

## DEAD ZONES ENHANCE KEY FISHERIES SPECIES BY PROVIDING PREDATION REFUGE

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**Abstract.** Natural stress gradients can reduce predation intensity and increase prey abundances. Whether the harsh conditions of anthropogenic habitat degradation can similarly reduce predation intensity and structure community dynamics remains largely unexplored. Oxygen depletion in coastal waters (hypoxia) is a form of degradation that has recently emerged as one of the greatest threats to coastal ecosystems worldwide due to increased rates of eutrophication and climate change. I conducted field experiments and surveys to test whether relaxed predation could explain the paradoxically high abundance of clams that have sustained a fishery in a degraded estuary with chronic hypoxic conditions. Hypoxia reduced predation on all experimental species but enhanced the long-term survivorship of only sufficiently hypoxia-tolerant prey due to periodic extreme conditions. As a consequence, only the harvested quahog clam (*Mercenaria mercenaria*) thrived in hypoxic areas that were otherwise rendered dead zones with depauperate diversity and low abundances of other species. This suggests that enhanced populations of some key species may be part of a predictable nonlinear community response that sustains ecosystem services and masks overall downward trends of habitat degradation.

**Key words:** biodiversity; bivalve; dead zone; ecosystem service; filtration; fishery; environmental stress models; hypoxia; *Mercenaria*, *Mya*, and *Mytilus*; Narragansett Bay, Rhode Island, USA; nonlinear ecosystem responses; predation refuge.

### INTRODUCTION

Large-scale habitat degradation is occurring at an accelerated pace due to human activities. For example, terrestrial desertification (Schlesinger et al. 1990), coral bleaching/mortality (Hughes et al. 2003, Pandolfi et al. 2005), conversion of wetlands (Farnsworth and Ellison 1997, Bromberg and Bertness 2005), and invasions by nuisance species (Mooney 2005) have all taken a tremendous toll on ecosystems worldwide. Habitat degradation is commonly characterized by downward trends in biodiversity and ecosystem functions including biological productivity, economic output, and ecosystem stability (Soule 1991, Vitousek 1994, Jackson et al. 2001, Lotze et al. 2006, Worm et al. 2006).

Despite this common focus on negative trends associated with degradation, some species could predictably benefit from the harsh conditions of degraded habitats. Along gradients of natural environmental stress, tolerant species often gain a refuge from their less tolerant predators that are either excluded or rendered less effective. For example, populations of sessile marine invertebrates persist in hyposaline subtidal (Witman and Grange 1998) and in high wave-shock intertidal (Menge 1978) environments. Water flow acts as an environmental stress to suppress the effectiveness

of predators in both tidal (Leonard et al. 1998) and freshwater (Peckarsky et al. 1990) rivers. In terrestrial environments, harsh conditions associated with increases in altitude reduce herbivory on mountain vegetation (Louda and Rodman 1983). This general relationship between environmental stress and predation has important consequences for the persistence of prey populations under naturally stressful conditions, and was summarized and later refined in a series of conceptual models put forth by Menge and colleagues (Menge and Sutherland 1976, 1987, Menge and Olson 1990).

Aside from noting blooms of noxious and/or invasive species however (Vitousek 1994, Jackson et al. 2001, Lotze et al. 2006, Worm et al. 2006), few studies have quantified how some species benefit from the harsh conditions of anthropogenic habitat degradation. Understanding how community-level ecological interactions such as predation are affected by environmental change is at the crux of predicting how large-scale environmental factors and organismal responses will interact to produce ecosystem-level consequences (Harley et al. 2006). If key species respond in a predictable and positive way to habitat degradation, then building their capacity for ecosystem services may become an important tool for conservation and restoration efforts that have traditionally focused on functionally extinct or threatened species (Soule 1991, Jackson et al. 2001, Lotze et al. 2006, Worm et al. 2006).

Oxygen depletion in coastal waters (hypoxia) is a form of anthropogenic habitat degradation that has recently

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emerged as one of the greatest threats to aquatic ecosystems worldwide. Increased rates of eutrophication and climate change have generated a doubling of hypoxic areas in recent years, and is evident by the creation of "dead zones" that represent general ecological collapse over areas of the bottom exceeding  $>20\,000\text{ km}^2$  (Blumberg and Ditoro 1990, Diaz 2001, Jackson et al. 2001, Rabalais et al. 2002, Grantham et al. 2004). Bleak indicators of hypoxic degradation include altered ecosystem fluxes (Baird et al. 2004), the local extinction of bivalve reefs and associated filtration (Lenihan and Peterson 1998, Meyers et al. 2000, Jackson et al. 2001, Altieri and Witman 2006), and fisheries losses that can exceed \$2 billion from a single hypoxic event (Figley et al. 1979, Diaz 2001, Rabalais et al. 2002). Contrary to these alarming effects of low-oxygen degradation, the chronically hypoxic estuary of Narragansett Bay, Rhode Island, USA, supports one of the largest quahog clam (*Mercenaria mercenaria*) fisheries in the United States (Desbonnet and Lee 1991). Quahogs are currently the most important fishery within the bay (DeAlteris et al. 2000), despite the recent and historic loss of other harvested bivalve species associated with declining water quality (Desbonnet and Lee 1991, Good et al. 2003, Oviatt et al. 2003, Altieri and Witman 2006).

