Nutrient enrichment and fisheries exploitation: interactive effects on estuarine living resources and their management

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Abstract Both fisheries exploitation and increased nutrient loadings strongly affect fish and shellfish abundance and production in estuaries. These stressors do not act independently; instead, they jointly influence food webs, and each affects the sensitivity of species and ecosystems to the other. Nutrient enrichment and the habitat degradation it sometimes causes can affect sustainable yields of fisheries, and fisheries exploitation can affect the ability of estuarine systems to process nutrients. The total biomass of fisheries landings in estuaries and semi-enclosed seas tends to increase with nitrogen loadings in spite of hypoxia, but hypoxia and other negative effects of nutrient over-enrichment cause declines in individual species and in parts of systems most severely affected. More thoroughly integrated management of nutrients and fisheries will permit more effective management responses to systems affected by both stressors, including the application of fisheries regulations to rebuild stocks negatively affected by eutrophication. Reducing fishing mortality may lead to the recovery of depressed populations even when eutrophication contributes to population declines if actions are taken while the population retains sufficient reproductive potential. New advances in modeling, statistics, and technology promise to provide the information needed to improve the understanding and management of systems subject to both nutrient enrichment and fisheries exploitation.

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Introduction

Estuaries are crossroads where land meets the sea, and where human influences on the terrestrial landscape and on aquatic food webs intersect. Both nutrient over-enrichment (Nixon & Buckley, 2002; Seitzinger et al., 2002) and declining populations of species targeted by fisheries (Jackson et al., 2001; Lotze et al., 2006) are common consequences of human influence in these coastal systems. Estuaries are particular targets for these and other stressors because of their proximity to population centers and because of their historical importance as sources of protein and as places for disposal of human waste (Kennish, 2002).

The term eutrophication encompasses a variety of ecological changes that occur when nutrient-stimulated primary production exceeds removal through biotic and physical processes (NRC, 2000). In estuaries, these changes are associated with or caused by an increase in the supply of organic carbon (Nixon, 1995) and include increased biomasses of phytoplankton, macroalgae, and epiphytes; increased occurrences of toxic and nuisance algal blooms; decreased dissolved oxygen concentrations (hypoxia and anoxia); and decreased abundance of submerged vascular plants (Cloern, 2001; Rabalais & Turner, 2001). More than two-thirds of the 122 U.S. estuaries evaluated in the National Eutrophication Assessment were rated as moderately or highly eutrophic due to nutrient over-enrichment (Bricker et al., 1999). Worldwide, nitrogen loadings resulting from human activities, as well as the number of estuaries and coastal seas reporting low dissolved oxygen concentrations have dramatically increased since the 1950s (Diaz, 2001; Boesch, 2002; Seitzinger et al., 2002; Diaz and Rosenberg, 2008; Fig. 1a).

In many of the same estuaries, but often over longer periods of time, fishing has contributed to declining abundances of species that spend all or part of their life cycle in estuaries (e.g., Secor & Waldman, 1999; Lotze et al., 2006). The historical progression of fishery expansion and collapse follows the temporal pattern of improvements in fishing technology (Pitcher, 2001) and spatial patterns of human population densities (Barrett et al., 2004; Kirby, 2004; Lotze et al., 2006).

The combined effect of eutrophication and fisheries exploitation is to simultaneously increase algal production, degrade habitat, and remove fish and shellfish biomass. In this review, we ask how nutrient enrichment affects fish (including mobile mollusks and crustaceans throughout this article unless otherwise noted) abundances and fisheries, how fisheries affect population responses to nutrient enrichment,

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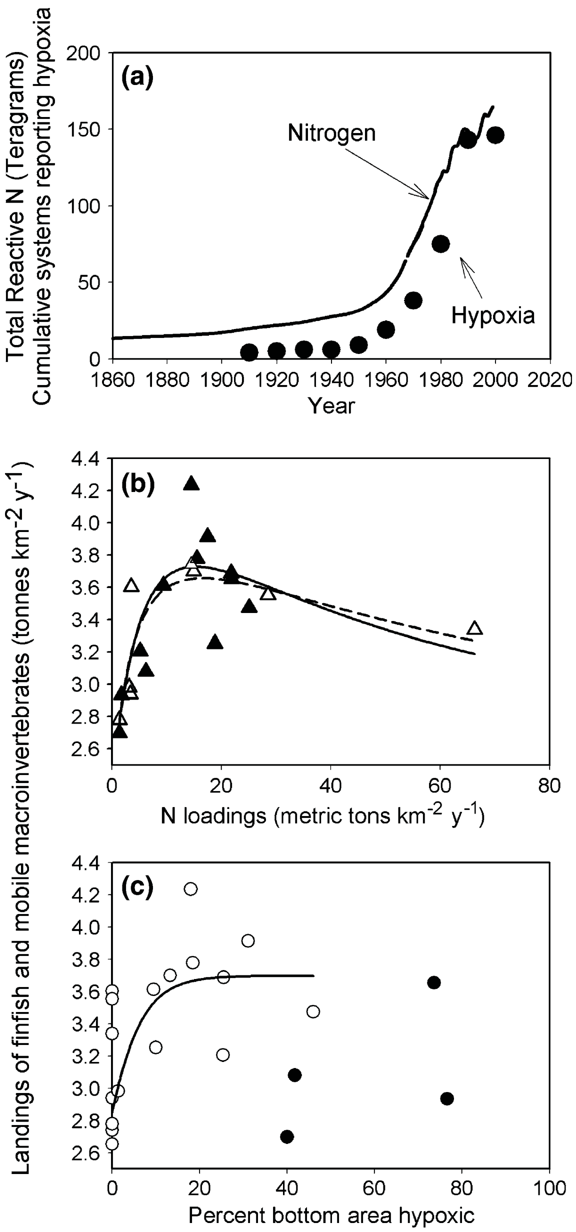


