

LOCAL EXTINCTION OF A FOUNDATION SPECIES IN A HYPOXIC ESTUARY: INTEGRATING INDIVIDUALS TO ECOSYSTEM

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Abstract. We integrated across individual, population, community, and ecosystem levels to understand the impact of environmental stress by tracking the foundation species *Mytilus edulis* in the hypoxic estuary Narragansett Bay, Rhode Island, USA. Our initial surveys revealed that the mussels occurred in nine extensive (2–28 ha) dense (814–9943 individuals/m²) subtidal reefs that attracted a diverse suite of predators (sea stars, crabs, gastropods). Hypoxia occurred in the summer of 2001, and a mussel transplant experiment revealed overall reduced growth rates of individuals, and higher mortality rates among larger mussels. At the population level, large decreases in densities and cover of mussels were correlated with dissolved oxygen concentrations, leading to extinction at one site and reductions of over an order of magnitude at others. Within one year, seven of the eight remaining populations were edged to extinction, and the previously extinct population was recolonized. At the community level, a predator exclusion experiment indicated that predation was an unimportant source of mussel mortality during the hypoxic period, in part due to the emigration of sea stars, as predicted by the Consumer Stress Model. However, mussels were too intolerant to hypoxia to have a net benefit from the predation refuge. The seasonal (summer) occurrence of hypoxia allowed sea stars to return following a lag, as predicted by a stress return time model, and the resumption of predation contributed to the subsequent extinction of mussel populations. At the ecosystem level, the initial filtration rate of the mussel reefs was estimated at 134.6×10^6 m³/d, equivalent to filtering the volume of the bay 1.3 times during the 26-d average residence time. That function was reduced by >75% following hypoxia. The effect of hypoxia on each level of organization had consequences at others. For example, size-specific mortality and decreased growth of individuals, and reduced filtration capacity of reefs, indicated a loss of the ability of mussels to entrain planktonic productivity and potential to control future eutrophication and hypoxia. Our study quantified patterns of loss and identified pathways within an integrative framework of feedbacks, summarized in a conceptual model that is applicable to similar foundation species subjected to environmental stress.

Key words: *Asterias forbesi*; benthic–pelagic coupling; bivalve; dissolved oxygen; disturbance; environmental stress; eutrophication; filtration; mussel; *Mytilus edulis*; predation; refuge.

INTRODUCTION

A perspective that integrates across levels of ecological organization is necessary to understand pattern and process in ecological systems, since the mechanism for change at a given level often lies at another (Werner 1998). Such a perspective has led to important conceptual breakthroughs and predictions. For example, the trophic cascade concept predicts how community level interactions between predators and grazers have ecosystem level effects on primary productivity in systems as different as lakes (Carpenter and Kitchell 1988), salt marshes (Silliman and Bertness 2002), and kelp forests (Estes et al. 1998). Likewise, ecosystem engineers demonstrate the way in which individuals and populations of some species can have a profound

effect on community composition and ecosystem level flow of energy and resources (Jones et al. 1997).

It has been recently suggested that a similar integrative approach can shed new light on how environmental stress generates ecological pattern, even in well-studied systems such as the rocky intertidal (Tomanek and Helmuth 2002). The elevated pace and magnitude of environmental change due to anthropogenic disturbance has renewed interest in the ecological responses of biological systems to environmental stress (Kareiva et al. 1993, Vitousek 1994), yet the approach of integrating across levels of organization remains underutilized. As a consequence, our ability to predict the impact of environmental changes is a limited (Lawton 2000).

Hypoxia (dissolved oxygen [DO] concentration <2.8 mg/L) is an environmental stress exacerbated by eutrophication, which has reached epidemic proportions in aquatic systems worldwide (UNEP 2004). Nutrient inputs stimulate primary production of organic matter, the microbial decomposition of which depletes dissolved oxygen (Andersson and Rydberg 1988, Justic et al. 1993,

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Turner and Rabalais 1994, Rabalais et al. 2002). The most striking ecological effects of hypoxia are mass mortality events and resulting lifeless areas (e.g., 27 000 km² "Dead Zone" in the Gulf of Mexico, Rabalais et al. 2002). With a doubling in the number of areas affected by hypoxia since 1990 (UNEP 2004) due to anthropogenically driven changes in climate, including global warming (Blumberg and Ditoro 1990), sea level rise (Van Der Zwaan and Jorissen 1991), and ocean circulation patterns (Grantham et al. 2004), hypoxia is emerging as one of the most pressing scientific and coastal management issues due to the predicted co-occurring biological impacts of mortality events and modified trophic webs (Diaz and Rosenberg 1995). Recent reviews of the ecological impacts of hypoxia advocate the importance of integrating across levels of organization (Diaz and Rosenberg 1995, Rabalais et al. 2002, Wu 2002). However, the integrative approach has not been applied to investigations of hypoxia in the field.

To address this void, and to examine the utility of the integrative perspective for studies of environmental stress in general, we tracked the dynamics associated with the foundation species (*sensu* Dayton 1972) *Mytilus edulis* (blue mussel) in the seasonally hypoxic estuary Narragansett Bay, Rhode Island, USA, at sites separated by 1–12 km. We focused on mussels because they were the only habitat-forming suspension feeder in potentially hypoxic areas of Narragansett Bay at the time of our study, although both oysters (*Crassostrea virginica*) and scallops (*Aequipecten irradians*) were historically abundant (Oviatt et al. 2003). Suspension feeders demand primary attention in studies of hypoxia because their populations have the potential to filter large volumes of water and control eutrophication (Officer et al. 1982), which in turn affects the prevalence of hypoxia. Mussels are foundation species since their reefs can play a central role in benthic habitats by modifying patterns of water flow and delivery of particulates to the benthos (Frechette et al. 1989), providing infauna with refuge from predation (Witman 1985) and abiotic stress (Suchanek 1986). They may also have a bottom-up effect on the size, distribution, and abundance of predators (Menge 1986, Witman et al. 2003). The effects of hypoxia on mussels, therefore, have clear implications for the entire system.

We addressed the overall question: How do the effects of hypoxia at one level of ecological organization affect processes at other levels? We answered that question by conducting surveys and experiments to address more specific questions including: (1) Does hypoxia affect the mussel's function of benthic–pelagic coupling through individual growth and mortality rates and reef filtration rates? (2) Does hypoxia affect predator–prey interactions by modifying prey availability and predator behavior as predicted by environmental stress models? (3) Does hypoxia affect reef persistence through differential rates of mussel mortality?

METHODS

Study system

Narragansett Bay is a large (328 km²) shallow (average depth 8.3 m) temperate estuary on the northwestern Atlantic (41.2° N latitude, 71.2° W longitude) with a volume of 2.7×10^9 m³ and an average flushing time of 26 days (Pilson 1985). Hypoxic events have been recently described as a predictable summer occurrence (Bergondo et al. 2005; C. Deacutis, D. Murray, W. Prell, E. Saarman, L. Korhun, and G. Cicchetti, *unpublished manuscript*), though observations of fish kills indicative of hypoxia date back to the late 1800s (Desbonnet and Lee 1991). Moreover, the bay has a legacy of eutrophication, including an estimated five-fold increase in dissolved inorganic nitrogen since European contact in the 1500s (Nixon 1997). It currently drains one of the most densely populated watersheds in the United States, with over 2758 people per km² (Basta et al. 1990).

We conducted our study at nine mussel reef sites (defined by >25% cover mussels at the start of the study) and seven non-mussel sites on gently sloping soft-sediment bottom at depths of 4–6 m (Fig. 1). To best capture the effects of hypoxia, we conducted our experiments during the summer (July and August), and spanned the hypoxic period with surveys in spring (June) and fall (September and October) 2001. To address the specific question of whether mussel reef dynamics varied idiosyncratically, we resurveyed mussel sites once again in fall 2002.

Oceanographic data

Oceanographic parameters including salinity, temperature, and dissolved oxygen were monitored continuously at two sites (A and J) located at the northern and southern ends of our study area (Fig. 1). Measurements were made in situ and recorded by moored data logging sondes (Yellow Springs Instrument [YSI], Yellow Springs, Ohio, USA; model 6600). We gained greater spatial resolution of those parameters by surveying five additional mussel sites on the night of 15 August 2001 during the period of predicted dissolved oxygen minimum according to the lunar tidal cycle (Bergondo et al. 2005). Boat-based teams comprising the Rhode Island Dissolved Oxygen Survey (Rhode Island Department of Environmental Management, Brown University, University of Rhode Island) used YSI 6000 and 6600 sondes to measure and record in situ temperature, salinity, and dissolved oxygen within one meter of the bottom.

