Kaushal et al., in press). This temperature rise would have reduced O_2 saturation level by ~ 0.25 mg/l and increased water column respiration by 0.06 mg l^{-1} d^{-1} (Sampou and Kemp 1994), probably insufficient changes to have caused the observed regime shift. Although reductions in phytoplankton biomass in the upper region of the Bay since the late 1970s may have allowed a larger fraction of Susquehanna River N loads to be transported seaward to fuel increased phytoplankton biomass in seaward regions (Harding and Perry 1997; Hagy et al. 2004; Paerl et al. 2004), nutrient transport estimates to support this hypothesis are lacking. The relative abundance and filtering capacity of

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the eastern oyster (*Crassostera virginica*) in Chesapeake Bay have declined dramatically over the past 150 years due to over-fishing and two disease outbreaks, with the largest reduction ($\sim 40 \times 10^6$ to $\sim 15 \times 10^6$ kg yr^{-1}) in upper Bay harvest occurring between 1890 and 1910 (Newell 1988). Despite these problems, a relatively stable, but much reduced, harvest (varying between 5 and 10×10^6 kg yr^{-1}) persisted from ca. 1930 to the early 1980s, when a final, drought-induced decline essentially eliminated the oyster fishery (Fig. 10, Kimmel and Newell 2007). Assuming that harvest provides a relative index of oyster abundance, the loss in phytoplankton filtering capacity associated with this final decline in harvest might have contributed to the 1980s jump in hypoxia per N loading (Newell and Ott 1999; Newell et al. 2007), especially if the drought of 1985-1986 caused high mortality of isolated, non-harvestable oysters (Kimmel and Newell 2007). The fact that historical records indicate no clear signal in phytoplankton abundance corresponding to the earlier oyster decline, however, raises questions about the potential for this smaller more recent oyster reduction to have caused the abrupt shift in hypoxia per N loading. The timing of other large changes in the Bay ecosystem, including reductions in nutrient-trapping capacity resulting from losses in abundance of marsh and seagrass communities (Kemp et al. 2005), while important, appear to be out of phase with this hypoxia regime shift.

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 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 organic nitrogen deposited to sediments is recycled to overlying water as NH_4^+ and mixed vertically into the euphotic zone where it can stimulate further algal growth (e.g., Kemp et al. 1990, 2005). This relationship arises because the coupled nitrification-denitrification process that transforms fixed nitrogen (NH_4^+) into N_2 gas (which is unavailable for algal assimilation) is restricted under hypoxic conditions (Kemp et al. 1990). This switch to increased N recycling to NH_4^+ is further enhanced by the loss of benthic macrofauna species from the anoxic region of the Bay bottom (Kemp et al. 2005), who have the ability to 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 (Testa et al., in prep). While this analysis suggests that hypoxia enhancement of benthic N recycling has played an important role reinforcing further O_2 depletion, 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 retrospective 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). The dramatic shift from negative to positive values for the winter index of the North Atlantic Oscillation (NAO) in the late 1970s (Fig. 10,

http://www.cgd.ucar.edu/cas/jhurrell/indices.html) 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 (Ogi et al. 2003) 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) region. The size of this low-O_2 zone has been mapped annually since the mid-1980s, when hypoxia was first recorded by direct observation (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. 2009 Greene et al. 2009) but that large-scale hypoxic zones likely did not occur prior to the 1970s (Justic et al. 2005; 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 km^2 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), produced no significant decrease in the extent of hypoxia in July (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. 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 nitrogen loading in a given year. Unfortunately, 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 (Dagg et al. 2007; Bianchi et al. 2008). The

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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 and biogeochemical nature of eroding wetland organic matter fluxes have been estimated, these organic fluxes have not been directly linked to increased Gulf hypoxia (Dagg et al. 2007). In addition, recent analyses indicate that, apart from increases associated with hurricanes in 2005, the rate of coastal land loss has been relatively constant for the last several decades (Barras et al. 2008). Others have emphasized the role of phosphorus (P) loading 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 predictor of hypoxia, inclusion of winter P concentrations in a multiple regression model did improve summer hypoxia predictions (e.g., Greene et al. 2009). However, the absence of any long-term trend in P loading (Sylvan et al. 2006) indicates that it is probably not responsible for the observed hypoxia regime 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., Justic 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 (not including the Atchafalaya River flow which is 30% of the total) enters the western shelf, whereas the remainder is directed eastward or otherwise lost to the open Gulf (Etter et al. 2004). Any change either in this fraction or in the rate of removal of water, nutrients, and sediments at the shelf margin (e.g., Bianchi et al. 2006) would likely impact the extent of hypoxia independently from the measured nitrogen 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 wind events (e.g., associated with frontal passage) 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. Thus far, however, no evidence has been presented to suggest decadal scale changes in these processes that would be needed to explain the observed shift in hypoxia per unit of N loading in this system.

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 following the intensification of agriculture in the watershed. Since 1993, observed hypoxic areas have been larger than expected from spring N loading alone, suggesting that one or more changes may have occurred in other potential ecological or physical drivers of hypoxia. Hypothesized causes include accumulation and preservation of labile sediment organic matter, relief of P-limitation on phytoplankton production, alternative organic carbon sources, and a sustained change in physical processes. Another possibility is that the

massive discharge from the Mississippi Basin in 1993 caused an ecological state change in the shelf ecosystem. To date, however, supporting empirical evidence and modeling analyses are insufficient to provide rigorous tests of these hypotheses.

7 Concluding Comments & Implications for Management

Our review of case studies around the world reveals the complexity of the hypoxia problem, from both the standpoint of understanding the controls on O_2 dynamics and also deciding what management actions are required to relieve depressed O_2. Persistent and growing hypoxia in many other regions of the world—e.g., East China Sea (Chen et al. 2007) and Long Island Sound (O'Donnell et al. 2008—remind the scientific community that efforts to understand and control hypoxia must continue during the next several decades, as human impacts on coastal systems continue to increase.

The varied trajectories of hypoxia responses to organic and nutrient loading in different systems, both hypothesized and realized, underscore the fact that managing and remediating hypoxia in coastal ecosystems must be system-specific. Physical features of the ecosystem (i.e., bathymetry, circulation, and stratification) appear to set limits on hypoxia extent by controlling O_2 replenishment via advective and diffusive O_2 inputs. These physical factors, thus, contribute to threshold responses of hypoxia to nutrient loading. Thresholds can also be ecological in nature when disruption of key feedback processes (e.g., grazing on algae, trapping of organic matter, and cycling of nutrients) alters the nature of the system's responses to loading. Where such thresholds exist, time-lags in ecosystem responses to reduced nutrient loading declines must be expected. Further time-lags may exist, for example, where accumulated nutrients take years to flush out of the system, or where benthic communities and associated food-webs require time to fully recover. In the case that benthic communities or other components of the food web are irreversibly altered, expectation of a return to historical conditions with remediation may be inappropriate. This is because climatic changes (i.e., increased temperature, altered freshwater input, changes in atmospheric circulation) during the degradation and remediation time periods may also induce a "shifting baseline", where even if nutrient loading is reduced, climatic forcing and ecosystem dynamics will differ from previous periods, possibly in ways that alter the ecosystem's susceptibility to hypoxia.