◀ **Fig. 1** Relationships among nitrogen loadings, hypoxia, and fisheries landings in estuaries. **a** Both anthropogenic loadings of nutrients to estuaries (adapted from Boesch, 2002) and the number of estuaries reporting hypoxia (from Diaz, 2001) have increased greatly since the mid-twentieth century. **b** Relationship between N loadings and fisheries landings. *Filled triangle* = systems with $\geq$10% of area hypoxic (dissolved oxygen concentration <3 mg l^{-1}); *open triangle* = systems with $<$10% bottom area hypoxic; *grey triangle* = Chesapeake Bay landings excluding Atlantic menhaden (*Brevoortia tyrannus*). The *solid line* is a four-parameter lognormal curve (SigmaPlot 9.0) including all landings of mobile species from Chesapeake Bay (highest landings in figure; adjusted $R^2 = 0.72$). The *dashed line* excludes Atlantic menhaden landings from Chesapeake Bay to make the data more comparable to other U.S. estuaries that do not have purse-seine fisheries ($R^2 = 0.76$). Systems plotted from lowest to highest N loadings: Azov Sea, Gulf of Bothnia, Black Sea, Adriatic Sea, Irish Sea, North Sea, Gulf of Finland, Baltic Proper (including Gulf of Riga), Kattegat/Skagerrak, Chesapeake Bay, Tampa Bay, Northern Gulf of Mexico, Long Island Sound, Corpus Christi Bay, Neuse River Estuary, Sea of Marmara, Danish Straits, Delaware Bay, and Galveston Bay. **c** Positive relationship between the spatial extent of hypoxia (dissolved oxygen concentration <3 mg l^{-1}) and fisheries landings in estuaries without persistent anoxic basins or widespread release of sulfides. *Open circle* = systems included in regression in the order of extent of hypoxia: 10 systems with $\ll$1% regularly occurring hypoxia (Aegean, Gulf of Bothnia, Balearic, Ionian, Irish, Levant, Sardinian, North Sea, Delaware Bay, and Galveston Bay), the Adriatic Sea, Kattegat/Skagerrak, Corpus Christi Bay, Chesapeake Bay, Northwest Gulf of Mexico, Gulf of Finland, Neuse River Estuary, and Long Island Sound, Danish Straits; *filled circle* = systems with persistent anoxic or severely hypoxic basins or widespread release of sulfides from lowest to highest spatial extent of hypoxia: the Sea of Azov, Baltic Proper, Sea of Marmara, and Black Sea. See supplementary material—Appendix—for the full list of references used for this figure

and how the co-occurrence of eutrophication and fisheries exploitation influences management options. We include a specific consideration of hypoxia, which is often caused or exacerbated by high loads of anthropogenic nutrients. Finally, we discuss recent advances in analysis and technology that may help predict the separate and combined effects of eutrophication and fisheries exploitation as well as outcomes of alternate management actions.

Several recent articles have addressed the effects of nutrient enrichment and fisheries removals in coastal systems (e.g., Diaz & Rosenberg, 1995, 2008; Peterson et al., 2000; Jackson et al., 2001; Nixon & Buckley, 2002; Lotze et al., 2006). The present synthesis differs by focusing on the potential interaction of these two stressors, and how the co-occurrence of nutrient enrichment and fisheries exploitation affects management options. We also emphasize eutrophication effects on finfish and mobile macroinvertebrates, which unlike sessile species have the potential to behaviorally avoid habitat patches negatively impacted by eutrophication. As a result of this behavioral flexibility, the responses of mobile species to eutrophication can be fundamentally different, and interactions with fisheries potentially more complex, than those of sessile species. Furthermore, unlike marine mammals and reptiles whose recovery is discussed by Lotze et al. (2006), fish and mobile macroinvertebrates generally continue to be managed for their harvest potential, rather than as species deserving of protection primarily because of intrinsic or ecological value. Our focus is on estuaries and semi-enclosed seas, although many of the issues we raise also apply to other aquatic systems.

Interactions between nutrient enrichment and fishing effects

Although seemingly disparate stressors, nutrient enrichment and fisheries removals are tightly coupled both ecologically and in management forums. Sustainable levels of fisheries removals are dependent on rates of production and mortality—both of which can be affected by the ecological changes associated with eutrophication (Fig. 2). Fisheries removals can affect both system and species' sensitivity to nutrient enrichment by altering the trophic structure, as well as the size and age distributions of key consumers (Pauly et al., 1998; Vallin & Nissling, 2000; Szmant, 2002; Birkeland & Dayton, 2005). Both nutrient enrichment and fisheries exploitation can cause similar changes in food webs, such as increased dominance of pelagic planktivores including gelatinous zooplankton (Caddy, 2000; de Leiva Moreno et al., 2000; Oguz, 2005). Since these stressors typically co-occur, mitigating management actions can be delayed or rendered less effective, as various stakeholders ascribe responsibility for declining fish landings to different causes and promote solutions that shift the greatest burden to other interest groups.

Nutrient enrichment effects on fish and fisheries

Production and mortality

Both cross-system comparisons and temporal trends indicate that nutrient enrichment in estuaries and semi-enclosed seas is associated with increases in total fisheries landings across a broad range of nutrient loading rates (Nixon, 1988; Nixon & Buckley, 2002; Fig. 1b). In much the same way that agricultural production increases with fertilizer use, fish landings are generally higher in systems with high nutrient loadings (Nixon & Buckley, 2002). This pattern suggests that nutrient enrichment typically increases fish growth, reproduction, or survival. Temporal patterns of fisheries landings and fish growth support this contention; in systems such as the Nile, Seto Inland Sea, North Sea, and until

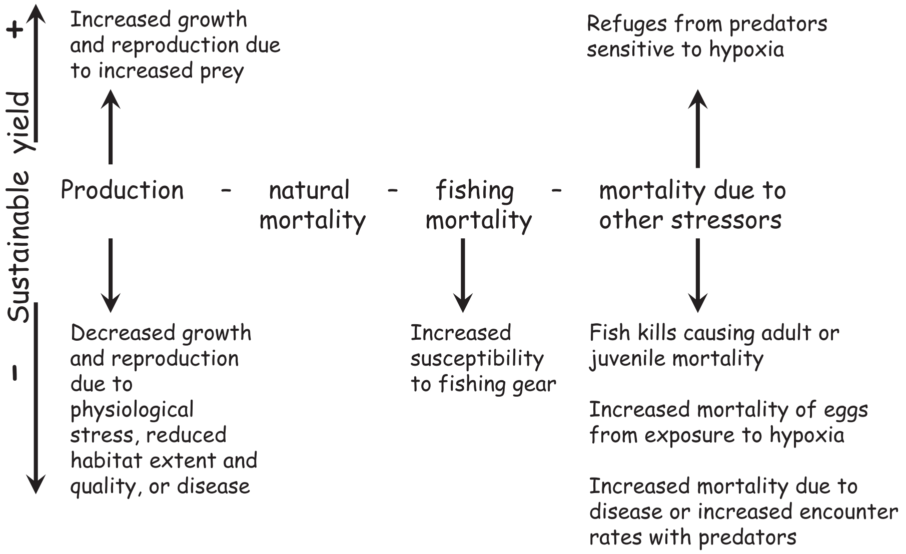


Fig. 2 Conceptual model of the relationship between eutrophication and sustainable fisheries yields. Nutrient enrichment can either increase (*upward arrows*) or decrease (*downward arrows*) sustainable yields of exploited species by affecting growth, reproduction, and fishing mortality as well as mortality due to other interacting stressors. The effect of nutrient enrichment on sustainable yields of fish species will depend on both the severity of eutrophication and whether critical habitat is negatively affected