Individual mussel response to hypoxia

To predict the effects of environmental stress on populations and communities, it is necessary to quantify the range of responses at the individual level (Helmuth 2002). The tolerance of mussels to hypoxia, and patterns of growth and size-specific mortality, were ex-

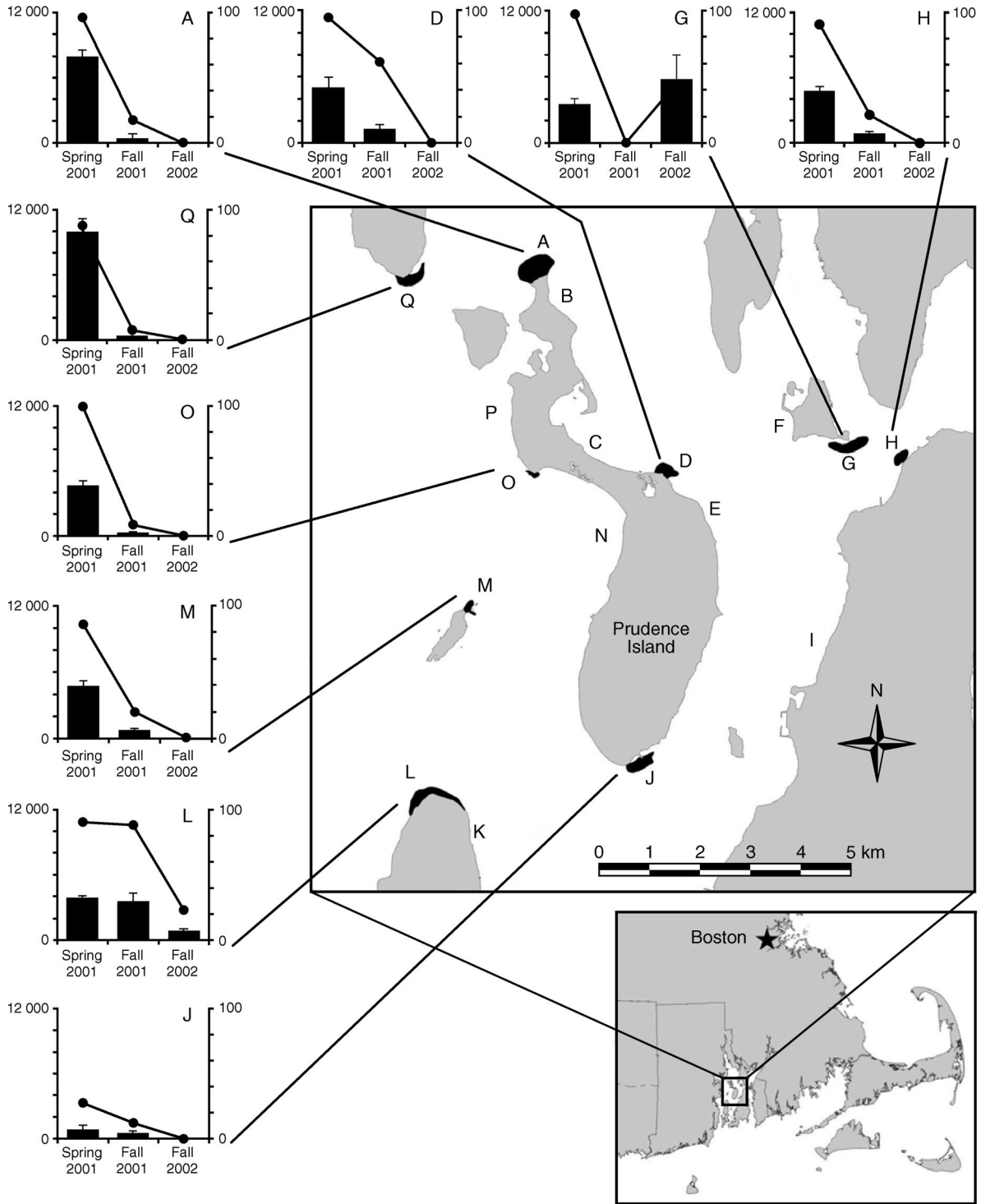


FIG. 1. Study sites and mussel reefs in central Narragansett Bay, Rhode Island, USA. Graphs for each site show mussel density (histograms, no./m²; mean + SE) on the left-hand axis and percent cover (lines) of mussels on the right-hand axis during each of the three sampling periods (spring 2001, fall 2001, and fall 2002). Color code: white, water; gray, land; black, mussel reefs. Mussel reef area (ha) is presented in Table 2. Study sites: A, Providence Point; B, Bear Cove; C, Potter's Cove; D, Mount Tom Rock; E, Homestead Point; F, Hog Island West; G, Hog Island East; H, Marker 6A; I, Portsmouth Abbey; J, T-Wharf; K, Conanicut Point East; L, Conanicut Point West; M, Hope and Despair Islands; N, Home Beach; O, Pine Hill Point; P, Rossi Farm Backside; Q, Warwick Point.

amined by transplanting mussels to mussel reef sites A, D, H, and M (Fig. 1) over a six-week period from early July to late August 2001. Transplanted mussels (20–40 mm length) were collected from a subtidal site (E) within the study region that was not otherwise included in the study. To record initial length of all mussels, the shell near the posterior lip was lightly sanded and marked with nontoxic paint. Five replicate mesh bags (mesh size 1 cm²), each containing 50 marked mussels, were placed at least 5 m apart at each site. Bags were suspended 10 cm above the bottom between PVC stakes to reduce access by predators (e.g., drills, sea stars, crabs) and to prevent surrounding mussels from crawling over the bags and smothering mussels within.

At the end of the experiment in late August, mussels were examined for survivorship and growth. The initial and final lengths of all live and dead mussels were recorded, and damage to shells of dead mussels was recorded to account for mortality due to predation (e.g., chipped shells due to crabs, drill holes due to whelks).

Mussel populations

In spring 2001, mussels (*Mytilus edulis*) formed discrete reefs extending from the mid-intertidal to the shallow subtidal of numerous sites throughout Narragansett Bay. All reefs in the study regions were located by either exploring the subtidal area adjacent to intertidal reefs or by towing a snorkeler behind a slow-moving boat. The spatial extent of mussel reefs was calculated in a Geographic Information Systems program (Arcview, version 3.3) from Global Positioning System points collected from the edge of reefs by a boat-based receiver shadowing a free-diver. Sites were designated as either mussel or non-mussel sites, based on mussel presence or absence during the spring survey. No mussel recruitment occurred at non-mussel sites during our study.

In spring 2001, fall 2001, and fall 2002, we conducted surveys to quantify the percent bottom cover, density, and size structure of mussel populations. Though density and cover are measures of mussel abundance that are often correlated, we quantified both since they can be decoupled by growth of individuals and/or populations comprised of stacked individuals (Petratis 1995). The percent cover of mussels at each site was estimated from the average proportion of 50 random points over live mussels in each of 15 haphazardly placed 1-m² quadrats (10 m minimum distance between replicates). All mussels within six haphazardly placed replicate cylindrical cores (177 cm²) were hand collected to characterize the density and size structure of the mussel population at each site. Reefs were three-dimensional structures consisting of multiple layers of mussels, and the core prevented adjacent mussels from falling into the collection area. The density of mussels was determined by counting all the mussels in each core and multiplying to a standard area of 1 m². The

size structure of mussels was estimated by measuring a randomly selected subsample of mussels to 0.1 mm using digital vernier calipers (minimum of 25 individuals per core).

Mussels at the community level

Predator surveys.—Predators can exhibit an “aggregative response” to prey availability in which their densities are higher in areas where prey are more abundant (Hassell and May 1974). To examine if mussels played a significant role as a prey resource in the distribution and behavior of predators, we contrasted predator densities at mussel and non-mussel sites by diver visual surveys in both spring (June) and fall (September/October) 2001. All species observed to feed on mussels in our system were considered predators in our study. This included a diverse assemblage of predators: sea stars (common sea star *Asterias forbesi*), crabs (spider crab *Libinia emarginata*, green crab *Carcinus maenas*, rock crab *Cancer irroratus*, Say’s mud crab *Dyspanopeus sayi*), drills (thick-lip drill *Eupleura caudate*, Atlantic oyster drill *Urosalpinx cinerea*), and whelks (knobbed whelk *Busycon carica*, channeled whelk *Busycotypus canaliculatus*). Neither drills nor whelks were differentiated to the species level for analyses due to potential misidentification in the field, and so are referred to as taxa rather than species. Divers counted predators along five replicate 15 × 2 m belt transects at each site (minimum 20 m between transects) using nondestructive methods such as moving occasional algae aside but not moving mussels or overturning shells. Two divers swam shoulder-to-shoulder along each transect, each recording consumers within 1 m of their respective side of the transect tape. The data collected by the two divers on a given 30-m² transect were pooled and treated as a single replicate.