As with strategies for management and remediation, expected responses to remediation should be adjusted to the specific system. In Long Island Sound, for example, despite reductions in municipal wastewater discharges, summer values for bottom O_2 have continued to decline because of long-term changes in wind velocity and associated increases in stratification (Wilson et al. 2008). In contrast, for shallow well-mixed coastal systems where point sources were the dominant contributor to hypoxia (e.g., the Scheldt, Forth and East River estuaries, Table 2), abrupt and large load reductions have induced successful remediation that followed relatively linear recovery trajectories. For other shallow coastal systems (e.g., upper estuaries of the Potomac and Thames Rivers) responses to point-sources nutrient remediation were substantial but delayed for a decade as these latter cases illustrate how adequate recovery time may need to be allowed prior to evaluating success of management actions.

Deep stratified systems have generally exhibited more complicated responses to remediation compared to shallower coastal systems. One of the few documented rapid and direct recoveries from hypoxia in a deep stratified system occurred in the northwestern shelf of the Black Sea, where severe political and economic shifts led to an unusually large and abrupt reduction in external nutrient loading. Similar systems, for which nutrient loads are primarily derived from diffuse sources (e.g., Chesapeake Bay, northern Gulf of Mexico, and Baltic Sea), have shown little recovery and in most cases, indicate continued expansion of hypoxia. Hysteresis recovery trajectories and long delays between management and ecological responses appear in these systems due to alterations in biological and physical processes. It appears that, in many cases, the loss of key ecosystem feedback effects (e.g., biogeochemical cycles or food-web interactions) and/or major alterations in climatic or oceanographic conditions may have muted or counteracted expected hypoxia decreases in response to reduced nutrient loading. In such situations, hypoxia remediation may be enhanced by restoration of habitats for key filter-feeding bivalve reefs, tidal marshes and seagrass beds—all of which tend to filter and retain nutrients and organic material. In addition, coupled management of point-sources and landscape modification may be necessary to remediate the nutrient loading that controls hypoxia. Full recovery in these systems may require additional time for restoration of nutrient-impaired biological functions to occur.

The temporal scales of hypoxia remediation may also be linked to the inherent physical properties and processes that constrain hypoxia development in coastal systems. For instance, in shallow well-mixed estuaries that experience seasonal or diel hypoxia, limited stratification and adequate vertical mixing naturally favor oxygenation, thus accelerating remediation time and favoring rapid linear recovery. Improvements in water clarity and restoration of benthic photosynthesis in these shallow systems may provide positive feedbacks that further accelerate recovery. In this case, decreased nutrients reduce phytoplankton biomass, improve water clarity, and enhance benthic algal and seagrass photosynthesis, which serves to oxygenate the water column and sequester nutrients within sediments. Deep, stratified, and enclosed estuaries are naturally more susceptible to hypoxic conditions and resistant to remediation. Stratified continental shelf regions have similar susceptibility to hypoxia; however, their comparatively open nature may make them more responsive to remediation because of characteristic stronger water exchange with deeper offshore regions. In systems with episodic hypoxia, the climatic conditions that favor brief hypoxic events may be unresponsive to remediation, but reduced nutrient loads could decrease the frequency and intensity of hypoxic events by limiting phytoplankton biomass.

Lessons learned from this comparative analysis of hypoxia responses to remediation 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 a particular coastal system 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. In addition to understanding oceanographic and ecological processes, managers will need to educate stakeholders to achieve realistic results regarding the speed, extent, and nature of hypoxia response to remediation. What appears to be unsuccessful remediation may simply result from time-lags in ecological

response to remediation actions. Successful remediation may require combinations of nutrient loading reductions, restoration of key ecological habitats, and hydrologic engineering solutions (e.g., river flow controls). Assuming that the scientific community is able to adequately understand factors regulating hypoxia, sustained remediation may require open communication among researchers, managers and stakeholders.

Acknowledgements

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Table 1. Characteristic categories of coastal hypoxia defined by time-scales of variability and partially controlled by water column depth.

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), [10]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).

Table 2: Summary of reported changes in oxygen for coastal ecosystems in response to remediation.
(Nut. = Nutrients, Reg. Shift = Regime Shift, No Red. = No Reduction in Nutrient Load)