recently, the Kattegat–Skagerrak, landings have increased and decreased in concert with temporal patterns of nutrient loadings (Nixon & Buckley, 2002; Nagai, 2003; Oczkowski & Nixon, 2008). These results are consistent with theoretical food-web models that indicate that a number of processes common in estuarine food webs such as cannibalism, density-dependent predator mortality, intraguild predation, grazer-resistance of algae, and predator-dependent functional responses tend to increase bottom-up effects (McCauly et al., 1988; Gatto, 1991; Ginzburg & Akçakaya 1992; McCann et al., 1998; Hart, 2002). Based on analyses of a large number of coastal systems (Fig. 1b; Caddy, 2000; Nixon & Buckley, 2002), fish data that represent a range of trophic levels, and a consideration of biomass removal by fisheries, we concur with the assessment by Nixon & Buckley (2002) that nutrient enrichment of estuaries generally increases fish biomass, a conclusion that differs from that of Micheli (1999).

High yields of fishable biomass characterize most highly nutrient-enriched estuaries in spite of the potential negative effects of nutrient over-enrichment (Fig. 1b, c). We compared nitrogen loadings (watershed, upstream, and direct atmospheric deposition), the spatial extent of hypoxia (percent of bottom area with <3 mg dissolved oxygen l^{-1}), and landings of finfish and mobile invertebrates (collectively referred to as "fish") in 19 estuaries and semi-enclosed seas in Europe and the United States, and hypoxic extent and fisheries landings in five additional European systems (see supplementary material—Appendix). Estuaries and semi-enclosed seas analyzed span more than an order of magnitude in N loadings (N km^{-2} $year^{-1}$) and two orders of magnitude in surface area. For the 13 systems with N loading rates <18 tonnes N km^{-2} $year^{-1}$, fisheries landings (i.e., total biomass of landings of mobile species km^{-2} $year^{-1}$) increased linearly with N loadings (equation: landings $= 0.39 \times$ N loadings $+ 0.27$; $R^2 = 0.87$; $P < 0.0001$) (Fig. 1b). Fisheries landings are not a perfect reflection of abundances and are affected by fishing regulations, historical overfishing, and economic and social influences. Nevertheless, fish production sets an upper bound on sustainable fisheries landings.

It is difficult to find compelling evidence for negative effects of hypoxia on fisheries for mobile species, even in systems with extensive and persistent oxygen depletion, *if system-wide conditions and total landings are the focus of the analyses*. The relationship between fisheries landings and the spatial extent of hypoxia is positive (although we certainly do not imply causality) if systems with persistent anoxic or severely hypoxic basins (the Baltic Sea proper, and the Black Sea, and the Sea of Marmara) or widespread release of sulfides (the Azov Sea) are excluded (Fig. 1c; quadratic regression: $R^2 = 0.50$, $n = 19$; SigmaPlot 9.0). Extensive hypoxia or anoxia, low fisheries landings, and clearly demonstrated effects of oxygen depletion on individual species targeted by fisheries in the Baltic, Black, and Azov Seas (Nissling et al., 1994; Caddy, 2000; Debol'skaya et al., 2005; Oguz, 2005) would seem to suggest that low landings in these three systems are caused by hypoxia or co-occurring negative effects of eutrophication. However, the Baltic, Black, and Azov Seas have low N loading rates (Fig. 1b). The relationship between total fish landings and N loadings in these systems, and in systems with $\geq$10% bottom area hypoxia, in general, is not different from that in estuaries and semi-enclosed seas with no or minimal hypoxia (Fig. 1b and regression of systems with N loadings of <18 tonnes km^{-2} $year^{-1}$ presented above).

The two systems in our dataset with the highest N loading rates, and that fell on the declining section of the relationship between N loadings and fisheries landings, were Delaware and Galveston Bays—systems with no or minimal ($\ll$1% total area) hypoxia. It is not clear whether landings in these systems are directly attributable to eutrophication and represent the declining productivity that Caddy (1993) predicted for highly enriched systems even though they lack severe oxygen depletion, or whether low fisheries landings reflect peculiarities of the systems or their fisheries. Four of the systems that fell on the declining slope of the curve relating N loadings and landings (in the order of increasing nitrogen loads: Corpus Christi Bay, the Neuse River, Delaware Bay, and Galveston Bay; Fig. 1b) are the smallest estuaries included in our analyses; small size may affect their propensity toward historical overfishing or other characteristics of their fisheries or fish production. These systems also lack purse-seine fisheries for Atlantic menhaden, which comprise >50% of landings of mobile species by weight in Chesapeake Bay.

The positive relationship between nutrient enrichment and fisheries yields measured at large spatial scales depends on an integrative, system-level view of the consequence of nutrient flow through marine food webs. Such an approach provides valuable information about the effects of nutrient enrichment on fisheries and provides a first-order estimate of the relationship between nutrients and fish production. However, calculations of system-wide landings involve spatial and temporal averaging by both researchers and the fish, themselves, that can mask habitat-, species-, and season-specific negative responses of fish and mobile macroinvertebrates to eutrophication.

In the majority of highly nutrient-enriched systems, eutrophication creates a spatial and temporal mosaic of habitats that vary in physiological suitability, species composition, spatial overlap of predators and prey, and prey abundance (Pihl et al., 1995; Breitburg, 2002; Craig & Crowder, 2005). High levels of nutrient enrichment can simultaneously stimulate prey production, creating areas of less favorable or completely unsuitable habitat by causing low dissolved oxygen concentrations, increasing macroalgal growth, and leading to the decline or disappearance of submerged macrophytes. In most systems, low dissolved oxygen concentrations are spatially and temporally limited, developing seasonally, and primarily affecting sub-pycnocline waters.