Populations of quahogs and other bivalves are commonly limited by intense predation (Mackenzie 1977, Peterson 1979, Wilson 1990, Olafsson et al. 1994, Micheli 1997, McCay et al. 2003, Witman et al. 2003). However, the predators of bivalves (e.g., sea stars, fish, and crustaceans) are highly susceptible to hypoxia and often flee hypoxic conditions (Pihl et al. 1991, Lenihan et al. 2001, Bell and Eggleston 2005, Altieri and Witman 2006). Predators that remain commonly perish or grow lethargic and cease feeding (Baden et al. 1990, Breitbart 1992, Bell et al. 2003, Grantham et al. 2004). This suggests that populations of bivalves in degraded hypoxic areas could be enhanced by reduced predation rates as generally observed along gradients of naturally occurring environmental stress.

Though a number of studies have considered the interaction between predation and hypoxia, it remains ambiguous whether prey populations benefit from hypoxia in aquatic ecosystems. Laboratory studies have generally observed reduced rates of predation under hypoxic conditions (Sandberg 1997, Taylor and Eggleston 2000, Brante and Hughes 2001, Sagasti et al. 2001, Mistri 2004), but have had mixed results depending on the duration of the experiment and on sublethal effects including vertical mobility of prey across oxygen gradients (Kolar and Rahel 1993, Taylor and Eggleston 2000, Seitz et al. 2003). Though useful for close observation of *potential* interactions, extrapolation of laboratory studies to field conditions is limited due to their (1) relatively short duration, (2) oversimplification of the community to a single (or few) predator and prey species, and/or (3) confinement of predators to small containers despite the large-scale emigration of preda-

tors from hypoxic areas commonly observed at the scale of natural ecosystems. Field studies generally infer reduced predation rates under hypoxic conditions from predator behavior, gut contents, and the relative distribution of predators and prey (Baden et al. 1990, Keister et al. 2000, Bell et al. 2003). Though prey communities are commonly surveyed in hypoxic areas, the lack of experimental predator manipulations has made it difficult to differentiate between stress intolerance and modified predation rates as mechanisms of changes in the prey community (Altieri and Witman 2006).

To determine whether prey can benefit from a predation refuge in hypoxic areas, I conducted field experiments and surveys of the benthic community in Narragansett Bay to answer several specific questions: (1) Are predation rates lower inside hypoxic areas than outside? (2) Is net survivorship of bivalve prey higher in hypoxic areas? (3) Do predation rates and stress tolerances interact to generate higher abundances but lower diversity of bivalves in areas with low dissolved oxygen? Here I present results that suggest an hypoxic area can provide a general predation refuge for the bivalve community, and that the paradoxically high population densities of the harvested quahog clam are due to their unique ability to exploit this refuge that is otherwise rendered a dead zone.

## MATERIALS AND METHODS

### *Study sites and organisms*

Hypoxic conditions occur along a spatial gradient in Narragansett Bay, Rhode Island, USA (Deacutis et al. 2006). I selected subtidal sites (each 3–5 m depth) along the gradient that were: (1) closed to the clam fishery consisting of rakers and divers, whose activity could interfere with the infaunal community and experiments (Peterson et al. 1987); (2) in the upper portion of the bay to minimize spatial variability of salinity and temperature (Altieri and Witman 2006, Deacutis et al. 2006); (3) all of a similar soft-sediment habitat to minimize confounding effects of sediment type or shell debris on predator efficacy (Lipcius and Hines 1986, Peterson et al. 1995) or as a representation of differences in sediment transport and other physical properties (Snelgrove and Butman 1994); and (4) at depths below the pycnocline where hypoxia consistently can occur and water temperature is less variable (Bergondo et al. 2005, Deacutis et al. 2006). According to those criteria, the four sites suitable for study, in order of decreasing hypoxia intensity were: south of Chepibanoxet Point (CHX) where the concentration of dissolved oxygen (DO) fell below 0.5 mg/L, northwest Greenwich Bay near navigational marker GC1 (green can number 1) where DO also fell below 0.5 mg/L but for less than half the duration of CHX, north of Conimicut Point (COP) where hypoxic conditions occurred but DO was consistently  $>1.0\text{ mg/L}$ , and northeast of Arnold Point Bay (APB) where DO was consistently  $>5.0\text{ mg/L}$ .

(Appendix A). All sampling and experiments were conducted on scuba.

Salinity, temperature, and DO at each site were measured in situ within 10 cm of the bottom every 15 min, June–October 2003–2004, by data-logging sondes (Yellow Springs Instruments model 6600-EDS [Yellow Springs Instruments, Yellow Springs, Ohio, USA]), except when serviced. Daily values of salinity and temperature varied among sites by less than  $2.00 \pm 0.08\text{‰}$  and  $1.84 \pm 0.07^\circ\text{C}$  (mean  $\pm$  SE), respectively (Appendix B).

I chose bivalves as the focal prey community because they have important ecological functions in Narragansett Bay including water-column filtration and provision of complex habitat for infauna (Altieri and Witman 2006, Lindsey et al. 2006, Altieri et al. 2007). They have also played a dominant economic role in regional fisheries for several centuries (Desbonnet and Lee 1991, Oviatt et al. 2003). Additionally, they are amenable to experimental manipulations and sampling due to their abundance in the natural system, relatively large size, and hard body parts.