| System	Hypoxia Type	Loading Source	Target	Response	Trajectory Type	Reference
Danish Coastal Waters	Seasonal Stratified	Diffuse/Point	Nut.	None	Reg. Shift	Conley et al. 2007
N. Gulf of Mexico	Seasonal Stratified	Diffuse	Nut.	No Red.	Reg. Shift	Turner et al. 2008
Lower Potomac	Seasonal Stratified	Diffuse/ Point	Nut.	None	Hysteresis	Jaworski unpubl.
Chesapeake Bay	Seasonal Stratified	Diffuse/ Point	Nut.	-	Reg. Shift	Hagy et al. 2004
NW Shelf Black Sea	Seasonal Stratified	Diffuse/ Point	Nut.	+	Hysteresis	Mee 2006
Baltic Sea proper	Permanently Stratified	Diffuse/ Point	Nut.	No Red.	None	Conley et al. 2009a
Lajaalahti Bay	Seasonal Mixed	Point	Nut./BOD	+	Linear	Kauppila et al. 2005
Boston Harbor	Seasonal Stratified	Point	Nut./BOD	+	Unknown	Diaz et al. 2008
Delaware estuary	Seasonal Mixed	Point	Nut./BOD	+	Linear	Patrick 1988
Scheldt estuary	Seasonal Mixed	Diffuse/ Point	Nut./BOD	+	Linear	Soetaert et al. 2006
Upper Potomac	Seasonal Mixed	Point	Nut./BOD	+	Linear	Jaworski unpubl.
Western LIS	Seasonal Stratified	Point	Nut./BOD	-	Hysteresis	Wilson et al. 2008