As a result of this spatial matrix of prey-enhanced and degraded habitats, eutrophication, in general, and hypoxia, in particular, fundamentally alter the way mobile organisms utilize space and move through systems. The net effect of eutrophication on fish and mobile macroinvertebrates is dependent on both these altered movement patterns and the limitations to movement (Breitburg, 2002). Effects on fish and fisheries depend on the way both eutrophication and co-occurring stressors alter the spatial matrix, the way that individual species requirements intersect with those spatial effects, and the way that fisheries practices intersect with both physiological and behavioral responses to this spatial mosaic (Fig. 3).

Spatial averaging of fish abundance or landings statistics can either accentuate or mask negative effects of nutrient over-enrichment depending on the

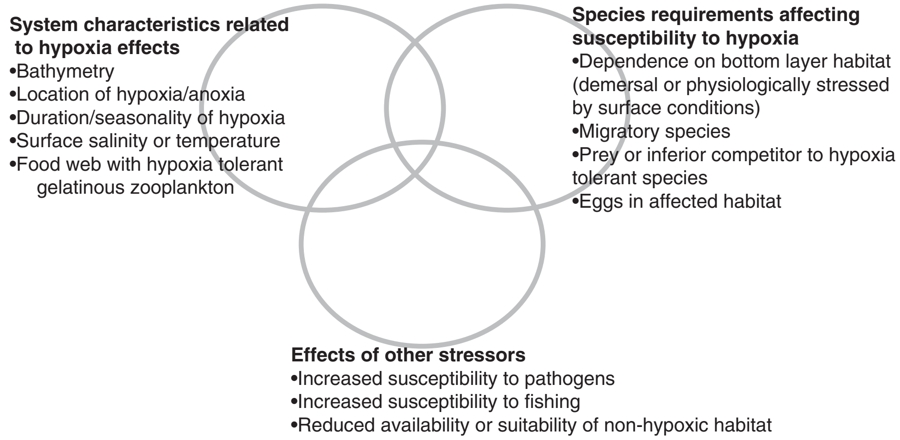


Fig. 3 Effects of nutrient enrichment on fish and fisheries depend on the intersection of habitat characteristics, species characteristics, and the co-occurrence of other stressors. System characteristics that modulate the effects of hypoxia include factors that influence the duration, timing, and location of hypoxia, the extent of shallow highly oxygenated waters, the suitability of highly oxygenated waters, and food web characteristics that may allow energy to be shunted into gelatinous zooplankton rather than fished species. Species' susceptibility to hypoxia is influenced by dependence on bottom layer habitat, migration patterns, whether the species is a prey or competitor of other species that are more tolerant of low oxygen, and whether eggs are deposited into or sink into hypoxic bottom waters. Hypoxia fundamentally alters the movement of individuals through the system, so species characteristics that limit the ability to appropriately respond to hypoxia by altering movement and space-use patterns can be especially important. The presence of co-occurring stressors that are worsened by hypoxia, or whose importance increases because of species responses to hypoxia, can increase the likelihood of population or fisheries declines. Stressors that reduce the suitability of habitat that would otherwise be a refuge from hypoxia may lead to population declines

scale and location of areas averaged. Behavior-induced averaging of spatial patterns of habitat quality by fish can be achieved through foraging and habitat-use behaviors. Opportunistic and adaptive behaviors of mobile species can reduce the potential negative effects of eutrophication-degraded habitat patches (Pihl et al., 1992; Brandt & Mason, 1994) if the scale and speed of response exceeds that at which habitat suitability declines (Breitburg, 1992). Avoidance of low dissolved oxygen concentrations and preferential use of habitat with high prey abundances provide the potential for growth rates to more strongly reflect conditions in favorable habitat patches than in unfavorable areas, although density-dependent interactions (Eby et al., 2005; Eggleston et al., 2005; Craig et al., 2007) and limits to behavioral responses (Stierhoff et al., 2006, in press; Tyler & Targett, 2007) affect the balance between positive and negative effects of nutrient enrichment. Over time, growth may also integrate temporal patterns in the positive effects of increased prey and negative effects of physiological stress and spatially limited reductions in prey abundance.

Negative effects of nutrient enrichment on fish and fisheries primarily reflect species-specific characteristics and requirements, and spatial processes that affect the location and timing of oxygen depletion. This difference between ecosystem and behavioral/population perspectives is an important consideration in the development of a framework for understanding and managing eutrophication effects. Some species that have supported commercial, recreational, or subsistence fisheries are especially susceptible because of their behaviors, life history characteristics, or physiological tolerances. Sewage and nutrient discharge patterns can determine whether those species' characteristics result in population declines.

On a local scale (i.e., within a portion of an interconnected estuarine system rather than system wide), hypoxia can sharply reduce both fish abundances and landings. Descriptions of physical conditions and biota in river segments with anoxic or severely hypoxic waters virtually throughout the water column prior to modern sewage treatment suggest that the release of raw sewage into tributaries may create the most severe impacts on fish and fisheries. Low dissolved oxygen is thought to have blocked the migration of anadromous fishes and contributed to the decline of the American shad (*Alosa sapidissima*) in the Delaware River Estuary before advanced sewage treatment was implemented in the city of Philadelphia (Weisberg et al., 1996, Albert, 1988). Release of raw sewage also led to widespread anoxia and loss of fish from large areas of both the Mersey (Jones, 2006) and Thames (Tinsley, 1998) Rivers prior to improved sewage treatment and reduced biological oxygen demand (BOD) of discharges. Entire year classes of smelt (*Osmerus eperlanus*) in the Elbe were lost in years when the timing and extent of low oxygen coincided with larval use of the affected habitat (Thiel et al., 1995). These cases are characterized by severe reductions in total fish biomass and fisheries at the local scale (i.e., within sub-estuaries rather than throughout the entire estuarine systems), and reductions in abundance and landings of severely affected species at a larger spatial scale.