#### *Bivalve transplant assay*

To quantify the relative contribution of predation and hypoxic stress in driving patterns of bivalve survivorship, I transplanted three species (quahog clams, *Mercenaria mercenaria*, of 1.5–2.0 cm length; softshell clams, *Mya arenaria*, of 1.8–2.3 cm length; and blue mussels, *Mytilus edulis*, of 2.5–3.0 cm length) with and without predator exclusions to the four study sites. Those species were chosen because they are ecologically and economically important bivalves that vary dramatically in their tolerance to hypoxic conditions, ranging from two days for mussels to over two weeks for quahogs at summer water temperatures (A. Altieri and D. Warren, unpublished data). Environmentally induced intraspecific variation in hypoxia tolerance is minor relative to interspecific differences (Altieri 2006; A. Altieri and D. Warren, unpublished data). To isolate the effects of hypoxia from other physical factors that are less temporally variable (e.g., salinity and temperature) the transplant assay was repeated 3 times in 2003 (late July, August, early October) and once in 2004. The assay was conducted with the moderately hypoxia-tolerant softshell clams during all assay intervals to develop general trends in hypoxia and predation mortality. To test for interspecific differences, mussels and quahogs were included in the 2004 assay.

Softshell and quahog clams were transplanted in baskets (30 cm wide  $\times$  30 cm long  $\times$  15 cm deep) constructed from aquaculture-grade plastic mesh (7-mm mesh size) and submerged in the sediment. Eight clams of a given species were inserted into each basket in the “siphon up” orientation at burial depths commonly observed in the study system. Baskets were randomly assigned to either predator-exclusion (covered with mesh) or predator-access (uncovered) treatments. Trans-

planted mussels were tethered to the same mesh material used in the clam assay to allow natural manipulation of predators and to aid in recovery of uneaten individuals (Leonard et al. 1998). Tethers consisted of 5-cm braided fishing line secured to the anterior portion of one valve with marine epoxy (Leonard et al. 1998). Mussels in predator access treatments were tethered to an open, flat piece of mesh, and in predator exclusion treatments were enclosed in mesh. For each species, there were 10 replicates of each predator treatment at each site. The proportion of transplanted bivalves surviving in each replicate was recorded at the end of the one-week transplant period.

The assays were sensitive to the broad community of predators including cancer crabs (*Cancer irroratus*), spider crabs (*Libinia emarginata*), mud crabs (*Dyspanopeus sayi*), green crabs (*Carcinus maenas*), whelks (*Busycon* spp.), drills (*Urosalpinx cinerea* and *Eupleura caudata*), and sea stars (*Asterias forbesi*), all of which were observed feeding on transplanted bivalves during the study.

#### *Natural infauna community and predator exclusions*

To quantify the diversity and abundance of the naturally occurring bivalve community at each site, and to quantify the relative contribution of predation and hypoxic stress in driving those patterns,  $3 \times 1$  m plots with or without predator-exclusion cages ( $n = 8$  plots per treatment) were established and sampled at each site before (in June) and after (in September/October) hypoxic summers in 2003 and 2004. Plots were  $>2$  m apart, and were assigned to caging treatments randomly.

Cages were constructed from aquaculture-grade plastic mesh (9-mm mesh size) placed 1–2 cm above the sediment surface to inhibit emergence and movement of stomatopods (*Squilla empusa*) as observed in taller cages in a pilot study. The squat stature of the cages also minimized boundary-layer flow interference (Arntz 1977). Flow interference was not found to be a significant issue in previous experiments in this system (Altieri and Witman 2006). The apparent lack of cage effects on densities of bivalve recruits and only positive effects on survivorship in the present study suggest that cages neither enhanced nor inhibited flow (Olafsson et al. 1994). Cage sides were 15 cm tall, and were inserted into sediment to prevent infiltration by predators (e.g., *Cancer* crabs and *Busycon* whelks) capable of shallow burrowing.

Infauna in each plot were sampled with four cylindrical cores (10 cm in diameter and 20 cm high) hand-collected by divers from a  $1 \times 0.5$  m area at the end of each plot during each sampling period. To prevent sediment removal by cores from affecting subsequent sampling, holes created by cores were immediately filled with sediment from outside of the plots, and experimental plots were shortened to exclude the area sampled along with a 20-cm buffer of undisturbed sediment.