Thames estuary	Seasonal Mixed	Point	BOD	+	Threshold	Andrews and Rickard 1980
Mersey estuary	Seasonal Mixed	Point	BOD	+	Unknown	Jones 2006
Forth estuary	Seasonal Mixed	Point	Nut./BOD	+	Linear	Balls et al. 1996
Lower Hudson	Seasonal Stratified	Point	Nut./BOD	+	Linear	Brosnan and O'Shea 1996
New York Harbor	Seasonal Stratified	Point	Nut./BOD	+	Linear	Parker and O'Reily 1991
East River	Seasonal Mixed	Point	Nut./BOD	+	Linear	Parker and O'Reily 1991
Charlotte Harbor	Seasonal Stratified	Point	Nutrients	+	Unknown	Turner et al. 2006
Los Angeles Harbor	Seasonal Mixed	Point	Nut./BOD	+	Unknown	Reish 2000
Raritan Bay	Seasonal Mixed	Point	Nut./BOD	+	Linear	Parker and O'Reily 1991
New River estuary	Seasonal Stratified	Point	Nut.	+	Linear	Mallin et al. 2006
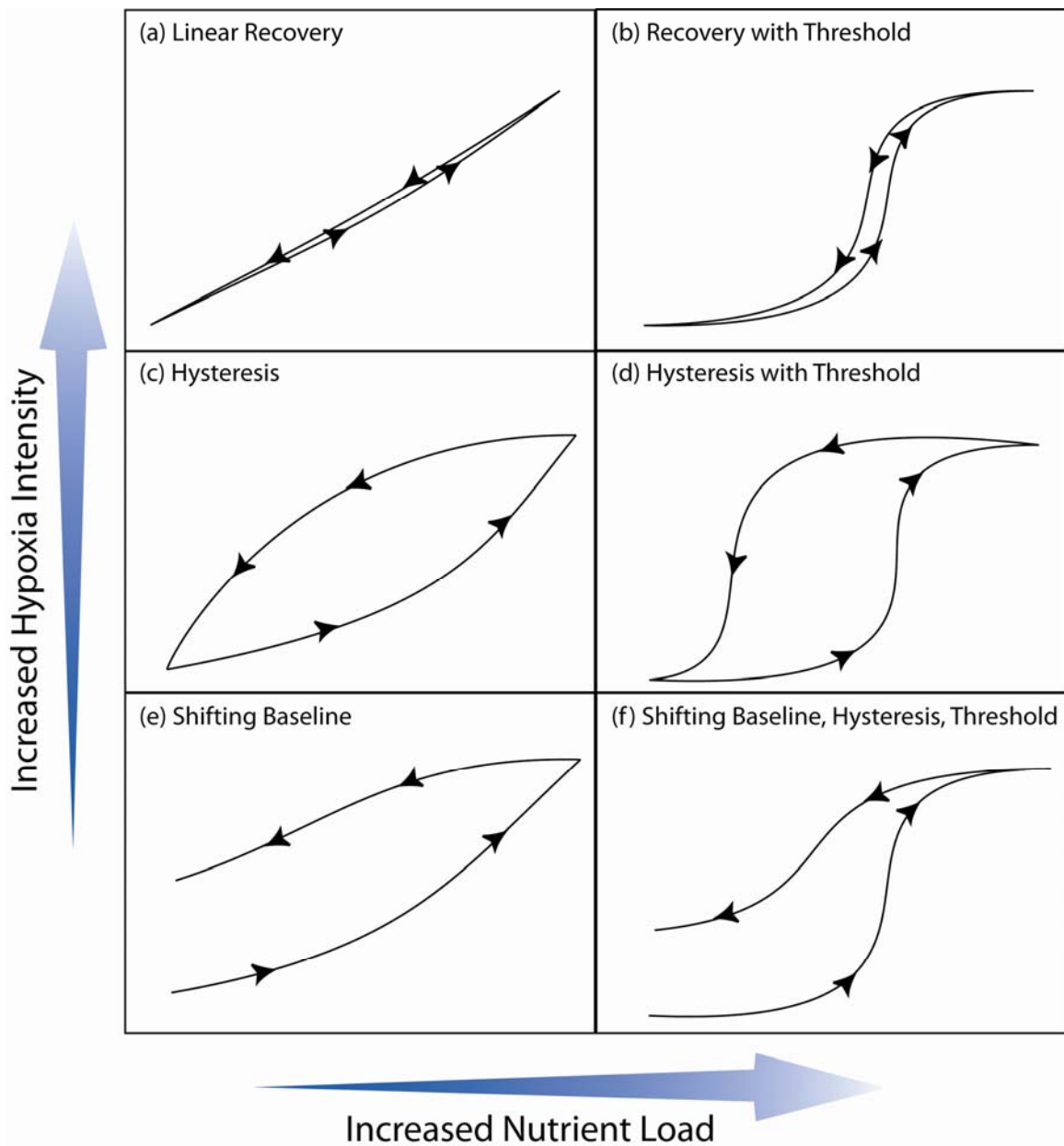
Figure 1: Six hypothetical response trajectories of oxygen conditions in relation to changes in nutrient load. Trajectories include: (a) linear relationship of hypoxia to load with immediate responses, (b) direct threshold response to nutrient load, (c) delayed (hysteretic) response to nutrient load, (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.