Oxygen depletion, along with other negative effects of nutrient over-enrichment, can sometimes affect recruitment and cause extensive mortality in mainstem areas of estuaries and semi-enclosed seas as well. For example, in the Baltic Sea, Baltic cod (*Gadus morhua*) eggs sink into bottom waters with lethally low dissolved oxygen concentrations, and temporal variation in this species' recruitment has been linked to variation in the depth of hypoxic waters in deep Baltic basins (Köster et al., 2005). Hypoxia causes mortality of adult Norway lobsters (*Nephrops norvegicus*) and may be especially problematic for juveniles, which require higher dissolved oxygen concentrations for survival as well as to dig or search for burrows (Eriksson & Baden, 1997). Stimulation of macroalgae by high nutrient loadings can exacerbate problems of hypoxia by further depressing oxygen concentrations (Deegan, 2002), producing exudates that reduce survival and growth of larvae and small juveniles (Larson, 1997), and reducing the extent of preferred unvegetated habitat (Pihl et al., 2005). Under such conditions, decreasing the nutrient loading sufficiently to increase dissolved oxygen concentrations and reducing macroalgae may increase the production of affected species.

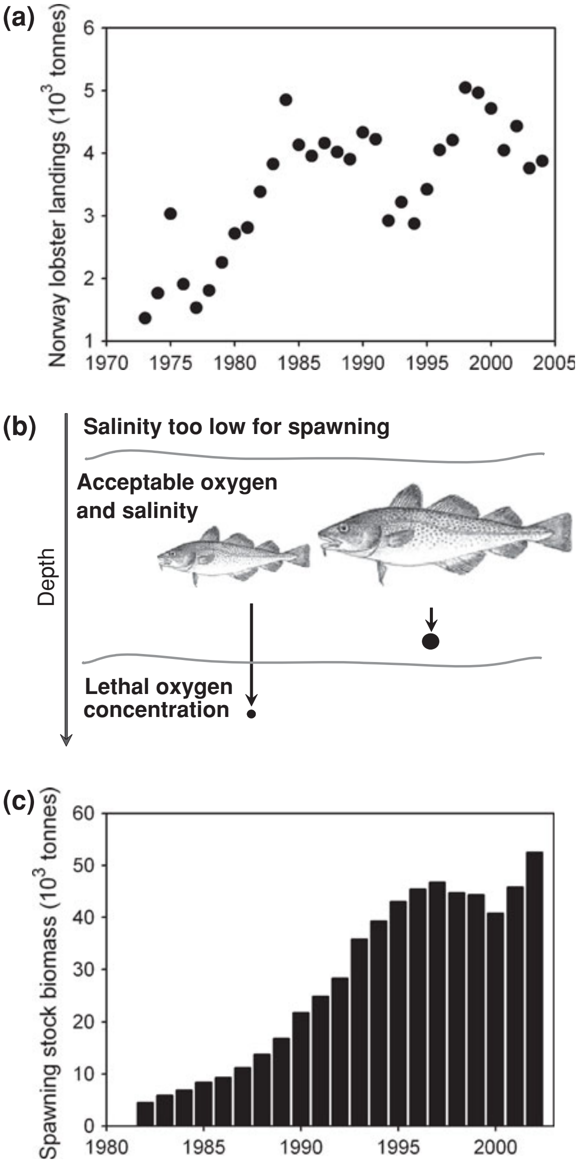
Since hypoxia primarily affects the bottom layer of the water column, demersal, epibenthic, and infaunal species tend to be more severely impacted than species that inhabit the upper water column (Caddy, 2000). Species composition of fish landings can change, and the economic value of fisheries (per unit biomass) can decline with increases in the ratio of pelagic to demersal species. Hypoxia thus reinforces patterns created by fisheries removals in which groundfish stocks tend to be depleted before stocks of small pelagic species. Avoidance of oxygen concentrations that lead to mortality or reduced growth can reduce the potential negative effects of habitat degradation due to nutrient over-enrichment (Breitburg, 2002; Tyler & Targett, 2007). Even so, both decreased growth and reproductive impairment have been reported in the field at the local scale and in small and shallow systems (Wu et al., 2003; Stierhoff et al., in press). Decreases in demersal species and increases in pelagic planktivores caused by nutrient enrichment may, however, have important economic and social consequences even when they occur on a local rather than a system-wide scale if historical fishing grounds are affected, and the consequence is a spatial separation of high-density population centers and fishing communities.

Sustainable fisheries landings and fisheries practices

Nutrient enrichment may buffer systems against fisheries removals by increasing fish growth, survival, and reproduction, thereby allowing for higher sustainable harvests. However, high landings can encourage fishing overcapitalization that can lead to overfishing, especially if nutrient loads are later reduced. The decline in anchovy (*Engraulis japonicus*) landings in the Seto Inland Sea that followed reductions in phosphorus loadings (Nagai, 2003) may have been the result of continued fishing pressure on a fish population with decreased anthropogenic nutrient-supplemented production.

Nutrient enrichment can also reduce sustainable harvests by reducing the growth, survival, and reproduction of targeted species where negative effects of eutrophication dominate (Fig. 2). Rates of fisheries removals that are sustainable in the absence of eutrophication-related reductions in production or survival may lead to overfishing and population declines in their presence. For example, macroalgal growth in nursery grounds of juvenile plaice (*Pleuronectes platessa*) in the Kattegat–Skagerrak may reduce recruitment to the fishery, and thus, slow the recovery of fish stocks even if fishing pressure is reduced or removed (Pihl et al., 2005). Eutrophication also can exacerbate effects of other stressors, resulting in greater than additive cumulative effects of multiple stressors, and reducing sustainable rates of fishing mortality more than either stressor alone (Breitburg & Riedel, 2005). Although this article focuses on mobile species, one of the clearest examples of a eutrophication–disease–fishery interaction is for a sessile bivalve. The eastern oyster (*Crassostrea virginica*) has declined in many Atlantic coast estuaries in the United States as a result of both overfishing and disease (NRC, 2004). Sublethal hypoxia can compromise the immune response of adult oysters and greatly increase mortality caused by *Perkinsus marinus*, the protistan parasite that causes Dermo (Anderson et al., 1998). As a result, sustainable rates of oyster harvests are likely to be reduced in areas in which *P. marinus* is common, if nutrient enrichment leads to even moderate levels of hypoxia.