We chose sea stars as a representative predator for more detailed study since they showed both a strong spatial relationship with mussels and easily quantifiable feeding behaviors. To establish a direct trophic link between mussels and sea stars, we contrasted in situ sea star observations at the nine mussel and seven non-mussel sites in spring and fall 2001. Average sea star size was quantified by measuring the radius of 100 individuals (or as many found in 90-minute search time) to the nearest 0.5 cm. Individuals were recorded as feeding if their stomachs were everted, and the identity of prey was noted.

Predator exclusion experiment.—Predation commonly limits the lower intertidal and subtidal distribution of mytilid mussels (Seed and Suchanek 1992). To quantify the importance of predation relative to other factors such as abiotic stress on reducing the density of live mussels, we conducted a predator exclusion caging experiment at three mussel reef sites (A, D, H) from mid-July to late August, a period when hypoxia commonly occurs. Within each mussel reef, we randomly assigned six replicates each of three treatments

(full cage, control cage, and open plot) to plots separated by 2 m. Full cages were cylindrical (1.0 m diameter \times 0.3 height), with walls and a roof constructed of PVC-coated galvanized steel (mesh size 2.4 cm²). Control cages were constructed similarly to full cages, but had four equal-size panels totaling 60% of side area cut away to allow predators access to the interior of cage. Predators that were targeted by our exclusion treatments and quantified by our surveys (e.g., crabs, sea stars, and large whelks) were observed to move freely through marked open plots and control cages, and were never observed inside exclusion cages. Cages were scrubbed with a nylon brush to keep them clear of light fouling that occurred over the course of the six-week experiment. Densities of mussels at the start of the caging experiment were determined by collecting six replicate 177-cm² cores from the surrounding mussel reef at each site. The experiment ended in late August when a similar core was collected from each replicate experimental plot.

Small predators and dislodgement.—To test the relative importance of two potential causes of mussel mortality not manipulated by the caging experiment, (1) predators that could potentially slip through the mesh of exclusion cages (e.g., drills and mud crabs) and (2) dislodgment, which can drastically reduce the density of mussels within reefs (Dayton 1971, Paine and Levin 1981), we quantified the change in density of all mussels in cores collected from unmanipulated mussel reef areas between spring and fall 2001 at the three predator exclusion sites. The density of all mussels included live mussels, whole dead mussels (valves articulated), and one-half the number of single valves. Shells that were broken (characteristic of predation by crabs) or had drill holes (characteristic of predation by drilling whelks) were excluded from the count of all mussels. If small predators and dislodgment significantly impacted mussel density, then the density of all mussels (live and undamaged dead) would be expected to drop over the study period due to outright removal from the site by dislodgment and/or removal from our count due to shell damage.

Mussel size refuge.—Subtidal mussel populations can persist in areas of high predator abundance if individuals grow too large to be handled by their predators (Reusch and Chapman 1997). To examine whether mussels at our study system attained a refuge in size (Paine 1976), a survey of sea stars and their prey was conducted in November of 2001. At each of the three caging experiment sites (A, D, and J), >100 sea stars were measured to 0.5 cm, and of those feeding on mussels, prey mussel lengths were measured in situ to the nearest millimeter using vernier calipers. The size of mussels available as prey at each site was quantified by measuring the length of mussels collected within six replicate cores as in earlier mussel surveys. Since it was observed that sea star density was noticeably higher during the November foraging survey than in a

post-hypoxia survey in previous months, we quantified their densities at those sites in a supplementary survey using transects as described for “Predator surveys” (*Methods: Mussels at the community level*).

Mussels at the ecosystem level

The filtration rate of each reef was estimated by multiplying the reef area \times the average density of mussels \times the individual filtration rate. The individual filtration rate (volume of water completely cleared of particles per individual per unit of time) was derived from Vahl (1973) as a function of mussel soft-tissue dry biomass. Vahl (1973) was chosen because the function was developed over a range of biomass and temperature values applicable to our system. The average soft-tissue dry biomass was determined for mussels collected during fall 2001 at three sites (A, D, J), and an exponential relationship between length and biomass was established from those data to estimate biomass for the remaining sites and dates for which only length data were collected.

RESULTS

Oceanographic data

Dissolved oxygen (DO) concentrations remained relatively constant and high (>5 mg/L) at site J in the southern part of the study region during the summer of 2001, whereas periodic hypoxia occurred at site A in the northern part of the bay (Appendix A: Fig. A1). At site A, DO exhibited a biweekly sawtooth cycle dictated by the tidal regime (Bergondo et al. 2005) and was lowest in mid-July and mid-August (Appendix A: Fig. A1) when it reached hypoxic levels of 2.8 mg/L as defined by Diaz and Rosenberg (1995). Concentrations of DO reached their lowest point on 17 August, two days after the multisite survey. Concentrations of DO encountered by mussels were likely lower than those recorded by instruments (which were suspended 0.5–1 m above the bottom), due to respiratory depletion of oxygen at the reef–water column interface (Nixon et al. 1971, Jorgensen 1980, Asmus et al. 1994).

Temperature and salinity were less variable than DO during the summer 2001 period (Appendix A: Fig. A1). However, there was a slight increase in salinity and decrease in temperature coincident with periods of hypoxia, indicative of denser bottom water possibly associated with a stratified water column characteristic of hypoxic estuaries (Breitburg 1990, Lenihan and Peterson 1998, C. Deacutis, D. Murray, W. Prell, E. Saarman, L. Korhun, and G. Cicchetti, *unpublished manuscript*).

Individual mussel response to hypoxia

The mussel transplant experiment revealed the influence of hypoxia as a physiological stress on patterns of growth and size-specific mortality of *Mytilus edulis*. The average initial length of mussels that survived the

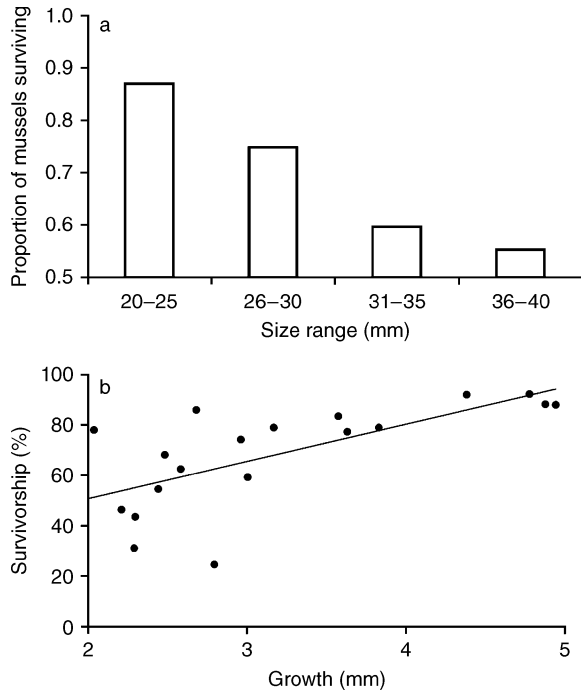


FIG. 2. Evidence for hypoxia affecting size structure of mussels through (a) mortality as a function of size and (b) growth rates. (a) Larger mussels had lower survivorship than smaller mussels when transplanted to hypoxic sites ($F_{1,11673} = 17.27$, $P < 0.0001$). Bars represent pooled data from all four experimental sites. (b) There was a correlation between survivorship and growth of mussels in the transplant experiment, suggesting a sublethal effect of reduced growth rates associated with hypoxic stress. Growth values are an average increase in length for all mussels alive at the end of experiment within a given replicated mesh bag, and survivorship values represent the proportion of mussels surviving in that same bag.

hypoxic period was shorter ($F_1 = 17.2662$, $P < 0.0001$) than those that perished (Fig. 2a). In addition to such direct effects on the size structure of the experimental population through selective mortality, sublethal effects of hypoxia led to reduced growth rates, with the effect of further decreasing the size structure of the mussel populations. Survivorship was correlated with the average growth of transplanted mussels pooled across sites ($P = 0.0006$, $R^2 = 0.49$; Fig. 2b).

Mussel populations

At the start of our study in spring 2001, nine extensive subtidal mussel reefs ≤ 27.6 ha in area were found to blanket portions of the subtidal zone in central Narragansett Bay with high percent cover ($\leq 99.7\%$) and density (≤ 9943 individuals per m^2) (Fig. 1). Reefs were conspicuously located around points where flow was likely accelerated, leading to increased flux of propagules and food (Hiscock 1983, Leonard et al. 1998). The length of mussels (mean \pm SE) ranged from 25.8 ± 0.2 mm (site J) to 42.7 ± 0.5 mm (site L). All distributions were unimodal, and mean size varied con-

tinuously within this range, suggesting that mussels from all sites were of the same cohort (Appendix B: Fig. B1). Differences among sites in mean size can be explained by site-specific growth rates (see mussel transplant experiment discussion in the following paragraphs). Only two of the nine sites (M and Q) showed an increase in mean length over the summer (Appendix B: Fig. B1).