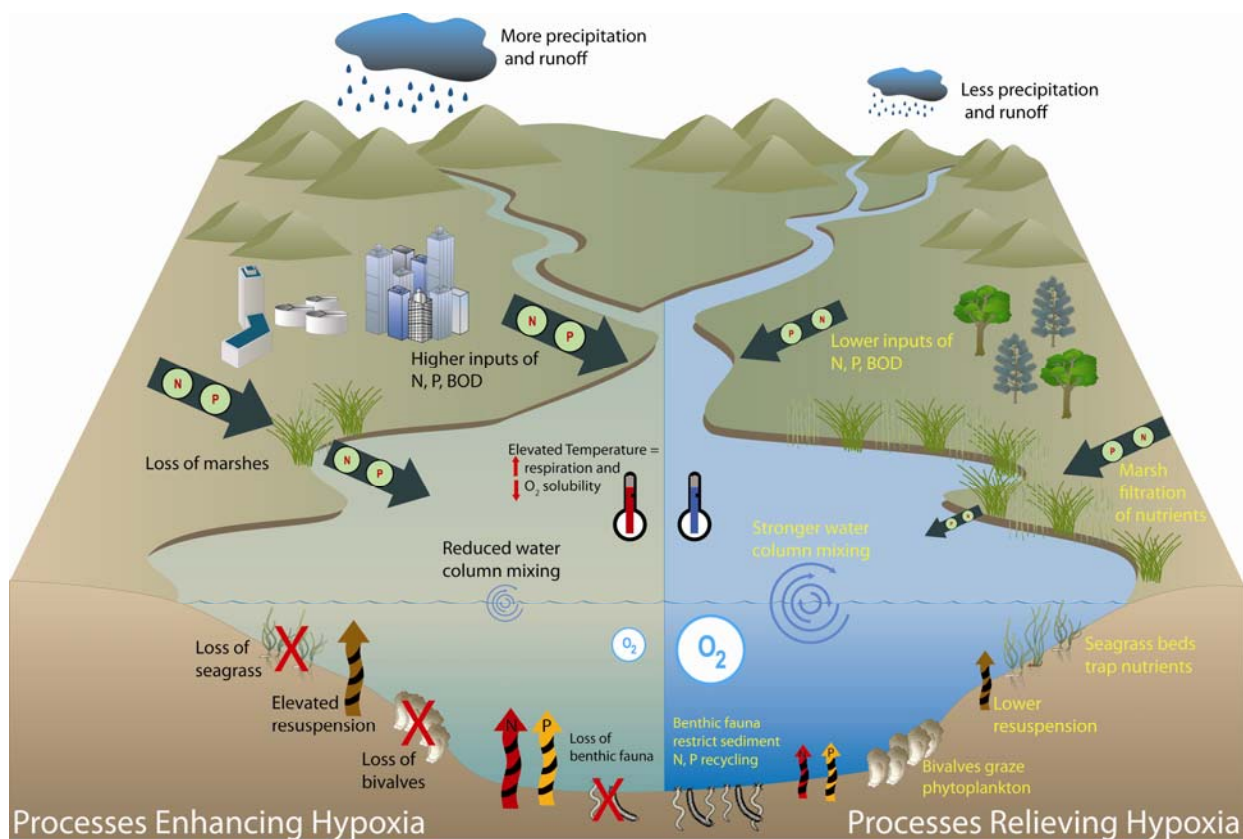
Figure 2: Conceptual diagram of processes influencing hypoxia. The left side represents the suite of processes which increase hypoxic conditions, while the right side details processes that relieve hypoxia. Hypoxia is enhanced in most all systems by higher freshwater inputs, higher nutrient and BOD loads from more human-impacted watersheds, reduced nutrient filtration with loss of marshes and submerged aquatic vegetation, reduced filtration of phytoplankton by depleted bivalve reefs, elevated temperature, reduced ventilation of deeper waters with atmospheric O_2, and enhanced sediment nutrient recycling ⬅ hypoxia-induced changes in biogeochemistry and loss of bioturbating benthic faunal.
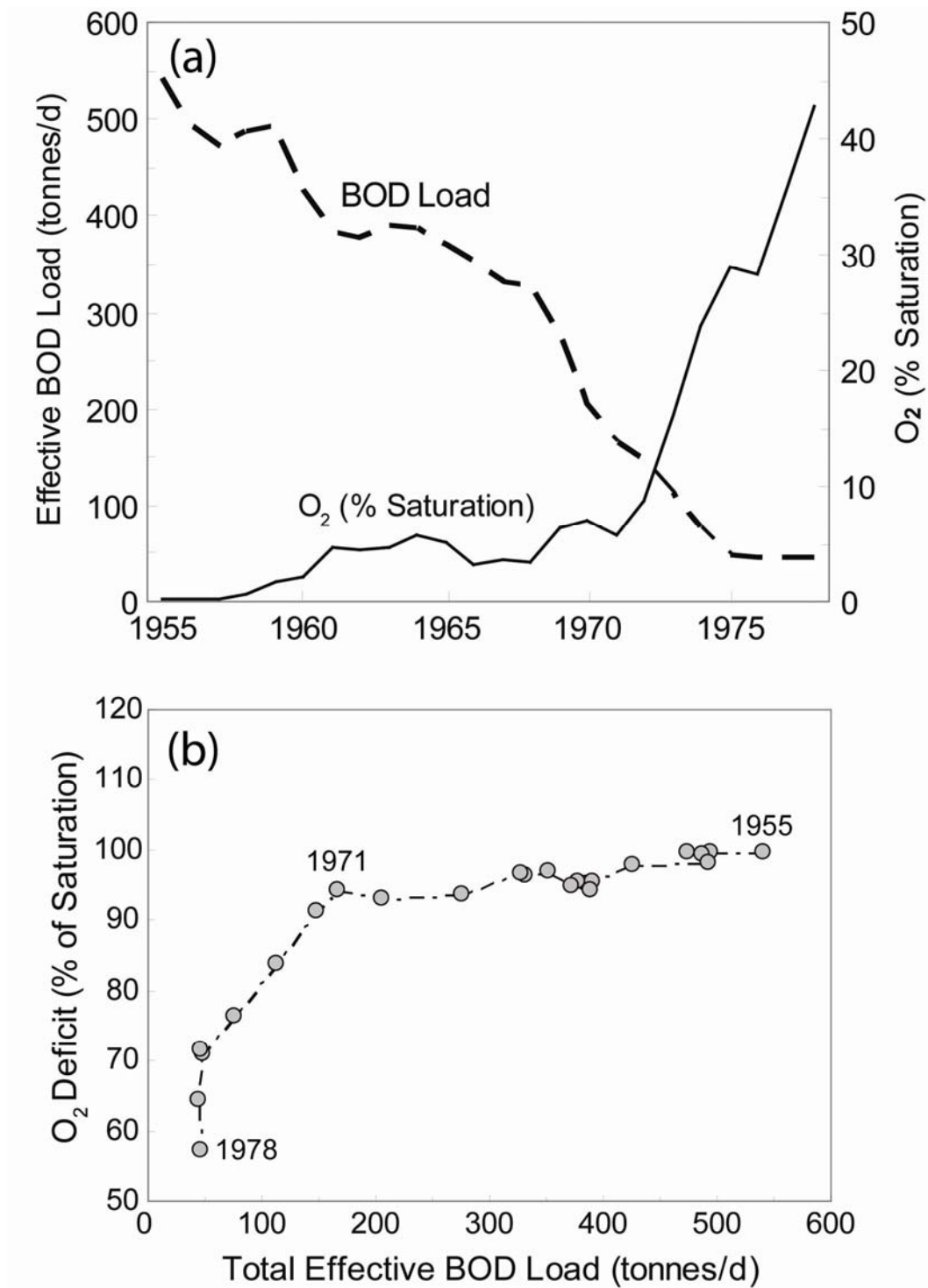
Figure 3: Time series (1955-1980) observations in the upper Thames River estuary (England) for (a) BOD load from major sewage treatment plants and summer O_2 % saturation and (b) relationship of O_2 % saturation deficit (concentration units below mean saturation) to BOD load showing threshold response of O_2 to reduced BOD load (b). Data sources referenced within text.