Behavioral avoidance of hypoxia can increase vulnerability to fishing gear, make fisheries more efficient, and result in increased catches. A well-documented example is the Norway lobster fishery in the Kattegat. Catch per unit effort peaked in 1982 as worsening hypoxia induced lobsters to leave their burrows, making them more accessible to capture (Baden et al., 1990). Fishers also adapt methods to local nutrient-related conditions, deploying gear in oxygenated refuge areas and along the edge of hypoxic zones where fish and mobile invertebrates aggregate. This practice may be widespread and has been noted in fisheries for crabs in the Neuse River Estuary (Selberg et al., 2001), flatfish in Osaka Bay (Jun Shoji, Hiroshima University, pers. comm.), and possibly for brown shrimp (*Farfantepaneus aztecus*) (Craig & Crowder, 2005) and menhaden (*Brevoortia patronus*) (Smith, 2001) in the Gulf of Mexico. However, we could find no documented cases with strong evidence of population declines resulting from hypoxia-related increases in vulnerability to fishing practices or gear. Even landings of Norway lobster in the Kattegat–Skagerrak system have remained at near peak levels more than 20 years after hypoxia-related mortality was first identified (Fig. 4a), although this could reflect changes in fishing locations and increased fishing effort (L. Pihl, Göteborg University, pers. comm.). Nevertheless, hypoxia-induced increases in sensitivity to harvest might keep landings high even if populations are declining—a situation that could lead to delays in the response of management.



◀ **Fig. 4** Strong interactions between fisheries mortality and eutrophication occur because of effects of eutrophication on behaviors, effects of fisheries removals on population size structure, and because of the magnitude of mortality caused by fisheries exploitation. **a** Behavior: Norway lobster. Behavioral responses to hypoxia can increase the susceptibility of organisms to fishing gear, and at least initially result in increased landings. Catch per unit effort of Norway lobsters in the Kattegat along the coast of Sweden peaked in the mid-1980s, as worsening hypoxia induced lobsters to leave their burrows, making them more accessible to nets (Baden et al., 1990). Nevertheless, landings of Norway lobster in the Kattegat–Skagerrak area have remained high. **b** Size distributions: Baltic cod. Fisheries regulations can indirectly influence the susceptibility of cod eggs to hypoxia-induced mortality by influencing the size of spawning females in the population. Large females produce large eggs that are sufficiently buoyant to be retained in oxygenated mid-depth waters; smaller females produce small eggs that sink and perish (Vallin & Nissling, 2000). Cod image http://stellwagen.noaa.gov/visit/welcome.html. **c** Reduced fishing mortality: Striped bass. Decisive management action taken to protect spawning stock biomass of striped bass in Chesapeake Bay is often cited as a successful example of fisheries management. Stringent fishing regulations allowed the population to rebound even though eutrophication and its potential to negatively affect striped bass growth and habitat persisted

Fishing effects on species and system responses to nutrient enrichment

Although eutrophication can strongly affect sustainable fisheries yields, the large number of estuarine species that have experienced reduced stock sizes as a result of fisheries exploitation (e.g., Jackson et al., 2001; Lotze et al., 2006) indicate that fishing is a more frequent direct cause of finfish and shellfish population declines in estuaries than eutrophication. Fishing can be a large source of direct mortality, while growing evidence suggests that direct mortality of juveniles and adults from hypoxia (i.e., fish kills), and other consequences of eutrophication (e.g., harmful algal blooms; HABs) is typically a relatively small proportion of total mortality. The primary effect of fishing is the removal of biomass, often of late juveniles or adults that have high reproductive value, and shifts in size structure to smaller body size. These effects may drive strong declines in abundance and, if they exceed the compensatory reserve of the population, decreases in population growth rates. In contrast, eutrophication can result in both increases and decreases in growth and survival over different spatial and temporal scales and life history stages, and it is the integration of these positive and negative effects that determines the net effect on population growth rates.

Fishing can, however, affect both system and species' sensitivities to nutrient enrichment. Slow-growing species, older and larger individuals, and top predators are often disproportionately impacted by fishing (Pauly et al., 1998; Jackson et al., 2001; Pitcher, 2001). Fisheries removal of piscivorous species can favor increases in short-lived mid-trophic level species that are more directly coupled, and likely to be more responsive, to nutrient enrichment (Oguz, 2005). Selective removal of species has the potential to simplify food webs, thereby increasing responsiveness to top-down control (including fishing) (Hart, 2002). A mechanism has also been identified by which fishing can increase egg mortality. A downward shift in female size distribution caused by size-selective fisheries removals can increase hypoxia-related mortality of Baltic cod eggs by affecting egg size and buoyancy (Vallin & Nissling, 2000; Fig. 4b). The importance of this mechanism to other species is unknown.

Fishing can also reduce the ability of estuarine systems to absorb increases in pelagic primary production by selectively removing herbivorous species. Some of the most important fisheries in temperate estuaries target suspension feeders, whose combined removal can have a direct effect on phytoplankton prey. In the United States, menhaden (*Brevoortia tyrannus* and *B. patronus*) and bivalves such as oysters and clams are among the most important estuarine fisheries by weight and dollar value, respectively (Houde & Rutherford, 1993). Removal of suspension feeders from temperate estuaries is thought to have reduced the capacity of these systems to process nutrients (Newell, 1988, 2004) in much the same way that reduced populations of herbivorous fishes and sea urchins sensitize coral reefs to nutrient effects (Szmant, 2002), although the effect of any single suspension-feeding species will be limited by its spatial distribution and feeding ecology (e.g., Pomeroy et al., 2006; Fulford et al., 2007). Harvesting suspension-feeder biomass has also been suggested as a tool to remove the consumed excess primary production and buffer coastal systems against nutrient enrichment effects. Calculations suggest, however, that biomass removal of wild populations by fishing is not a large enough factor, *at least at sustainable removal levels,* to affect the severity of eutrophication (Boynton et al., 1995).

Effects of fisheries on eutrophication, and of eutrophication on fish yields, may be strongest in systems with extensive aquaculture production. Excess feed and feces associated with intensive cage culture of fish can cause localized hypoxia and harmful algal blooms, resulting in losses of both cultured and wild fish production (Rosenthal, 1985; Naylor et al., 2000). Bivalve aquaculture, in contrast, removes phytoplankton and can sometimes reduce negative effects of nutrient enrichment. Removal of farmed suspension-feeder biomass may have a greater potential than fisheries exploitation of wild populations to reduce eutrophication because high rates of aquaculture removals need not cause the population declines and fisheries collapses characteristic of wild fish fisheries. Diversion of human sewage to aquaculture operations, as in the Kulti Estuary in India, can also simultaneously increase fish production and improve water quality. Aquaculture operations may, however, be particularly susceptible to mortality resulting from negative effects of eutrophication such as harmful algal blooms. *Chattonella* spp. blooms killed about 14 million yellowtail (*Seriola quinqueradiata*) in the eastern Seto Inland Sea in 1972, resulting in a financial loss equivalent to US$ 106 million in 2004 dollars (Anderson et al., 2001).