Over the course of the summer, the percent cover and density of live mussels declined by more than an order of magnitude at some sites (Fig. 1). Mussels were completely eliminated at site G. There was a negative linear relationship between DO during the 15 August survey and reduction in both density ($P = 0.0081$, $R^2 = 0.88$) and percent cover ($P = 0.0470$, $R^2 = 0.58$) of live mussels (Fig. 3), suggesting that hypoxia played a primary role in the loss of mussels over the course of the summer. Reduction in mussel density was not correlated with salinity or temperature ($P = 0.9067$, $R^2 = 0.0036$ and $P = 0.1833$, $R^2 = 0.32$, respectively).

Individual populations of mussels showed idiosyncratic dynamics with regard to changes in density, extinction, and colonization (Fig. 1). Of the nine populations surveyed in spring 2001, one was extinct by fall 2001. Seven of the eight remaining populations had

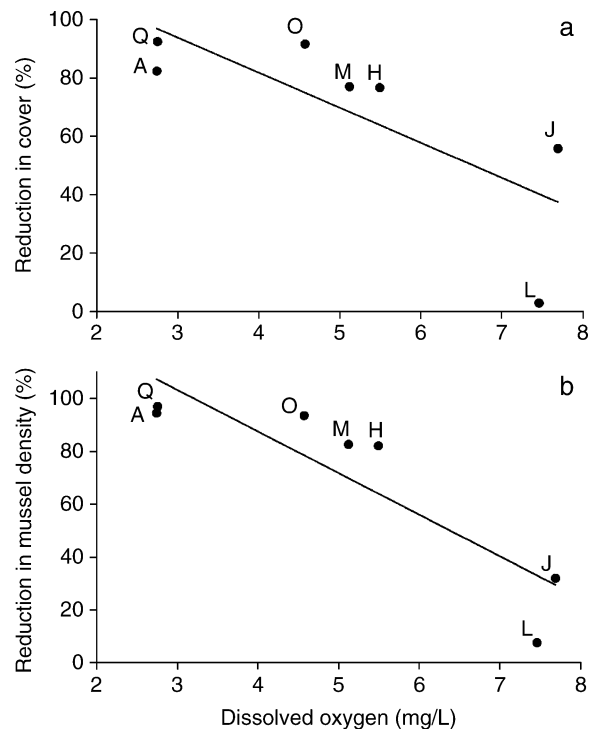


FIG. 3. The reduction in (a) percent cover and (b) density of live mussels between spring 2001 and fall 2001 was correlated with representative dissolved oxygen concentrations ($R^2 = 0.58$, $P = 0.0470$ and $R^2 = 0.88$, $P = 0.0081$, respectively) from seven sites (A, H, J, L, M, O, Q) spanning the hypoxia gradient. Oceanographic data were not available for mussel sites D and G.

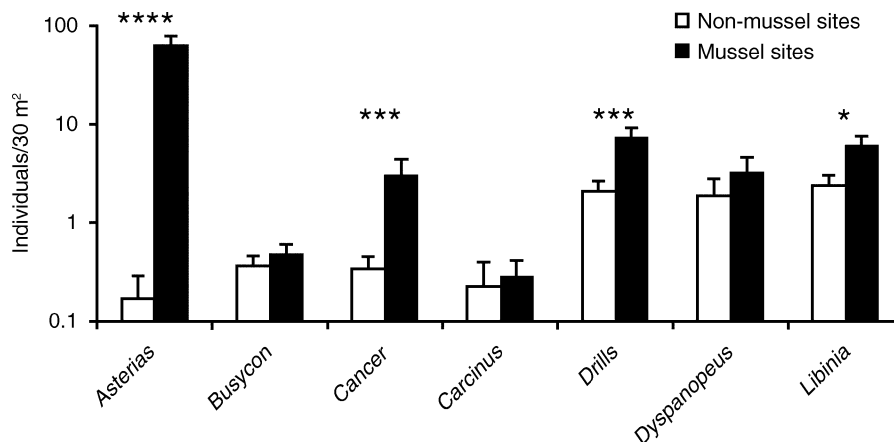


FIG. 4. Relative to non-mussel sites, predator densities at mussel sites in pre-hypoxia spring surveys were higher for four predator taxa (sea stars *Asterias forbesi*, rock crabs *Cancer irroratus*, spider crabs *Libinia emarginata*, and drills *Urosalpinx cinerea/Eupleura caudate*) and were similar for the remaining three predators (whelks *Busycon canaliculatus/carica*, green crabs *Carcinus maenas*, and mud crabs *Dyspanopeus sayi*), suggesting that mussels as a food resource had a bottom-up effect on the abundance and/or distribution of consumers. Note that the y-axis is log scale. For ANOVA, individual survey sites were nested within the factor of mussel presence/absence to account for the hierarchical nature of replicate transects within sites and replicated sites within the factor of mussel presence/absence. Predator densities for each transect were log-transformed [$\log_{10}(\text{density} + 1)$] to meet ANOVA assumptions of homogeneous variance.

been edged to extinction by fall 2002, and the previously extinct population (Site G) had been recolonized by larval recruitment (evident by size distribution and mean size shifted toward smaller animals, Appendix B: Fig. B1). The only mussel population to persist through the entire study period was at site L.

Mussels at the community level

Predator surveys.—Four of the seven predator taxa (sea stars, cancer crabs, spider crabs, and drills) were more abundant at mussel sites than at non-mussel sites in spring 2001 (Fig. 4, Appendix C: Table C1) suggesting that mussels enhanced local populations of predators through higher rates of recruitment and/or net immigration of adults. The abundance of the remaining three predator taxa did not differ between mussel sites and non-mussel sites.

Of all the predator taxa, sea stars showed the greatest difference in average abundance between mussel and non-mussel sites (greater than two orders of magnitude higher at mussel sites), and details of their populations provide additional evidence that mussels had a positive bottom-up effect (Menge 1992) on predator populations. Stars feeding at mussel sites fed only on mussels, while those at non-mussel sites fed on either slippersnails (*Crepidula* spp.) or barnacles (*Semibalanus/Balanus* spp.). The average radius of sea stars was greater at mussel sites than at non-mussel sites ($F_1 = 235.04$, $P < 0.0001$, Appendix D: Table D1), suggesting higher sea star growth rates fueled by mussels, as observed elsewhere in New England (Menge 1986, Witman et al. 2003).

Of the four predator taxa with higher densities at mussel than non-mussel sites, only sea star populations

declined between the spring and fall 2001 surveys, a decrease correlated with both the reduction in mussel density ($P = 0.04$, $R^2 = 0.26$) and dissolved oxygen ($P = 0.05$, $R^2 = 0.56$) (Fig. 5a and b, respectively). This suggests that food limitation, hypoxic stress, or both led to decreased sea star abundances at mussel sites. The rebound of sea star densities observed in November surveys due to emigration (evident by the large size of sea stars) suggests that hypoxic stress was the most likely explanation (Appendix E: Table E1).

Predator exclusion experiments.—The mean proportion of mussels alive ranged from 0.66 to 0.99 across all sites at the start of the experiment, and declined to less than 0.30 by the end of the experiment just six weeks later (Fig. 6). The predator exclusion experiment revealed that predators played a relatively unimportant role in the mussel decline, indicated by the overall drop in density of live mussels across treatments, and the site \times treatment interaction ($P = 0.03$, $F_4 = 2.93$), which represents inconsistent treatment (i.e., predator) effect across sites (Fig. 6).

Small predators and dislodgement.—As mussels died, their shells remained with negligible shell damage, indicating that neither predators nor dislodgement contributed significantly to the dramatic drop in the number of live mussels over the experimental period (Table 1). There was no difference ($P = 0.36$, $F_1 = 0.86$) in the total number of mussels (including both alive and dead, and excluding those few that were cracked or drilled by small predators) between the start and end of the experiment at any of the three sites.