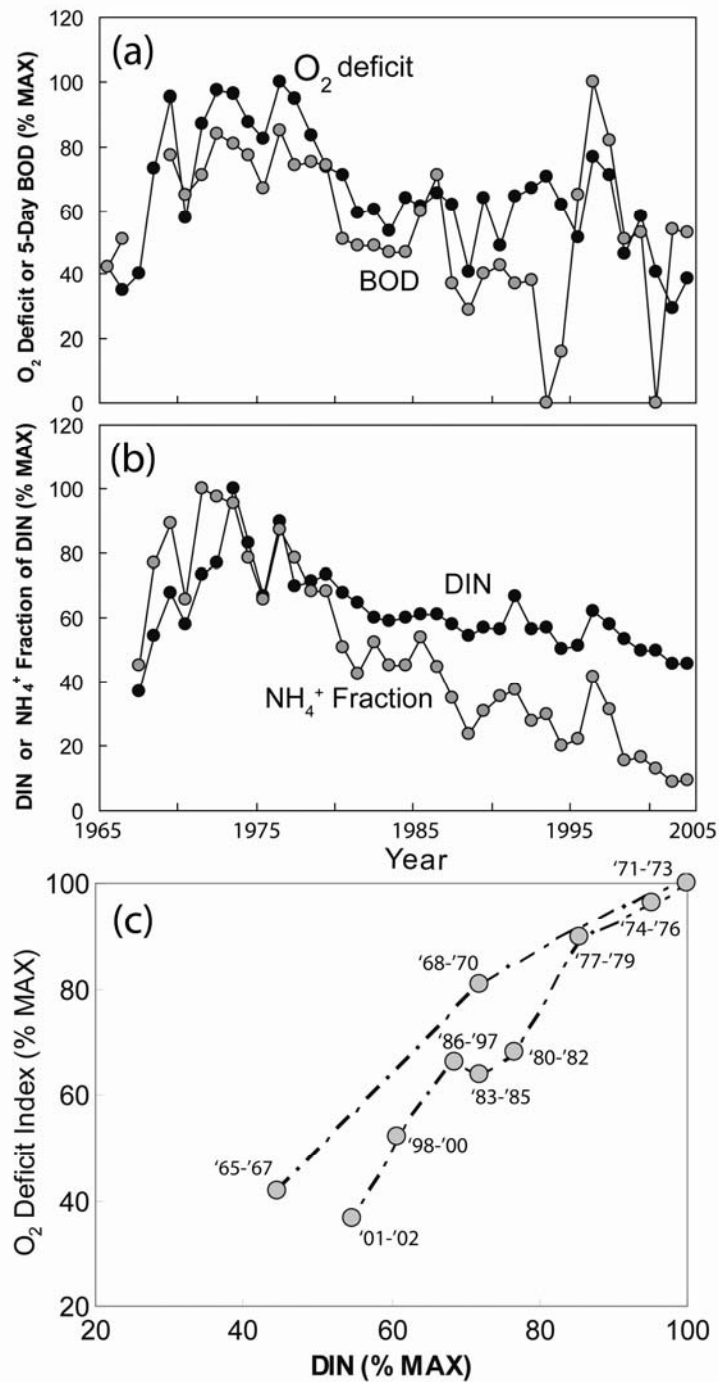
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Figure 4: Time series (1965-2002) observations in the Scheldt River estuary (Netherlands) for (a) BOD and O_2 % saturation deficit, and for (b) DIN concentrations and fraction as NH_4^+ and (c) relationship of O_2 deficit index to DIN concentration, showing a favorable linear shifting baseline response of O_2 to reduced DIN and BOD loads. Data sources referenced within text.
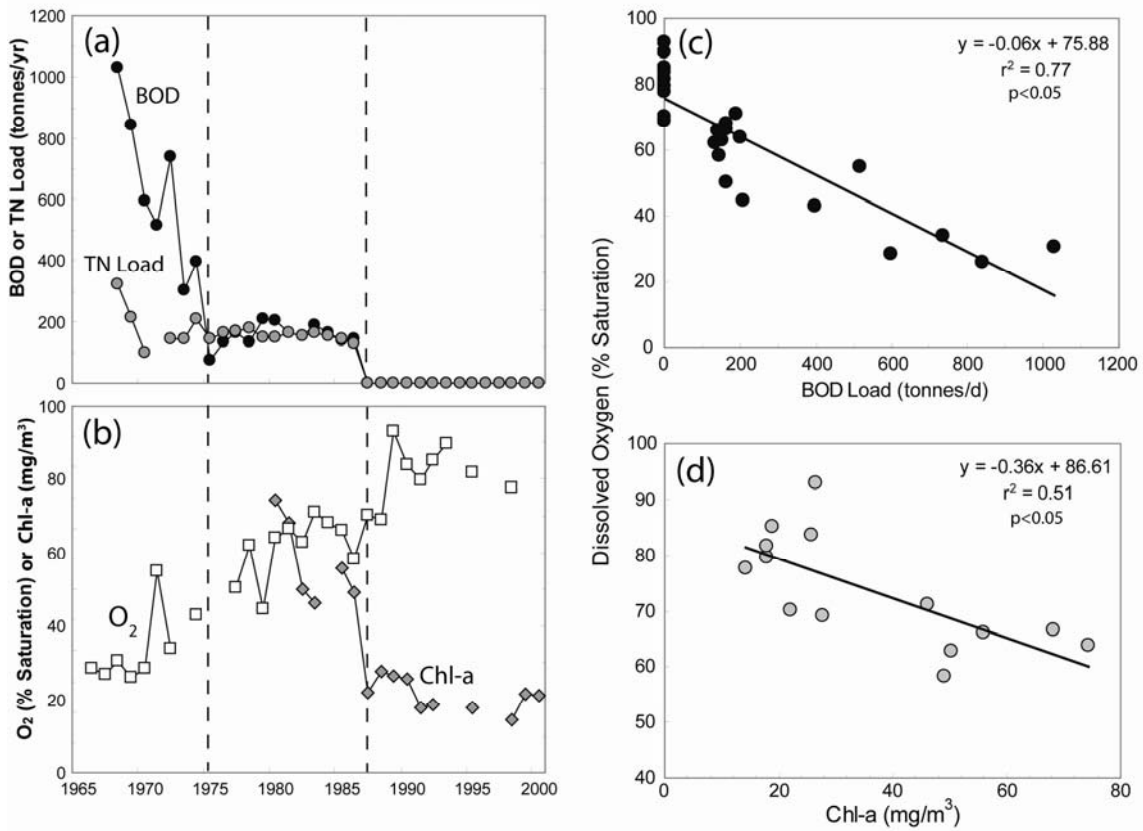
Figure 5: Time series (1965-2000) observations in Laajalahti Bay (Finland) of (a) BOD and TN loads and of (b) O_2 % saturation and chlorophyll-a. Relationship of (c) O_2 % saturation to BOD Load and (d) O_2 % saturation to chlorophyll-a. Data sources referenced within text.
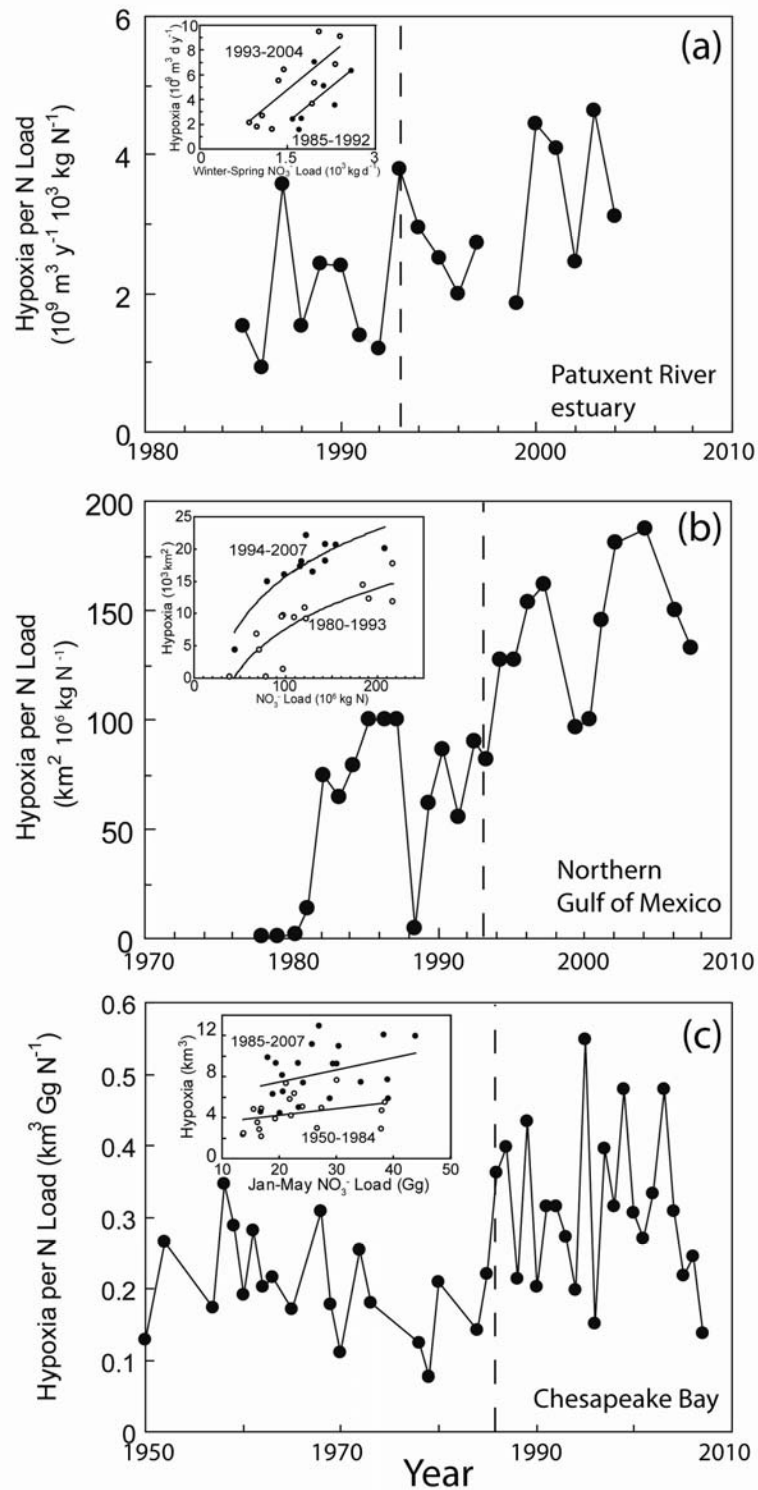