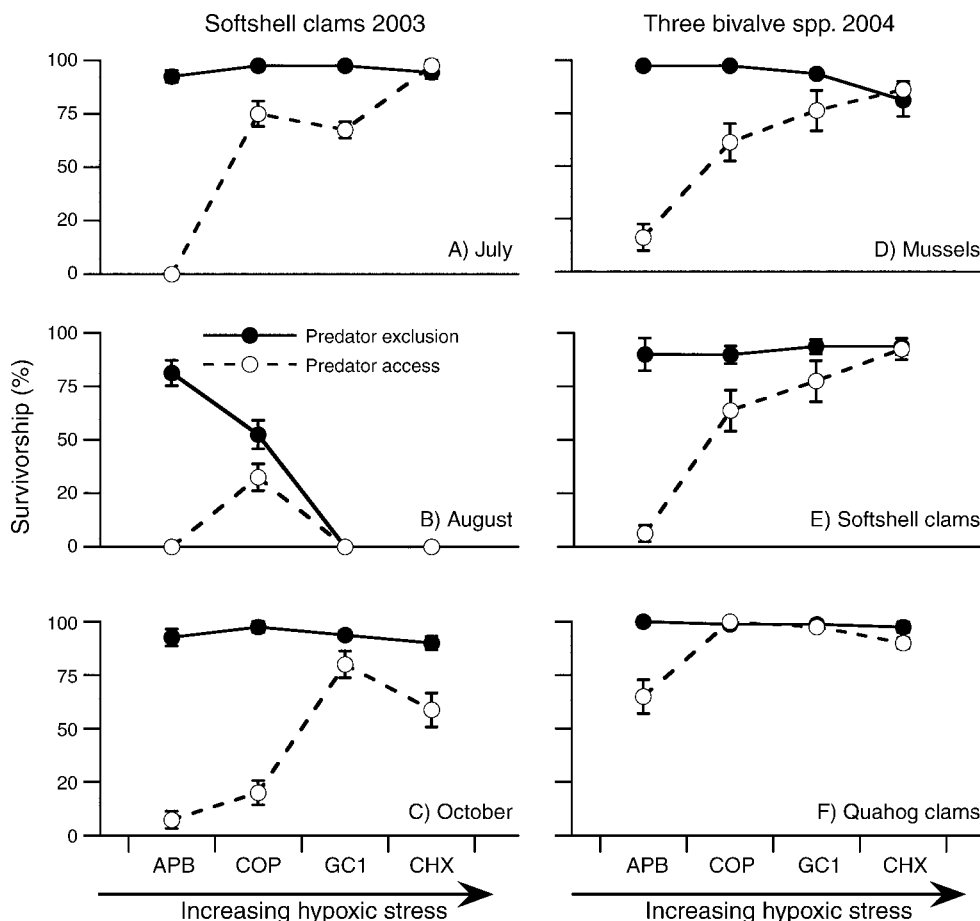


FIG. 1. Bivalve survivorship along the hypoxic gradient at four hypoxic sites in Narragansett Bay, Rhode Island, USA. (A–C) There was temporal variation in the net effect of hypoxia on softshell survivorship. (D–F) All three species exhibited decreased predation with increasing hypoxic stress. Differences in survivorship between predator-access (open circles) and predator-exclusion (solid circles) treatments were assessed with two-way ANOVAs. Data were arcsine square-root transformed to meet ANOVA assumptions of normality. Predation varied across the hypoxic gradient for all experimental periods and species ( $F_{3,70-72} > 14.4$ ,  $P < 0.001$  for site  $\times$  predation in all analyses). Data are survivorship (mean  $\pm$  SE) in 10 replicates. Sites on the x-axis are in order of increasing hypoxic stress: APB = Arnold Point Bay, CPO = Conimicut Point, GC1 = Greenwich Cove (navigational marker number 1), and CHX = Chepiwanoxet Point.

All cores were sieved (mesh size 1 mm) live in seawater, and legal-sized quahogs (width  $\geq 2.54$  cm) were quantified following collection. The bulk content of one core from each plot was randomly selected for detailed quantification. Contents were relaxed with  $MgCl_2$  and stained with rose bengal for 5 h at 4°C, fixed in buffered 10% formalin for 6 d, and transferred to 70% ethanol until sorting. All bivalves were identified to the species level except *Macoma* spp. to the genus level. Bivalves  $\leq 5$  mm were designated as “recruits” unless maximum size was  $< 1$  cm).

RESULTS

Predation on all three bivalve species in the transplant assays was consistently highest at the non-hypoxic site Arnold Point Bay (APB), and was reduced or absent under hypoxic conditions at the other sites (Fig. 1). During moderate hypoxic conditions in July 2003,

predation was the primary source of mortality for transplanted softshells, and decreased in importance along the gradient of increasing hypoxic stress (Fig. 1A). When hypoxia reached its most severe levels in August 2003, softshells at the intermediately hypoxic site Conimicut Point (COP) continued to have a net benefit from reduced predation despite some hypoxia-induced mortality (Fig. 1B). However, they were completely eliminated during that same period at the two most severely hypoxic sites along the gradient, indicating that any benefit of a predation refuge associated with hypoxia during previous transplant periods was subsequently nullified by direct effects of hypoxic stress. Just five weeks later, when seasonal hypoxic conditions subsided, predation on the clams at the most hypoxic site resumed (Fig. 1C). During the moderately hypoxic summer of 2004, oxygen stress was not sufficiently severe to cause mortality in any of the three transplanted