Mussel size refuge.—At all three sites, the average size of mussels being consumed by sea stars did not differ from those available in the surrounding reef (P

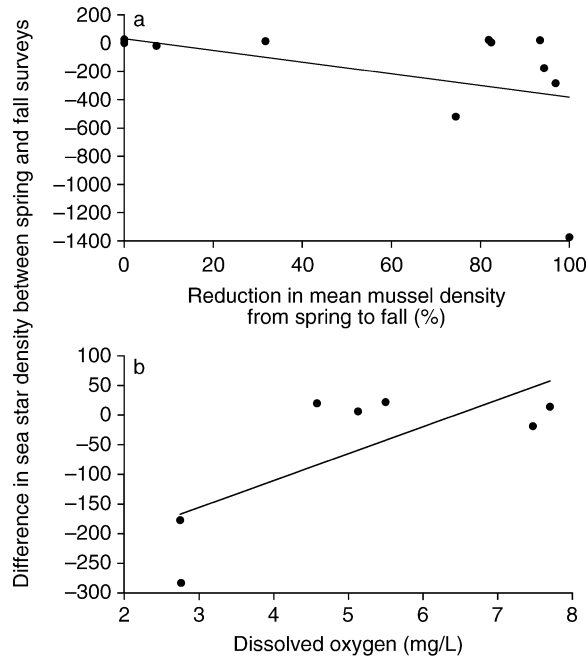


FIG. 5. A decline in sea star abundance between the fall and spring surveys was observed to be correlated with both (a) the change in mussel densities (food resource) associated with hypoxia ($R^2 = 0.30$, $P = 0.04$) and (b) representative DO concentrations from the hypoxia survey ($R^2 = 0.56$, $P = 0.05$). The latter is the more likely explanation, because density of sea stars was found to rebound following the fall survey (Appendix E).

$= 0.95$, $F_1 = 0.0048$), and the size range eaten coincided with the range of those available for a given site (Appendix F: Table F1). This result suggests that mussels in our study area did not have a refuge in size from

TABLE 1. Total number of mussels (sum of live mussels, articulated valves, and half the number of unarticulated valves) at the Narragansett Bay (Rhode Island, USA) study sites.

Site	No. mussels/m ² (mean \pm SE)	
	Before die-off	After die-off
A	14 107 \pm 1247	12 029 \pm 904
D	5203 \pm 1009	5899 \pm 1435
H	6153 \pm 480	4962 \pm 412

Note: The total number of mussels (live and dead) did not differ ($F_{1,27} = 0.86$, $P = 0.36$) before and after the hypoxic event at the three caging experiment sites, suggesting that the die-off was due to neither dislodgement nor predators, such as crabs and fish, that could have damaged or removed shells.

predation, nor were sea stars altering the size distribution of the mussel population, despite the potential for foraging patterns of individual sea stars to be influenced by mussel size (Campbell 1983).

Mussels at the ecosystem level

At their initial high densities, mussels had the potential to exert a strong influence on the plankton community through their enormous filtering capacity. Estimated filtration rates for individual reefs in our study ranged from 2.5 to 41.5×10^6 m³/d, representing an aggregate capacity of 134.6×10^6 m³/d (Table 2). At that rate, the mussel reefs could filter the equivalent of the entire volume of Narragansett Bay (2724.3×10^6 m³) 1.3 times during the average residence time of 26 days. The initial filtration capacity was reduced by >75% to 33.1×10^6 m³/d during the summer 2001 due to mass mortality of the mussels, and further to 24.0×10^6 m³/d one year later.

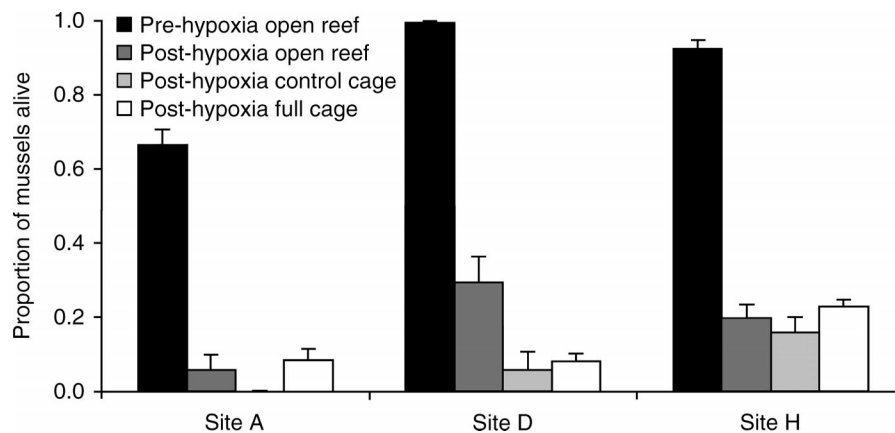


FIG. 6. There was a sharp decline in the proportion of live mussels through the summer in all experimental treatments. Predators had a negligible role in their demise over the hypoxic period; there was no consistent treatment effect across sites (site \times treatment interaction $F_{4,45} = 2.93$, $P = 0.03$). Caging treatments and site effects on the proportion of mussels alive were analyzed by a two-factor ANOVA including an interaction term to determine if the difference between experimental treatments varied between sites. Proportion values were arcsine-transformed to reduce heterogeneity of variances. The proportion of mussels alive (rather than the absolute density of live mussels) was used as a more conservative response variable since the density of mussels was known to vary among sites at the outset of the experiment and could have erroneously led to a site \times treatment interaction. Error bars represent SE.

TABLE 2. Estimated filtering capacity of mussel reefs at Narragansett Bay study sites.

Site	Reef area (ha)	Filtration rate (millions of m ³ /d)		
		Spring 2001	Fall 2001	Fall 2002
A	27.6	41.5	2.5	0
D	8.7	13.4	3.1	0
G	14.5	11.6	0	17.4
H	5.9	7.9	1.4	0
J	11.2	2.5	1.8	0
L	17.4	24.5	22.0	6.6
M	3.6	5.8	1.2	0
O	2.0	2.9	0.2	0
Q	11.1	24.4	0.9	0
Total	102.0	134.6	33.1	24.0

Notes: Mussel reef filtering capacity decreased by >80%, with the greatest loss occurring during the hypoxic summer of 2001. Locations of reefs, and densities and percent cover of mussels within each reef, are presented in Fig. 1.

DISCUSSION

Mussel function as a foundation species

Our initial surveys revealed that mussels in Narragansett Bay functioned as a foundation species (sensu Dayton 1972) in several ways. First, mussels formed large discrete reefs with areas >27 hectares, mean densities of 9900/m², and 100% cover of the bottom, and thus were a significant feature in the benthos.

Second, the reefs of suspension-feeding mussels coupled the benthic–pelagic systems with an estimated aggregate filtration rate $>1.3 \times 10^8$ m³/d, which was equivalent to filtering the entire volume of Narragansett Bay 1.3 times during the average flushing time of 26 days (Pilson 1985). That capacity for benthic–pelagic coupling was likely enhanced by the effects of the reef structure on boundary layer flow and delivery of particulates to the bottom (Frechette et al. 1989). The high conversion rate of pelagic resources to benthic biomass by mussels generates a level of productivity that can rival that of tropical rain forests (Leigh et al. 1987). Mussels can represent >80% of the benthic soft-tissue biomass in the Narragansett Bay (Nixon et al. 1971).

Third, mussels served as a prey resource that had an influence on the subtidal food webs, consistent with bottom-up forcing (Menge 1992). Sea stars (*Asterias forbesi*), spider crabs (*Libinia emarginata*), rock crabs (*Cancer irroratus*), and drills (*Urosalpinx cinerea/Eupleura caudata*) were more abundant at mussel sites than non-mussel sites, with sea stars exhibiting a difference in density of over two orders of magnitude (Fig. 4). Such an “aggregative response” (Hassell and May 1974) is predicted for *A. forbesi* since their movement rate is inversely correlated with the density of mussels, leading to retention of sea stars within mussel reefs (Campbell 1983), and may have led to higher densities of the other predator species as well. Moreover, the body size of *A. forbesi* was greater at mussel sites than non-mussel sites (Appendix D: Table D1), which has the potential to lead to higher reproductive output and

subsequent recruitment, as observed at sites with high mussel availability in the nearby Gulf of Maine (Menge 1986, Witman et al. 2003).

Fourth, mussel reefs are known to increase the diversity and abundance of infauna by providing refuge from predation (Witman 1985) and abiotic stress (Suchanek 1986). Although our surveys did not address this common function directly, a companion study (Lindsey et al. 2006) in the same system found that the structure of mussel reefs led to higher abundance of an infaunal crab species.

Impact of hypoxia on mussels

The most striking effect of hypoxia detected by our study was the bay-wide die-off of mussels (Fig. 1), evident by the correlation between the reduction in mussel densities and DO concentrations (Fig. 3b). At the most severely affected sites, the density of mussels dropped by over an order of magnitude and led to local extinction at site G. The concomitant drop in percent cover of live mussels indicates the magnitude of decline in the mussel reef structure. Although we did not sample frequently enough to elucidate the exact timing of mussel mortality, both our in situ observations and the DO record (Appendix A: Fig. A1) indicate that mussel mortality occurred during a 10-d period in mid-August. The low tolerance of mussels to hypoxic conditions is sufficient to explain mussel mortality during that period. For example, subtidal mussels from Narragansett Bay experienced 80% mortality after 36 h in laboratory conditions of 0.5 mg/L of O₂ and 22°C (typical summer temperature) (A. Altieri, unpublished data).