Figure 6: Multi-decadal time series data for hypoxia per unit nitrogen load in the (a) Patuxent River estuary, USA, (b) northern Gulf of Mexico, USA, and (c) Chesapeake Bay, USA. Inset figures are relationships between N load and hypoxia for each system during periods before and after statistically significant change points (vertical dashed lines) in time-series of hypoxia per unit N load. Data sources referenced within text.
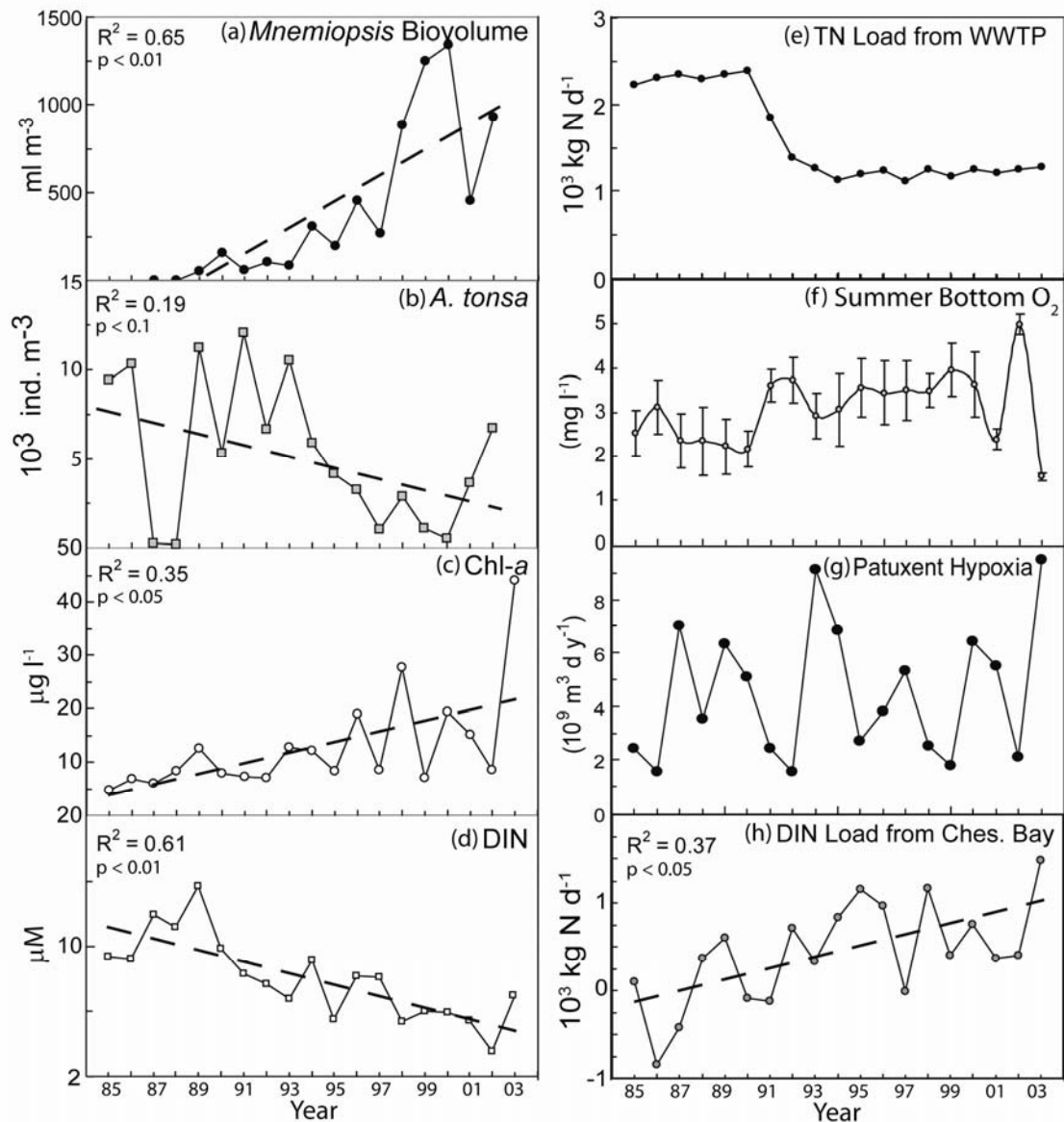
Figure 7: Time series and trend lines (1985 to 2003) of annual mean June-August concentrations (a) *Mnemiopsis* spp. biovolume, (b) *Acartia tonsa* abundance, (c) chlorophyll-a, and (d) DIN, and (e) mean annual DIN loads from upstream sewage plants, (f) upper Patuxent summer (June-August) mean concentrations 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 sources referenced within text.
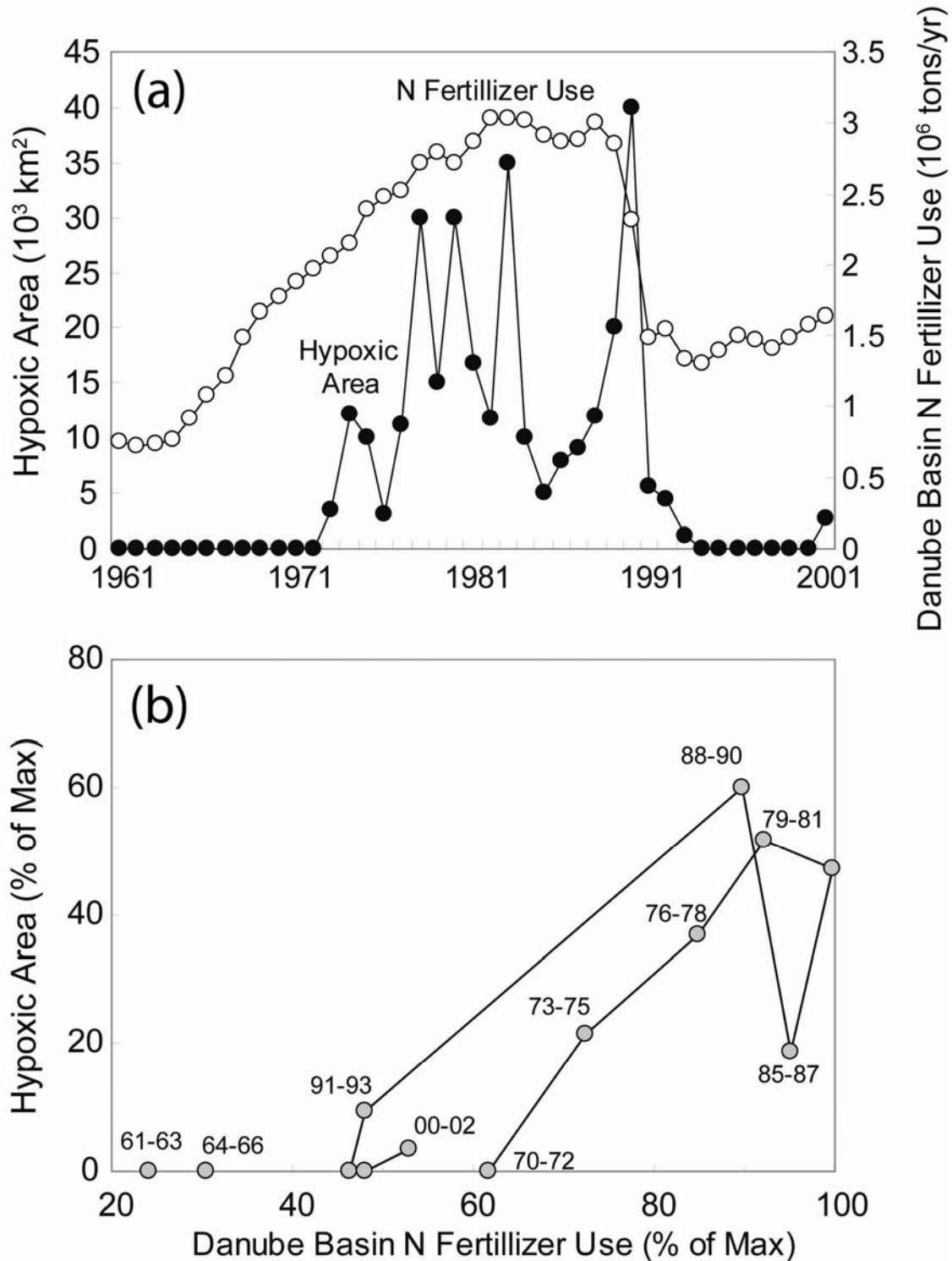
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Figure 8: Time series (1960-2001) observations for (a) Danube River watershed nitrogen fertilizer use and summer hypoxic area in the northwest shelf of the Black Sea and (b) response trajectory