Restoring and managing fishes in estuaries and semi-enclosed seas

Better coordinated and joint management of water quality and fisheries is important not only because the effects of fisheries removals and nutrient enrichment are tightly linked, but also because tools associated with the management of one stressor may help ameliorate problems caused by the other. Reducing fishing mortality can be a rapid, effective tool for increasing depleted populations even where eutrophication contributes to population decline. The most rapid route to the recovery of depressed populations is often through increased survival to reproductive sizes or ages and reduced mortality of reproductive individuals. Where fishing mortality contributes to low reproductive potential of the population, both results may be rapidly accomplished through appropriate fishing regulations if they are adopted and implemented in a timely manner.

Recent experience with striped bass (*Morone saxatilis*) management in Chesapeake Bay, USA, suggests that reducing fishing mortality can allow populations to recover even in systems where nutrient enrichment reduces the suitability and extent of habitat by increasing hypoxia (summarized from Richards & Rago, 1999; Fig. 4c). Both fisheries landings and numbers of juvenile striped bass declined during the 1970s and early 1980s. A number of factors—including low dissolved oxygen, contaminants, and acidic precipitation, as well as overfishing—were suggested as causes of reduced growth and survival. Nevertheless, management agencies responded to declining striped bass numbers by taking the most direct and immediate action available—reducing fishing mortality. In 1981, the Atlantic States Marine Fisheries Commission (ASMFC) adopted the Interstate Fisheries Management Plan for the Striped Bass, which called for coast-wide size limits and spawning area closures; this was adopted by most states during 1981–1984. Maryland and Delaware declared moratoria on striped bass fishing and other jurisdictions imposed high minimum size limits in 1985; Virginia imposed a moratorium in 1989. Strong year classes, indicating high levels of successful reproduction, occurred in 1989 and 1993. In spite of the resumption of limited fishing in 1990, striped bass continued to rebound. The Chesapeake striped bass stock was declared fully recovered in 1995, and remains high today although water quality problems that potentially reduce striped bass growth and habitat quality persist. This example indicates the potential for reduced fishing mortality to allow fished stocks to increase even when multiple stressors affect the targeted population, and for rapid implementation of fisheries restrictions to be an effective management action while research is conducted to sort out the relative contribution of potential causes of an observed population decline.

The question of how to balance or coordinate nutrient and fisheries management to prevent further system degradation and to meet restoration goals is complicated by fundamental differences in nutrient and fisheries management, as well as the need to better predict outcomes of strategies for coordinated management of multiple stressors. Nutrient management is challenged with a spatial and functional mismatch between the source of the problem and its effects that is not typical in fisheries management. Individuals and businesses that generate nutrients are often separated from the water bodies those nutrients affect by meaningful distances. They often do not utilize, and are not financially dependent on, those water bodies. In contrast, fishers depend on bodies of water in which they fish, and are affected financially if targeted stocks are depleted. There are also large differences in costs to taxpayers of meeting nutrient and fisheries management goals. For example, the Chesapeake Bay Commission (2003) recently estimated the cost of water quality protection and restoration in the Bay at nearly US$ 11.5 billion. Implementing fishing regulations can be far less expensive.

There can also be large differences between nutrient and fisheries management in the time scales between the identification of the problem, implementation of management actions, and system response. Regulations to reduce fishing can, in theory, be rapidly implemented while reductions of nitrogen require longer time periods, as sewage treatment plants are upgraded, riparian buffers are restored, and farming practices are changed. Less than 15 years elapsed between the initiation of fishery management planning and the full recovery of the Chesapeake Bay striped bass stock (Richards & Rago, 1999), as compared to a 45-year projected time frame for achieving water quality goals in the Chesapeake (Richard Batiuk, Chesapeake Bay Program, pers. comm.). In practice, however, there are many examples of long delays in implementing fisheries management strategies. The rapid recovery of striped bass in Chesapeake Bay required that fishing mortality be greatly reduced, while the population still had the reproductive capacity to rebound rapidly (Secor, 2000).

There has generally been an institutional disconnect between fisheries and water quality management despite their shared goals. In the United States, responsibility for water quality and fisheries management rests with different governmental agencies even though water quality criteria are set to protect fish populations and key habitats, and despite an increasing emphasis in fisheries management on habitat considerations and ecosystem-based management. The efficacy of separate management of nutrients and fisheries is compromised because each management branch (i.e., fisheries versus water quality) works within a shared landscape that is constantly changed by the other. Nutrient loading can affect sustainable yields of fisheries, and fishery removals and aquaculture can affect the ability of ecosystems to process anthropogenic nutrient loadings and can directly affect water quality. In addition, public and political support for nutrient management can be influenced by perceived effects of water quality conditions on fisheries and aquaculture.

New tools and approaches

Accelerating progress is being made toward the ultimate goal of ecosystem-level understanding and quantitative modeling (water quality to fish) that goes beyond correlative approaches. While immediate management remedies to water quality and fisheries issues need not be based on complete mechanistic understanding, long-term sustainability requires the identification of the causes and interplay between water quality and fish community dynamics, and mechanistic understanding greatly aids in garnering stakeholder support for management actions. New methods for data collection and modeling are enabling increased understanding of nutrient and food-web dynamics in estuaries, and will lead to increased capabilities for quantifying the interactions between eutrophication and fisheries. These new data collection and modeling methods promise to meet three critical needs for improved understanding and management of systems stressed by both nutrient enrichment and fisheries exploitation: (1) the ability to scale up from effects measurable on a local or individual scale to population, fisheries, and whole-ecosystem responses in order to better understand the effects of eutrophication on fished populations and vulnerability to overfishing; (2) the ability to track active movement and transport of all life stages to evaluate environmental and fisheries risks; and (3) the ability to better predict outcomes of alternative management actions for species and systems exposed to both nutrient enrichment and fisheries exploitation. The citations below represent only a sampling of promising approaches.

Advances in water quality monitoring have refined our measurements and expanded the temporal and spatial scales of observations. We are improving our ability to make synoptic system-wide measurements of water quality conditions via remote sensing (Walker & Rabalais, 2006). Continuous monitoring of physicochemical conditions via ocean observing systems is being developed for many locations (Ocean US, 2002), and fishing effort can now be tracked via vessel monitoring systems (Gallaway et al., 2003; Murawski et al., 2005).