Our mussel transplant experiment, conducted to examine individual level response to hypoxia, revealed higher mortality rates among larger mussels and overall reduced growth rates. Size-dependent oxygen uptake and reduced growth are typical effects of hypoxia detected by aquatic organisms exposed to hypoxia in laboratory conditions (Wu 2002), and the former is predicted by the positive correlation between oxygen demand and body size among *M. edulis* (Vahl 1973). Reduced mussel growth due to hypoxia has not been detected prior to our study. This probably results from a reduction in feeding rates, which are negatively correlated with concentrations of dissolved oxygen in laboratory conditions (Wang and Widdows 1993).

We addressed a number of alternative hypotheses for the mussel mortality, an aspect often overlooked in studies of hypoxia due to the overwhelming impacts associated with the stress and/or lack of adequate a priori data. Predation and dislodgment are the two most common factors in the rapid destruction of mussel reefs (see review by Seed and Suchanek 1992), however neither appeared to be a significant factor during our study. The loss of live mussels from our sites was accounted for by an increase in the density of shells of dead mussels (Table 1), indicating that mussels died in place rather than being swept away. Likewise, results from

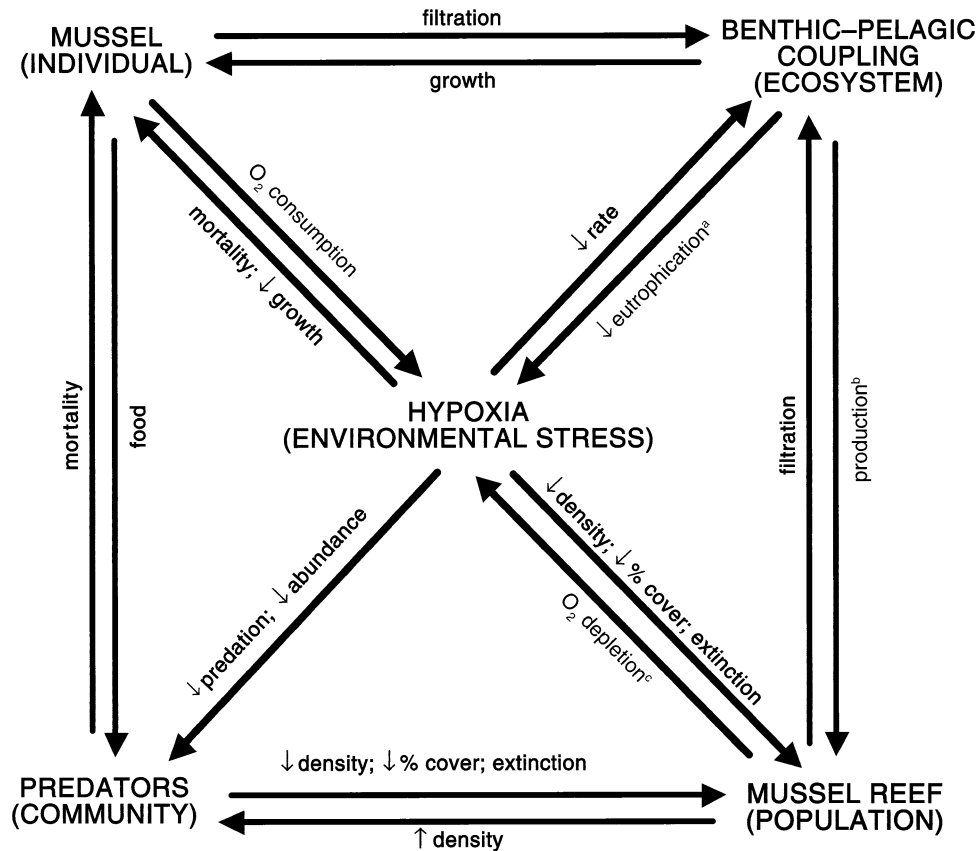


FIG. 7. A conceptual model that predicts the way in which changes at one level of organization can have consequences at other levels, often mediated by dissolved oxygen conditions. Hypoxia is at the hub to emphasize the central role it plays in this perspective. Major levels of ecological organization are at the corners, and pathways of interactions are indicated by the large arrows. Mechanisms by which levels of organization interact with one another directly, or indirectly via hypoxia, are indicated with text along those arrows. Small arrows immediately preceding text indicate whether the mechanism is one of increase (up arrow) or decrease (down arrow). Boldface type indicates relationships quantified in this study. Superscript letters indicate references: a, Ulanowicz and Tuttle (1992), Jackson et al. (2001), and Baird et al. (2004); b, Nixon et al. (1971) and Leigh et al. (1987); c, Nixon et al. (1971), Asmus et al. (1994), and Jackson et al. (2001).

the predator exclusion suggest that predation was not a significant factor in mussel mortality over the six-week period spanning the massive die-off (Fig. 6). It is possible that predators had an effect on mussel populations in the caging experiment that was masked by subsequent hypoxia-induced mortality, but that sequence of events seems unlikely, as the densities of mussels changed least at sites L and J, where DO remained high and predator abundance was similar to other mussel sites. Salinity and temperature appear to have been insignificant factors from the lack of correlation between either factor and mussel mortality, and their narrow range over the study area (salinity 28.6–31.0 ppt; temperature 19.2–22.2°C).

*Significance of hypoxia on mussels:
an integrated perspective*

Hypoxia had a dramatic effect on the mussels of our system, but the broader significance of the event can be discerned only by integrating across levels of eco-

logical organization, as suggested in general terms by Werner (1998) and Lawton (2000) and alluded to in reviews on hypoxia (Diaz and Rosenberg 1995, Rabalais et al. 2002, Wu 2002). We highlight some of the dominant conclusions that emerge from the integrative perspective in this section and summarize those relationships and others in a conceptual model (Fig. 7).

Effects of hypoxia through reduced growth and mortality of individual mussels had implications for the ecosystem level function of water column filtration and benthic–pelagic coupling. Decreased growth indicates that hypoxia suppressed productivity of mussels and inhibited energy transfer from the water column to the benthos at the individual level, as is expected by the negative correlation between DO concentration and feeding rate in *Mytilus edulis* (Wang and Widdows 1993). The overall result at the population level was that seven of the nine reefs (all but M and Q) showed no increase in average size over the hypoxic summer (Appendix B: Fig. B1), despite the expectation for

growth rates to be highest in summer when metabolism peaks with warm temperatures and food is most available (Kautsky 1982).

Moreover, the capacity for benthic–pelagic coupling was reduced at the population/reef level due to mortality of individuals (Table 2). The magnitude of the loss of potential productivity is indicated by the estimated combined filtration rate, which declined by >75% over the hypoxic period. Despite the long-term loss in benthic–pelagic coupling, the mussel die-off represented a short-term increase in the flux of energy to benthic microbial decomposers and facultative scavengers, as commonly occurs following mass mortality events (Britton and Morton 1994). Dead mussels still containing soft tissue represented <0.1% area cover in visual surveys conducted within weeks of the mussel mortality (A. Altieri, *unpublished data*), indicating a rapid transfer of resources into the benthic food web.

Hypoxia also affected community level trophic interactions as detected at the population level of mussel prey and predatory sea stars. Sea stars showed a decline in abundance between the spring and fall 2001 surveys that can be explained by either the direct effects of hypoxia (Fig. 5b), and/or the indirect effects of hypoxia via large decreases in mussel food sources (Fig. 5a). The former is most likely since sea star densities at the three sites resurveyed two to three months following the fall 2001 survey rebounded to levels similar to or higher than the spring 2001 survey (Appendix E: Table E1). Likewise, Pihl and colleagues (1992) observed that fish and crustacean predators returned to feed on remaining prey, whereas predators apparently failed to return to oyster reefs lacking prey in Pamlico Sound following hypoxia (Lenihan et al. 2001).

A model of stress return time by Witman and Dayton (2001) predicts predation as a function of predator mobility and the return time of the limiting stress. Our results indicate the return time for sea stars is on the order of several months, which is adequate to exploit the remaining mussel prey in the time between hypoxic summers, although even their temporary absence represents lost opportunities for energy transfer from mussels to predator. Sea stars may have recolonized from adjacent depths where hypoxia was not as severe (C. Deacutis, D. Murray, W. Prell, E. Saarman, L. Korhun, and G. Cicchetti, *unpublished manuscript*). A decline in density of other predators (i.e., crabs and drills) following the hypoxic period was not detected by our surveys, despite the tendency for predators in our system, such as spider crabs (Pavela et al. 1978) and green crabs (Taylor and Butler 1973), to flee from hypoxic areas. The densities of those highly mobile species may have declined in response to hypoxia as sea stars did, followed by rapid immigration to exploit mussel prey before our fall 2001 surveys.