of hypoxic area on the northwest shelf of the Black Sea to interannual changes in nitrogen fertilizer use derived from time series data. Data sources referenced within text.
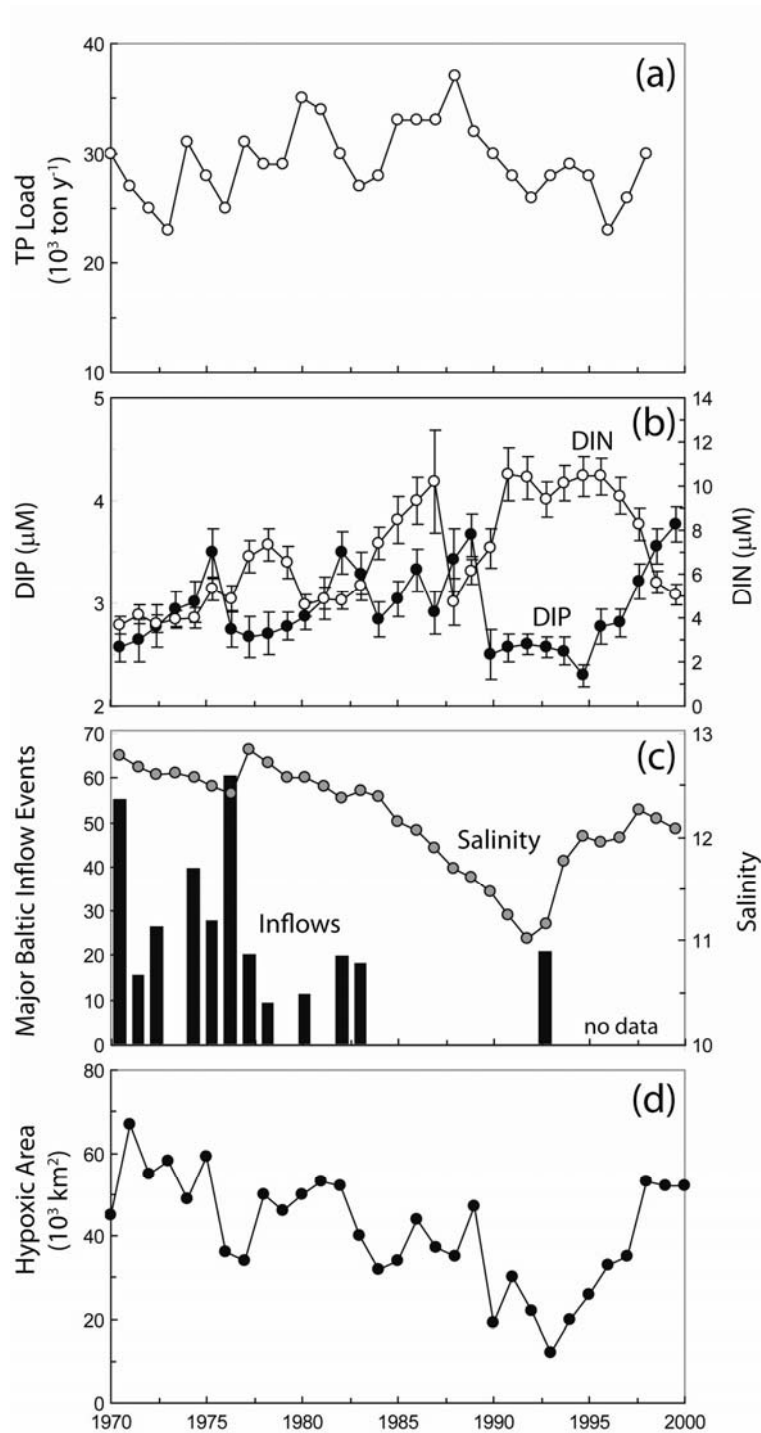
Figure 9: Time-series (1970 to 2000) of (a) annual TP loads to the Baltic Sea, (b) annual concentration of DIP (solid circles) and DIN (open circles) in the Baltic Proper for depths <100m, (c) index of water inflow to the Baltic (solid bars) and deep water (200m) salinity (grey circles) in the Gotland Deep, and (d) hypoxic area in the Baltic Proper, Gulf of Riga, and Gulf of Finland from 1970 to 2000. Data sources referenced within text.
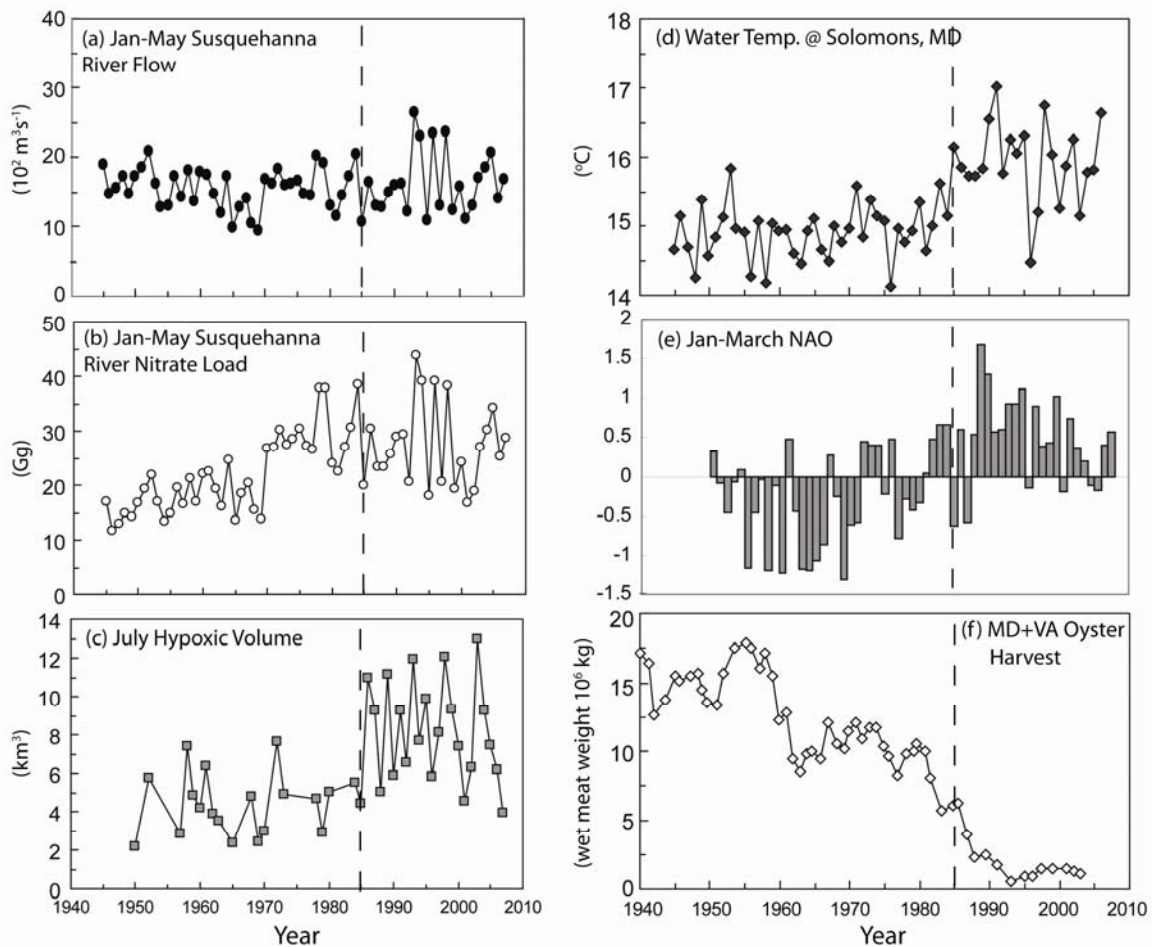
Figure 10: Time-series (1945-2007) of (a) Susquehanna River Flow at Conowingo, MD, (b) January-May NO_3^- loads to Chesapeake Bay, (c) July hypoxic volume in Chesapeake Bay, (d) mean annual water temperature at Solomons, MD, (e) January to March North Atlantic Oscillation, and (f) annual Maryland (MD) and Virginia (VA) oyster harvest. Data sources referenced within text.