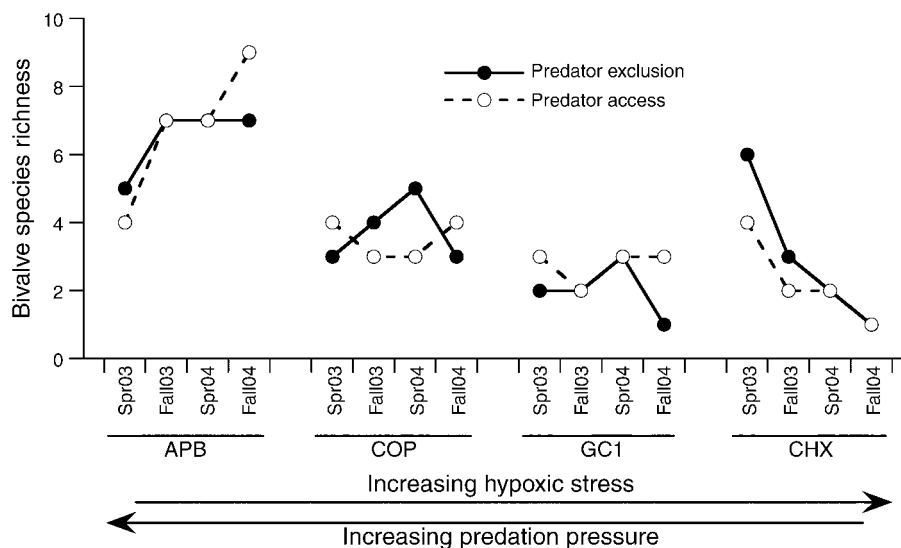


FIG. 2. Diversity of bivalves at sites spanning the hypoxic gradient. Each value was derived from asymptotic species-accumulation curves in the EstimateS (version 6.8) software program, with eight replicate samples run through 100 iterations for each curve. Sampling periods are listed adjacent to the *x*-axis (e.g., Spr03 = Spring 2003). Open circles represent the predator-access treatment, and solid circles represent the predator-exclusion treatment. Abbreviations are as in Fig. 1.

bivalve species, but still led to a distinctive refuge from the more sensitive predators. As a consequence of this general predation refuge, the survivorship of all three bivalve species in 2004 was similarly high in both predator-access and predator-exclusion treatments at the most hypoxic sites (Fig. 1D–F).

As predicted by transplanted softshell clams, which perished under extreme conditions (Fig. 1B), sites at the degraded end of the hypoxia gradient were rendered largely dead zones. Bivalve diversity declined until only quahogs remained at the most severely hypoxic site (Fig. 2). Bivalves other than quahogs were generally lowest in abundance at the two most hypoxic sites (Fig. 3A, B). In contrast, the highest levels of bivalve diversity were found at the non-hypoxic site APB (Fig. 2). The community of bivalves at low-diversity sites was a subset of the species found at more diverse sites. The persistence of a diverse bivalve community despite predation in less hypoxic areas is consistent with the functional response of predators that generally allows clams to persist at low densities in soft-sediment habitats (Seitz et al. 2001). As hypoxic stress decreased across the spatial gradient, predation played an increasingly important role as detected by bivalves in the transplant experiment (Fig. 1D–F) and in the natural community following a recruitment pulse at site COP (Fig. 3). This suggests that many bivalve species would benefit from a hypoxic refuge if they were sufficiently tolerant to the associated stress.

Quahogs are known as “facultative anaerobes” due to their extreme hypoxia tolerance (Hochachka and Somero 2002), and were unique among bivalves in their ability to persist in the hypoxic conditions that provided a general predation refuge. Unlike other bivalves,

densities of legal-harvest-sized quahogs were highest at the most hypoxic site, and declined along the gradient of decreasing hypoxic stress (Fig. 4A). Similarly, sub-legal-sized quahogs were consistently found at only the two most hypoxic sites (Fig. 4B). Predation on sub-legal quahogs was evident only at the less hypoxic of those two sites, Greenwich Cove (green can 1, GC1) and can explain why fewer quahogs reached legal size there than at the more hypoxic Chepiwanoxet Cove (CHX) site (Fig. 4). Direct effects of predation on populations of legal-sized quahogs is uncommon, as observed in this study (Fig. 4A), due to a size-refuge from predators (Mackenzie 1977, McCay et al. 2003). However, predation on smaller quahogs commonly limits the abundance of individuals that advance to larger size classes (Mackenzie 1977, McCay et al. 2003), a demographic bottleneck that apparently occurred at GC1 but not the more hypoxic CHX (Fig. 4).

#### DISCUSSION

Low-oxygen conditions can reduce overall predation rates. Under hypoxic conditions, the benefits of this predation refuge can outweigh the deleterious effects of stress-induced mortality for basal trophic levels. Survivorship of transplanted bivalves was found to be higher at moderately hypoxic sites than non-hypoxic sites. However, periodically severe hypoxic conditions overwhelmed the tolerance of most bivalves in the natural community. As a consequence, only the harvested quahog clam is enhanced in hypoxic areas of Narragansett Bay (Rhode Island, USA) that are otherwise rendered dead zones with depauperate diversity and low abundances of other bivalves. The apparent success of quahogs, which sustains ecosystem services including the