The exclusion of sea stars from hypoxic areas suggests that hypoxia provided a refuge from predation as predicted by the Consumer Stress Model (Menge and

Sutherland 1976, 1987, Menge and Olson 1990) similarly to other physiological stresses such as aerial exposure (Robles 1987), temperature (Sanford 1999), and salinity (Witman and Grange 1998). For those predators that remained, it is likely that lethargy and “clumsiness” associated with hypoxia decreased predation rates as has been observed for species in our system, including green crabs (Brante and Hughes 2001) and *Asterias forbesi* (Nystrom 2004) feeding on *Mytilus edulis*. Periodic emigration of mobile consumers from hypoxic areas in other systems provides further evidence that hypoxia could provide a refuge in benthic systems (Pihl et al. 1991, Breitburg 1992, Lenihan et al. 2001). Although hypoxic stress outweighed the potential benefits of a refuge from predation for *M. edulis*, we predict a net benefit in hypoxic areas for prey species in the system such as soft-shell (*Mya arenaria*) and quahog clams (*Mercenaria mercenaria*), which have tolerances three and nine times greater, respectively, than *Mytilus edulis* (A. Altieri and D. Warren, *unpublished data*).

Hypoxia may have also affected the foraging behavior of predators indirectly by affecting the size distribution of prey through reduced growth and greater mortality of larger mussels. Smaller mussels may have increased the proportion of the prey population available to size-limited predators in our system, such as small sea stars (Campbell 1983) and green crabs (Elner 1978), and led to suboptimal foraging by selective predators such green crabs (Elner and Hughes 1978).

The additive effects of hypoxic stress and subsequent predation on mussel reefs led to the local extinction of mussel populations. In the fall 2001 survey following hypoxia, one of the nine populations was extinct, and the density of several other populations was reduced by over an order of magnitude (Fig. 1). One year later, seven of the eight remaining populations had been edged to extinction, and the previously extinct population at site G had been recolonized (Fig. 1), apparently by larval recruitment due to the small mean size of mussels (Appendix B, Fig. B1). Only the population at site L, where both hypoxic stress remained low and initial recruitment was high, persisted through the study period as predicted by the Consumer Stress Model (Menge and Sutherland 1976, 1987, Menge and Olson 1990), though it too was in decline, likely due to attrition from predation and lack of continued recruitment. Most studies to date have treated a species occurrence within hypoxic areas as a single demographic population, yet our study revealed that spatially discrete populations behaved idiosyncratically with respect to extinction and recolonization, suggesting that insights on hypoxia could be gained by adopting a metapopulation perspective (Levins 1969). Such a spatially explicit approach has been called for in a recent review by Breitburg (2002) to better predict the impact of hypoxia on coastal systems, particularly fish populations and dependent fisheries.

Conceptual model

By consuming phytoplankton, suspension feeders have the potential to control eutrophication, which fuels the development of hypoxia (Officer et al. 1982). Therefore, the decreased function (benthic–pelagic coupling and filtration) and outright loss of mussels in Narragansett Bay could lead to an increased prevalence of hypoxia and further mortality of suspension feeders through a positive feedback loop. Such a cycle has been sparked in estuaries of the southeastern United States by the functional extinction of oysters (*Crassostrea virginica*), which in turn has contributed to hypoxia and the failure of oysters to return (Ulanowicz and Tuttle 1992, Lenihan and Peterson 1998, Jackson et al. 2001, Baird et al. 2004).

The pathways generating this cycle, and the consequences for the system, emerge in a conceptual model by integrating the effects of hypoxia across levels of organization from the individual to the ecosystem (Fig. 7). It becomes clear that predicting the effects of change within components (e.g., increases in prevalence of hypoxic stress) and the significance of interaction among components (e.g., predator and mussel prey) requires consideration of responses in the other components. Moreover, the model is useful in generating novel hypotheses. For example, mussel reefs can exacerbate hypoxia by depleting O₂ levels, which in turn can decrease predation rates of consumers, including sea stars.

Conclusions

Reef-forming suspension feeders are both an indicator and linchpin of coastal areas threatened by hypoxia. The observed loss of the foundation species *Mytilus edulis* from a hypoxic estuary gained new significance by integrating across individual, population, community, and ecosystem levels of ecological organization. For example, both individual level growth rates and size-specific mortality, and population level declines in density, had implications for the ecosystem level function of benthic–pelagic coupling. The approach reveals the connectedness of the system summarized in our conceptual model, and the emergent relationships allow for generalizations to other systems and new predictions for further study. The basis for a predictive approach to studies of hypoxia was further strengthened by the response of predator–prey relationships to hypoxia as predicted by environmental stress models. While a perspective that crosses levels of organization can, and should be, explicitly applied to any ecological investigation, in this study it proved especially fruitful in the context of a foundation species and environmental stress.

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LITERATURE CITED

- Andersson, L., and L. Rydberg. 1988. Trends in nutrient and oxygen conditions within the Kattegat: effects of local nutrient supply. *Estuarine Coastal and Shelf Science* **26**:559–579.
- Asmus, R., H. Asmus, A. Wille, G. F. Zubillaga, and K. Reise. 1994. Complementary oxygen and nutrient fluxes in seagrass beds and mussel banks? Pages 227–237 in K. R. Dyer and R. J. Orth, editors. *Changes and fluxes in estuaries: implications from science to management*. Olsen and Olsen, Fredensborg, Denmark.
- Baird, D., R. R. Christian, C. H. Peterson, and G. A. Johnson. 2004. Consequences of hypoxia on estuarine ecosystem function: energy diversion from consumers to microbes. *Ecological Applications* **14**:805–822.
- Basta, D. J., M. A. Warren, and T. R. Goodspeed. 1990. Estuaries of the United States: vital statistics of a national resource base. National Oceanographic and Atmospheric Administration, Rockville, Maryland, USA.
- Bergondo, D., D. R. Kester, H. E. Stoffel, and W. L. Woods. 2005. Time series observations during the low sub-surface oxygen events in Narragansett Bay during summer 2001. *Marine Chemistry* **97**:90–103.
- Blumberg, A. F., and D. M. Ditoro. 1990. Effects of climate warming on dissolved-oxygen concentrations in Lake Erie. *Transactions of the American Fisheries Society* **119**:210–223.
- Brante, A., and R. N. Hughes. 2001. Effect of hypoxia on the prey-handling behaviour of *Carcinus maenas* feeding on *Mytilus edulis*. *Marine Ecology-Progress Series* **209**:301–305.
- Breitburg, D. L. 1990. Near-shore hypoxia in the Chesapeake Bay: patterns and relationships among physical factors. *Estuarine Coastal and Shelf Science* **30**:593–609.
- Breitburg, D. L. 1992. Episodic hypoxia in Chesapeake Bay: interacting effects of recruitment, behavior, and physical disturbance. *Ecological Monographs* **62**:525–546.
- Breitburg, D. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries* **25**:767–781.
- Britton, J. C., and B. Morton. 1994. Marine carrion and scavengers. *Oceanography and Marine Biology: an Annual Review* **32**:369–434.
- Campbell, D. B. 1983. Determination of the foraging strategy of *Asterias forbesi* (Echinodermata: Asteroidea). Dissertation. University of Rhode Island, Kingston, Rhode Island, USA.
- Carpenter, S. R., and J. F. Kitchell. 1988. Consumer control of lake productivity. *Bioscience* **38**:764–769.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**:351–389.
- Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichment to the benthos of McMurdo Sound, Antarctica. Pages 81–95 in