Improved techniques have refined growth and mortality rate estimates and are providing new information on fine-scale spatial distributions and behavior (Rose et al., 2001). Acoustic methods produce three-dimensional views of fish distributions that can be overlain onto fine-scale spatial maps of environmental variables (Brandt & Mason, 1994; Roy et al., 2004). Otolith ageing has provided a new level of resolution to our ability to determine causes of fluctuations in year-class strength of finfish populations (Limburg et al., 1999). New methods for marking individual fish and microchemical analysis of skeletal material have refined estimates of mortality and movement (Secor et al., 1995), and ultrasonic telemetry now allows for almost continuous tracking of the movements of individuals through time and space (Szedlmayer, 1997; Bell et al., 2003). Molecular and genetic-based analysis provides information on the degree of mixing of populations (Carvalho & Hauser, 1994; Manel et al., 2003). We can monitor the physiology, behavior, growth, and energetic status of free-ranging animals on increasingly fine temporal and spatial scales through a variety of methods (Cooke et al., 2004; Makris et al., 2006), including RNA:DNA ratios (Stierhoff et al., in press) and implantable sensors that directly detect oxygen concentrations encountered (Svendsen et al., 2006).

Theoretical advances have occurred in our conceptual thinking about ecosystems and in the resolution and melding of water quality and fish models. Shifts in our conceptual view of estuarine ecosystems include the recognition of the importance of the microbial food web and sediments to nutrient recycling (Cornwell et al., 1999; Cloern, 2001), how indirect effects that are not simply bottom-up or top-down can affect ecosystems (Cury et al., 2000), and the increasing understanding of how regional and global climate patterns affect local conditions (Hoffman & Powell, 1998). Two seemingly large shifts in our theoretical basis for viewing ecosystems have been the shift from equilibrium analysis to dynamic and stochastic analysis (Turchin, 1995), and viewing ecosystems as complex systems (Bascompte & Sole, 1995). The shift from equilibrium to dynamic systems began several decades ago, while the complexity theory view is just beginning to enter the mainstream thinking. Complexity theory suggests that the non-linear responses of systems to perturbations and change, which keep on surprising us (Paine et al., 1998), are in fact expected responses from a complex system and that local small-scale interactions lead to many of the macroscopic properties we attribute to communities and ecosystems.

A broader array of statistical and analytical methods is becoming available to researchers (Venables & Dichmont, 2004; Hobbs & Hillborn, 2006). Numerical models of water quality, hydrodynamics, and lower trophic-level food webs have advanced dramatically and are being developed at a resolution not imagined computationally possible a few years ago (e.g., McGillicuddy et al., 2003). Such detail is becoming important to capture the complicated hydrodynamics and nutrient and plankton dynamics typical of coastal ecosystems. At the same time, fish models have been progressing with finer spatial resolution and the tracking of individuals (DeAngelis & Mooij, 2005). Individual-based modeling nicely accommodates the spatial mosaic imposed by variation in water quality and habitat. The mass-balance trophic network model, Ecopath with Ecosim, can be used to examine the relationship between primary production and fisheries production (Christensen and Walters, 2004), although it does not easily accommodate the effects of hypoxia on foraging. Water quality models that start at the base of the food web and fish models that start near the top of the food web are slowly but steadily converging (Runge et al., 2004; Rose et al., 2008). In addition, it will become increasingly important to address processes not typical for separate applications of water quality and fisheries models, such as the movement of adult fish within a high-resolution three-dimensional unstructured grid. Just over the horizon are models that include humans as fully dynamic components (Massey et al., 2006).

Conclusions

Estuaries continue to provide valued ecosystem services such as nutrient processing and protein production even when they are challenged by moderate levels of nutrient additions and fisheries removals. Even in severely degraded systems, reductions in nutrient loading lead to improvements in water quality and increases in fish populations negatively affected by nutrient enrichment (Albert, 1988; Thomas, 1998; Mee et al., 2005; Jones, 2006). Similarly, reductions in fishing mortality can lead to increased populations where suitable habitat and reproductive potential in the population remain sufficient (Richards & Rago, 1999).

This resilience of estuaries may result from their basic nature. Estuaries are spatially heterogeneous, open systems that exhibit dynamic within-year and among-year variability. Nutrients are flushed out of the system, and migratory species are replenished from broadly distributed coastal populations. In the vast majority of estuaries, hypoxia is disrupted annually or more frequently by seasonal destratification and wind mixing of the water column. Estuarine organisms are adapted to these dynamic conditions, are generally plastic in their tolerances and behaviors, and typically have high egg production rates that facilitate population increase under favorable conditions. Resilience of estuaries may be facilitated by limits on the magnitude of fishing and eutrophication effects on fish and mobile invertebrate species; although there are exceptions (e.g., sturgeons: Niklitschek & Secor, 2005), neither stressor typically results in complete extirpations of these species throughout interconnected estuarine systems. More closed systems, including some semi-enclosed seas included in our analysis and discussion, lack some of the properties that impart resilience in estuaries connected to oceans or other large water bodies.

Of particular concern are co-occurring stressors, or levels of fisheries removals and nutrient loadings that lead to threshold responses that are resistant to remediation through fisheries and nutrient management (Scheffer et al., 2001; Breitburg & Riedel, 2005). These threshold responses may be particularly likely where multiple stressors reinforce the direction of ecosystem change and reduce the likelihood that a system can retrace the same trajectory during restoration as during degradation. Since eutrophication and fisheries exploitation co-occur, there is the potential for eutrophication and fishing to interact, each affecting the way populations and estuarine ecosystems respond to the other stressor and to management actions. Parallels between agricultural systems and nutrient-enriched estuaries may include reduced stability and heightened susceptibility to natural and anthropogenic stressors. Determining the potential for nutrient enrichment to affect the susceptibility of species and systems to overfishing, the spatial dislocation of fisheries and fishing communities, and the economic value of fisheries is critically important.

We raise the issue of cumulative effects of eutrophication and fisheries not only because of the increased understanding of the potential interactions among these stressors, but also because we now have measurement and modeling techniques to better analyze their individual and simultaneous effects on coastal systems. Joint or coordinated management of nutrients and fisheries is warranted by the intertwined effects of these two stressors as well as because we are well along the way to developing the means to improve the management of both water quality and fisheries by managing them jointly.

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