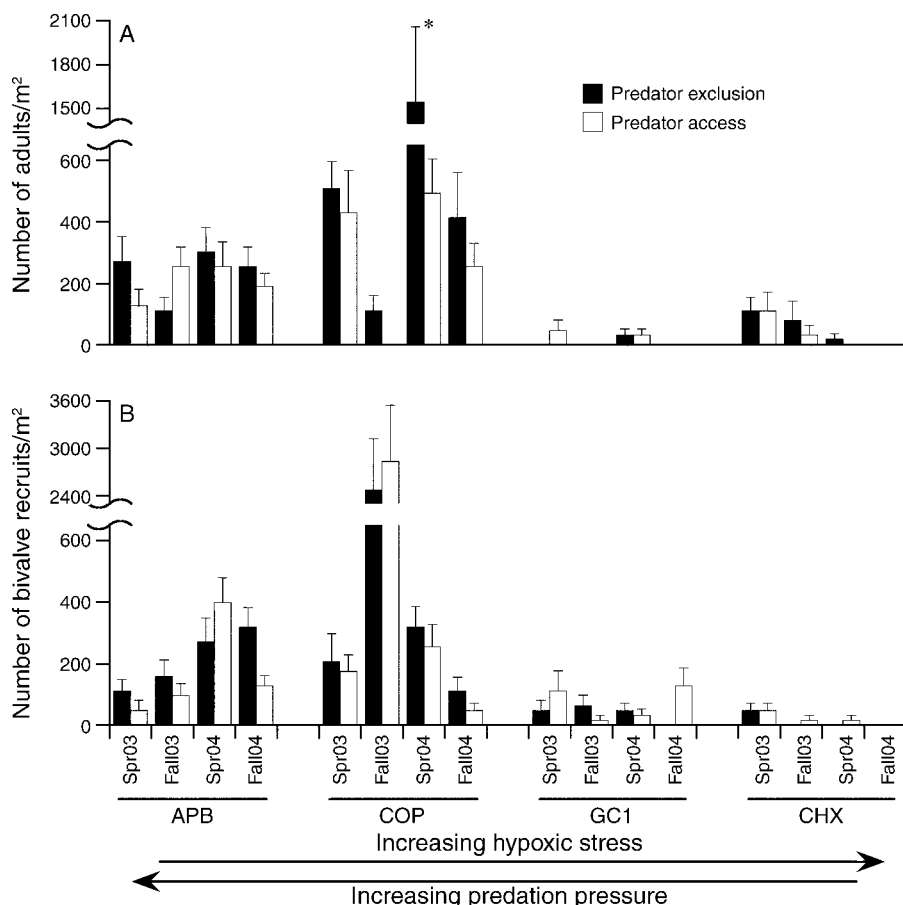


FIG. 3. Bivalve abundances along the hypoxia gradient. The abundance of (A) bivalve adults and (B) recruits in predator-access (open circles) and predator-exclusion (solid circles) treatments decreased along the gradient of increasing hypoxic stress. Data are densities (mean  $\pm$  SE) in eight replicates for all species pooled except quahogs. Differences in densities were analyzed by a three-way ANOVA (predation  $\times$  site  $\times$  season), and post hoc analyses were by Tukey's hsd test. Data were  $\log_{10}(x + 1)$ -transformed to meet ANOVA assumptions of normality. The asterisk (\*) denotes a significant effect of predation ( $F_{6,166} = 2.4, P < 0.05$ ) during the period at the site. Sampling periods (x-axis) are as explained in Fig. 2.

Bay's currently most important fishery and water column filtration, belies significant impacts of hypoxic habitat degradation on the composition and interactions of the benthic community.

*Hypoxia provides predation refuge: A net benefit?*

I found hypoxia to be an abiotic stress that reduces predation rates as commonly observed along gradients of natural environmental stresses. This relationship between hypoxia and predation intensity fits the qualitative predictions of the "environmental-stress models" (ESMs) proposed by Menge and Sutherland (Menge and Sutherland 1976, 1987). However, support for the ESMs' predictions for prey survivorship is less straightforward due to interspecific variation in the ability of prey to tolerate the stressful conditions within the predation refuge. For quahogs, and the other transplanted species under only moderate hypoxic conditions, enhanced survivorship appeared to follow the expectations of the "consumer stress model" (CSM),

which predicts a positive relationship between stress and prey survivorship when prey are more stress tolerant than their predators (Menge and Olson 1990). For transplanted softshells under severe hypoxic conditions, and most bivalves in the natural community, a negative relationship between stress and survivorship followed expectations of the "predator stress model" (PSM), which predicts a negative relationship between stress and prey survivorship due to the additive or synergistic combination of predation and stress-induced mortality (Menge and Olson 1990). Thus there was a net benefit associated with hypoxic conditions only for quahog clams. The seasonal summer occurrence of hypoxia and the associated refuge is ecologically significant since predation rates are greatest during the summer season (Micheli 1997, Beal et al. 2001).

In addition to the spatial gradient in predation pressure associated with hypoxia, the series of transplant assays with softshell clams revealed considerable temporal variability in survivorship within a given hypoxic