- B. C. Parker, editor. Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press, Lawrence, Kansas, USA.
- Desbonnet, A., and V. Lee. 1991. Water quality and fisheries Narragansett Bay. Rhode Island Sea Grant, Narragansett, Rhode Island, USA.
- Diaz, R. J., and R. Rosenberg. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Pages 245–303 in *Oceanography and Marine Biology—an Annual Review*. Volume 33.
- Elnor, R. W. 1978. The mechanics of predation by the shore crab, *Carcinus maenas* (L.), on the edible mussel, *Mytilus edulis* (L.). *Oecologia* **36**:333–344.
- Elnor, R. W., and R. N. Hughes. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. *The Journal of Animal Ecology* **47**:103–116.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**:473–476.
- Frechette, M., C. A. Butman, and W. R. Geyer. 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. *Limnology and Oceanography* **34**:19–36.
- Grantham, B. A., F. Chan, K. J. Nielsen, D. S. Fox, J. A. Barth, A. Huyer, J. Lubchenco, and B. A. Menge. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* **429**:749–754.
- Hassell, M. P., and R. M. May. 1974. Aggregations of predators and insect parasites and its effect on stability. *Journal of Animal Ecology* **43**:567–594.
- Helmuth, B. 2002. How do we measure the environment? Linking intertidal thermal physiology and ecology through biophysics. *Integrative and Comparative Biology* **42**:837–845.
- Hiscock, K. 1983. Water movement. Pages 58–96 in R. Earll and D. G. Erwin, editors. *Sublittoral ecology*. Clarendon Press, Oxford, UK.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**:629–638.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**:1946–1957.
- Jorgensen, B. B. 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effects on the benthic community. *Oikos* **34**:68–76.
- Justic, D., N. N. Rabalais, R. E. Turner, and W. J. Wiseman. 1993. Seasonal coupling between riverborne nutrients, net productivity and hypoxia. *Marine Pollution Bulletin* **26**:184–189.
- Kareiva, P. M., J. G. Kingsolver, and R. B. Huey, editors. 1993. *Biotic interaction and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Kautsky, N. 1982. Growth and size structure in a Baltic *Mytilus edulis* population. *Marine Biology* **68**:117–133.
- Lawton, J. H. 2000. *Community ecology in a changing world*. Ecology Institute, Oldendorf/Luhe, Germany.
- Leigh, E. G., R. T. Paine, J. F. Quinn, and T. H. Suchanek. 1987. Wave energy intertidal productivity. Proceedings of the National Academy of Sciences of the United States of America **84**:1314–1318.
- Lenihan, H. S., and C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecological Applications* **8**:128–140.
- Lenihan, H. S., C. H. Peterson, J. E. Byers, J. H. Grabowski, G. W. Thayer, and D. R. Colby. 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. *Ecological Applications* **11**:764–782.
- Leonard, G. H., J. M. Levine, P. R. Schmidt, and M. D. Bertness. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* **79**:1395–1411.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**:237–240.
- Lindsey, E. L., A. H. Altieri, and J. D. Witman. 2006. Influence of biogenic habitat on the recruitment and distribution of a subtidal xanthid crab. *Marine Ecology Progress Series*, in press.
- Menge, B. A. 1986. A preliminary study of the reproductive ecology of the seastars *Asterias vulgaris* and *A. forbesi* in New England. *Bulletin of Marine Science* **39**:467–476.
- Menge, B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores. *Ecology* **73**:755–765.
- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* **5**:52–57.
- Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* **110**:351–369.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* **130**:730–757.
- Nixon, S. W. 1997. Prehistoric nutrient inputs and productivity in Narragansett Bay. *Estuaries* **20**:253–261.
- Nixon, S. W., C. A. Oviatt, C. Rogers, and K. Taylor. 1971. Mass and metabolism of a mussel bed. *Oecologia* **8**:21–30.
- Nystrom, M. 2004. The impact of hypoxia on the mortality, sublethal behavior, and predator-prey interaction of *Mytilus edulis* and *Asterias forbesi*. University of Rhode Island, Kingston, Rhode Island, USA.
- Officer, C. B., T. J. Smayda, and R. Mann. 1982. Benthic filter feeding: a natural eutrophication control. *Marine Ecology Progress Series* **9**:203–210.
- Oviatt, C., S. Olsen, M. Andrews, J. Collie, T. Lynch, and K. Raposa. 2003. A century of fishing and fish fluctuations in Narragansett Bay. *Reviews in Fisheries Science* **11**:221–242.
- Paine, R. T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* **57**:858–873.
- Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* **51**:145–178.
- Pavela, J. S., J. L. Ross, and M. E. Chittenden, Jr. 1978. Sharp reductions in abundances of fishes and benthic macroinvertebrates in the Gulf of Mexico off Texas associated with hypoxia. *Northeast Gulf Science* **6**:167–173.
- Petratis, P. S. 1995. The role of growth in maintaining spatial dominance by mussels (*Mytilus edulis*). *Ecology* **76**:1337–1346.
- Pihl, L., S. P. Baden, and R. J. Diaz. 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Marine Biology* **108**:349–360.
- Pihl, L., S. P. Baden, R. J. Diaz, and L. C. Schaffner. 1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and crustacea. *Marine Biology* **112**:349–361.
- Pilson, M. E. Q. 1985. On the residence time of water in Narragansett Bay. *Estuaries* **8**:2–14.
- Rabalais, N. N., R. E. Turner, and W. J. Wiseman. 2002. Gulf of Mexico hypoxia, aka “the dead zone”. *Annual Review of Ecology and Systematics* **33**:235–263.

- Reusch, T. B. H., and A. R. O. Chapman. 1997. Persistence and space occupancy by subtidal blue mussel patches. *Ecological Monographs* **67**:65–87.
- Robles, C. 1987. Predator foraging characteristics and prey population structure on a sheltered shore. *Ecology* **68**:1502–1514.
- Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* **283**:2095–2097.
- Seed, R., and T. H. Suchanek. 1992. Population and community ecology of *Mytilus*. Pages 87–169 in E. Gosling, editor. *The mussel *Mytilus edulis*: ecology, physiology, genetics and culture*. Elsevier, Amsterdam, The Netherlands.
- Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences of the United States of America* **99**:10500–10505.
- Suchanek, T. H. 1986. Mussels and their role in structuring rocky shore communities. Pages 70–96 in P. G. Moore and R. Seed, editors. *The ecology of rocky coasts*. Columbia University Press, New York, New York, USA.
- Taylor, E. W., and P. J. Butler. 1973. The behaviour and physiological responses of the shore crab *Carcinus maenas* during changes in environmental oxygen tension. *Netherlands Journal of Sea Research* **7**:496–505.
- Tomanek, L., and B. Helmuth. 2002. Physiological ecology of rocky intertidal organisms: a synergy of concepts. *Integrative and Comparative Biology* **42**:771–775.
- Turner, R. E., and N. N. Rabalais. 1994. Coastal eutrophication near the Mississippi river delta. *Nature* **368**:619–621.
- Ulanowicz, R. E., and J. H. Tuttle. 1992. The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. *Estuaries* **15**:298–306.
- UNEP. 2004. *Global Environmental Outlook (GEO) Year Book 2003*. United Nations Environment Programme (UNEP), Nairobi, Kenya.
- Vahl, O. 1973. Pumping and oxygen consumption rates of *Mytilus edulis* L. of different sizes. *Ophelia* **12**:45–52.
- Van Der Zwaan, G. J., and F. J. Jorissen. 1991. Biofacial patterns in river-induced shelf anoxia. Pages 65–82 in R. V. T. and T. H. Pearson, editors. *Modern and ancient continental shelf anoxia*. The Geological Society, London, UK.
- Vitousek, P. M. 1994. Beyond global warming: ecology and global change. *Ecology* **75**:1861–1876.
- Wang, W. X., and J. Widdows. 1993. Metabolic responses of the common mussel *Mytilus edulis* to hypoxia and anoxia. *Marine Ecology Progress Series* **95**:205–214.
- Werner, E. E. 1998. Ecological experiments and a research program in community ecology. Pages 3–26 in W. J. J. Resatarits and J. Bernardo, editors. *Experimental ecology: issues and perspectives*. Oxford University Press, Oxford, UK.
- Witman, J. D. 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. *Ecological Monographs* **55**:421–445.
- Witman, J. D., and P. K. Dayton. 2001. Rocky subtidal communities. Pages 339–366 in M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. *Marine community ecology*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Witman, J. D., S. J. Genovese, J. F. Bruno, J. W. McLaughlin, and B. I. Pavlin. 2003. Massive prey recruitment and the control of rocky subtidal communities on large spatial scales. *Ecological Monographs* **73**:441–462.
- Witman, J. D., and K. R. Grange. 1998. Links between rain, salinity, and predation in a rocky subtidal community. *Ecology* **79**:2429–2447.
- Wu, R. S. S. 2002. Hypoxia: from molecular responses to ecosystem responses. *Marine Pollution Bulletin* **45**:35–45.

APPENDIX A

Figures of trends in dissolved oxygen, temperature, and salinity data at two sites representing extremes in hypoxia conditions in the study area (*Ecological Archives* E087-042-A1).

APPENDIX B

Size frequency histograms of mussels for each survey site and period (*Ecological Archives* E087-042-A2).

APPENDIX C

A table of ANOVA comparing densities of predators at mussel and non-mussel sites (*Ecological Archives* E087-042-A3).

APPENDIX D

A table of sea star sizes at mussel and non-mussel sites (*Ecological Archives* E087-042-A4).

APPENDIX E

A table of sea star densities and sizes before and after hypoxia (*Ecological Archives* E087-042-A5).

APPENDIX F

A table of sizes of mussels eaten by, and available to, sea stars (*Ecological Archives* E087-042-A6).