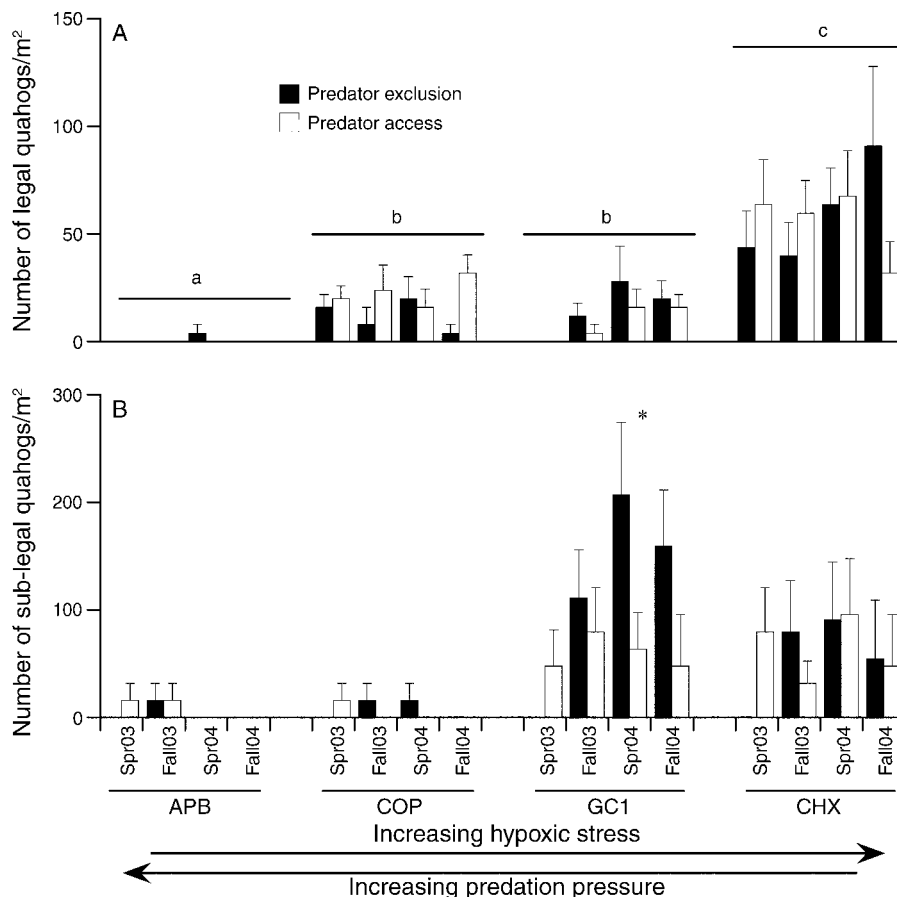


FIG. 4. Quahog clam abundances along the hypoxia gradient. The abundance of (A) legal-harvest-sized and (B) sub-legal-sized quahogs in predator-access (open circles) and predator-exclusion (solid circles) treatments increased along the gradient of increasing hypoxic stress. Sampling periods ( $x$ -axis) are as explained in Fig. 2. Data were analyzed as described in Fig. 3 and are presented as densities (mean  $\pm$  SE) of eight replicate plots. The asterisk (\*) denotes a significant effect of predation ( $F_{3,166} = 3.0$ ,  $P < 0.05$ ) at the site. Different lowercase letters above sites indicate differences in adult quahog densities ( $F_{3,166} = 29.4$ ,  $P < 0.0001$ ).

site. Sites CHX and GC1 had the highest survivorship during three of four transplant assays due to a predation refuge, but had 0% survivorship in August 2003 during a severely hypoxic episode. Such periodic extreme events that lead to total loss of a population can have effects on community structure lasting far longer than the event itself, and can explain the cumulative decline in bivalve diversity at hypoxic sites over the course of the study period. The significance of rare and extreme environmental events and their ecological impacts has long been an area of interest, and emphasizes the necessity of long-term monitoring programs to capture abiotic drivers of biological dynamics (Gaines and Denny 1993, Romme et al. 1998, Gutschick and BassiriRad 2003, Benedetti-Cecchi et al. 2006). Extrapolating biological impacts from oxygen levels and biota sampled only once a year as recently suggested (Strobel and Heitmuller 2001) would be misleading since a majority of documented hypoxic coastal ecosystems experience intermittent low-oxygen levels (Diaz 2001, UNEP 2004).

#### *Nonlinear community responses*

Though the CSM has generally been supported by empirical studies in marine systems and the PSM by studies in terrestrial habitats (Menge and Olson 1990), I found that both models applied to the hypoxic estuary Narragansett Bay due to interspecific variation among prey in their physiological tolerances to hypoxia. These divergent responses highlight why predicting the direct effects of hypoxia via stress-induced mortality and indirect effects via modified predation rates requires careful field experimentation and an ecophysiological perspective as suggested for other stressful habitats (Tomanek and Helmuth 2002). Competition is another ecological interaction that could potentially be modified by hypoxia. Exploitative competition for food resources can limit bivalve growth in soft-sediment communities (Peterson 1982), and the differential mortality among bivalve species in Narragansett Bay may allow hypoxia-tolerant species access to more resources. Recent syntheses and empirical studies have emphasized the

potential for large-scale environmental degradation to have nonlinear consequences for ecosystems due to such modified ecological interactions (Jackson et al. 2001, Hughes et al. 2003, Silliman et al. 2005, Harley et al. 2006, Lotze et al. 2006, Worm et al. 2006). Modeling efforts have furthered that effort in hypoxic ecosystems by quantifying the consequences of modified community structure and interactions for energy fluxes (Pearson and Rosenberg 1992, Baird et al. 2004).

Like hypoxia, recruitment was a structuring force in the benthic community of Narragansett Bay that varied significantly in both space and time. A major recruitment event in the fall of 2003 was observed only at site COP. The population of adult bivalves that had largely perished at that site in the previous hypoxic summer was replenished as the newly recruited cohort grew into the adult size class by spring 2004 despite some predation between summers. Previous observations of local extinction due to hypoxia followed by recolonization through larval recruitment has led to the suggestion that a meta-population perspective should be applied to shed insight into hypoxic ecosystems (Altieri and Witman 2006). Recruitment rates at the other three sites were much lower however, and were insufficient at sites GC1 and CHX to rescue the bivalve communities from the effects of mortality during the hypoxic summers of 2003 and 2004. Other studies in Narragansett Bay have similarly documented highly variable patterns of benthic recruitment (Frithsen 1989, Gaines and Bertness 1992, Oviatt 2004, Lindsey et al. 2006).

For the hypoxia-tolerant quahog, which showed a spatial pattern of abundance opposite to the other bivalves, three lines of evidence suggest that post-settlement mortality (i.e., predation), and not propagule limitation, was responsible for the overall lower abundance of quahogs at less hypoxic sites. (1) Recruitment was uniformly low across all sites. (2) Three of the four quahogs that did recruit during the 18-month study period were found at the non-hypoxic site APB, which had consistently low densities of both sub-legal and legal-sized individuals. (3) The density of legal-sized quahogs was higher at the intermediately hypoxic site COP than the non-hypoxic site APB despite similar numbers of sub-legal-sized quahogs at both sites, suggesting lower survivorship of quahogs during the sub-legal-size stage at non-hypoxic APB.

Salinity and temperature are two additional factors that potentially could modify predation rates and prey-mortality patterns in estuarine conditions. Both factors remained well within the physiological limits of the bivalves utilized in the experimental portion of the study and their dominant predators (e.g., Wells 1961, Ansell 1968, Castagna and Chanley 1973, Bourget 1983, Charmantier and Charmantier-Daures 1991, Seed and Suchanek 1992, and references therein). Previous work in Narragansett Bay found that mass mortality of mussels was correlated with oxygen levels but not with temperature or salinity (Altieri and Witman 2006).

Warm summer temperatures, however, may have increased the susceptibility of bivalves and their predators to hypoxic stress (Matthews and McMahon 1999, Hicks and McMahon 2005). This relationship suggests that the impact of a given level of hypoxia on mortality in benthic communities could be amplified by warming seas.

*Biodiversity and ecosystem services:  
a historical perspective*

That quahog clams are a standout among contemporary bivalves in their ability to tolerate low-oxygen conditions and exploit the predation refuge created by hypoxic conditions has important implications for ecosystem services, including fisheries output and water-column filtration capacity. The diversity of the bivalve community declined at the two most hypoxic sites, and by the end of the two-year study period quahogs were the only species remaining at the most severely hypoxic of the two sites. Similarly, quahogs are an exception among the historic assemblage of commercially harvested species to persist and flourish in the degraded Narragansett Bay system. Oysters (*Crassostrea virginica*) and scallops (*Argopecten irradians*) were mainstays of the region's fisheries-based economy for centuries until the combined effects of habitat degradation and over-exploitation led to their collapse in the mid-1900s (Desbonnet and Lee 1991, Oviatt et al. 2003). Softshell clams and blue mussels are two additional exploitable species that have been marginalized and recently suffered bouts of mass-mortality as a result of hypoxia (Good et al. 2003, Altieri and Witman 2006).

A commercial fishery has been sustained by shifting to the less desirable quahogs in Narragansett Bay (Desbonnet and Lee 1991, Oviatt et al. 2003) as in other degraded estuaries such as Chesapeake Bay (USA; Mann et al. 2005). In addition to sustaining fishery services, quahogs provide a filtration function that is critical for countering the effects of eutrophication (Jackson et al. 2001, McCay et al. 2003, Altieri and Witman 2006). Though the historic diversity and functional redundancy of bivalves in the ecosystem has partially buffered against the complete loss of some ecosystem functions, the overall decline in bivalve diversity has a number of potentially important consequences. For example, the loss of bivalve diversity likely decreased the aggregate water-column filtration function of the benthic community (Worm et al. 2006). Moreover, dependence on the one remaining harvestable species in hypoxic areas has left the bivalve fishery vulnerable to collapse should quahog clams be driven to local extinction by increased hypoxic stress or another factor.

In addition to enhanced fisheries through reduced predation (top-down control) as suggested by the present study, several investigators have indicated that fisheries could be enhanced by the higher primary productivity (bottom-up control) associated with the eutrophication that commonly drives low-oxygen conditions. One of the



more notable of these syntheses is the Caddy model (Caddy 1993), which proposes a positive relationship between eutrophication and fisheries yield to a point, after which deleterious secondary effects including hypoxia cause a negative relationship. A recent review of observational studies revealed mixed support for the Caddy model at the ecosystem-wide scale for reasons including variation in fisheries effort, location, and target species that co-occurred with changes in eutrophication rates (Kemp et al. 2005). The loss of major fisheries has been associated with hypoxic conditions in numerous coastal ecosystems, and has often resulted in a shift in effort towards remaining species that occupy different habitats or trophic levels (Diaz 2001). Within an ecosystem, Breitburg (2002) proposed that the effects of eutrophication on fisheries would likely be localized along a gradient, with positive bottom-up effects further from a nutrient source, and negative effects due to hypoxia nearer to a source. Consideration of the top-down perspective in the present study reveals the opposite pattern for sufficiently tolerant species—positive effects of eutrophication can occur in the more degraded hypoxic area due to a predation refuge.

### Conclusions

A general understanding of emergent community-level responses to habitat degradation is essential for anticipating the consequences of anthropogenic environmental change on economically critical ecosystem services (Costanza et al. 1997, Harley et al. 2006). This study revealed that apparently positive indicators, such as the high abundance of a harvested species, can be part of a general trend towards system-wide habitat degradation. Predator–prey interactions disrupted by hypoxia contribute to the success of quahogs and the maintenance of associated ecosystem services including fisheries and water-column filtration, even as bivalve diversity and historically abundant species have declined. Conservation efforts focused on the general recovery of ecosystem services should identify and enhance such seemingly paradoxical positive indicators in addition to restoring lost components of the ecosystem. Moreover, increased communication among scientists, managers, and fishery harvesters may be necessary to motivate restoration in such instances when apparently satisfactory indicators mask a trajectory of overall ecosystem demise.

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#### APPENDIX A

A map of the study sites in Narragansett Bay, Rhode Island, USA (*Ecological Archives* E089-159-A1).

#### APPENDIX B

A figure showing oceanographic conditions (daily averages) at the four study sites, summer–fall 2003–2004 (*Ecological Archives* E089-159-A2).