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Trophic interactions under stress: hypoxia enhances foraging in an estuarine food web

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ABSTRACT: Ecosystem-level effects of stressors are critical to understanding community regulation, and environmental stress models are useful in describing such effects. Hypoxia is an important stressor in aquatic ecosystems that usually decreases abundance and biomass of benthic fauna. In field surveys, predator abundance is low in hypoxic areas, and in lab experiments, predators reduce their feeding rates under hypoxic conditions, leading to the hypothesis that consumer stress models (CSMs), rather than prey stress models (PSMs), apply to the systems. We tested predictions from these models with manipulative field experiments wherein we varied predator access to marked *Macoma balthica* clams at deep and shallow sites in the York River, Chesapeake Bay, before (June) and during (August) hypoxic episodes. In June, dissolved oxygen in deep and shallow sites was normoxic (>2 mg l^{-1}) for most of the experiment. In August, the shallow zone remained normoxic, while the deep zone experienced several hypoxic episodes. During hypoxia, predation rates in hypoxic sites were more than twice those in normoxic sites, whereas mortality due to physical stress did not differ between time periods or depths. Ambient clam densities were lower at the deep sites than at the shallow sites, and in August than in June. We conclude that hypoxia increased the susceptibility of benthic prey to predation, enhancing infaunal secondary production available to predators, but concurrently reducing the resilience of the benthic community. These findings are inconsistent with the predictions of CSMs, indicating that PSMs better describe this system.

KEY WORDS: Environmental stress models · Food web · Hypoxia · Predation · Predator–prey · *Macoma balthica*

INTRODUCTION

Predation and hypoxia

Environmental stress is a major determinant of community structure (e.g. Menge & Sutherland 1987). Species respond differently to the same stressor, such that an increase in the magnitude of a stressor is expected to shift the outcome of interactions between species to favor the one with greater tolerance. This expectation has been expressed in consumer stress models (CSMs), conceptual models which predict that a stressor will reduce predation when consumers are less tolerant of a stressor than their prey (Menge & Sutherland 1987). Alternatively, prey stress models (PSMs) predict that a stressor will increase predation when consumers are more tolerant of, or resilient to, the stressor than their prey (Menge & Olson 1990).

Anthropogenic eutrophication of estuaries has had widespread effects on these ecosystems (Kemp et al. 2005), including development of hypoxic, or oxygen-depleted, bottom waters (Diaz & Rosenberg 1995). Hypoxia (here defined as dissolved oxygen [DO] concentrations <2 mg l^{-1}) is an important stressor of benthic communities, and its effects are well documented in many systems (e.g. Diaz et al. 1992, Powers et al. 2005). Typically, abundance, biomass, recruitment, and diversity decrease, and there is a shift from large,

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long-lived species to small, opportunistic species. The magnitude of these effects generally increases with the severity of hypoxic stress.

Hypoxia has a multitude of non-lethal effects. Metabolism, and thus oxygen demand, decreases (Wu 2002), reducing growth and reproductive output (e.g. Grove & Breitburg 2005, Long 2007). Infaunal organisms migrate vertically in the sediment, stretching their siphons or palps above the benthic boundary layer into higher DO concentrations, and they may expose themselves on the surface or float in the water column (Brafield 1963, Rosenberg et al. 1991, Taylor & Eggleston 2000, Seitz et al. 2003). Almost all species decrease oxygen demand by decreasing activity and feeding rates (Sagasti et al. 2001).

These effects, especially the behavioral responses, potentially increase the availability of benthic fauna to their predators. The closer proximity of infaunal prey to the sediment surface and extension of siphons and palps decrease predator searching time. However, the responses of predators to hypoxia may jeopardize their ability to take advantage of stressed prey. Many predators in these systems are highly mobile, and have a much lower tolerance for hypoxia than do sessile prey (Das & Stickle 1993, Seitz et al. 2003). Field studies on predator abundance show a migration of motile predators out of hypoxic areas, often followed by a reinvasion shortly after hypoxia abates (Pihl et al. 1991, Das & Stickle 1994, Bell & Eggleston 2005, Powers et al. 2005). Almost universally, laboratory experiments show a decrease in predation rate under hypoxic conditions (Breitburg et al. 1994, Breitburg et al. 1997, Sagasti et al. 2001, Seitz et al. 2003), mostly due to a decrease in predator activity.

Either CSMs or PSMs could apply to hypoxic systems. Some authors (Sagasti et al. 2001, Powers et al. 2005) argue that, because the predators have lower tolerances for hypoxia than their prey and avoid hypoxic zones, hypoxia is likely to act as a refuge for prey species, as predicted by CSMs. Others suggest that PSMs are more appropriate and that predators consume prey stressed by hypoxia, either during a hypoxic episode (Rahel & Nutzman 1994) or immediately afterwards, before the prey have time to recover (Nestlerode & Diaz 1998). Foraging can occur during hypoxia; fish in a freshwater lake foraged in hypoxic waters (Rahel & Nutzman 1994), and predation on tethered polychaetes in the York River, Chesapeake Bay (USA), occurred at low levels during hypoxia (Nestlerode & Diaz 1998). Gut contents of predators in the York River shifted to include larger and deeper-burrowing prey items after hypoxic events (Pihl et al. 1992). These studies suggest that PSMs are appropriate, but the studies did not quantify the rate of predation, so they could not distinguish between PSMs and CSMs. To date, the only field study to definitively support CSMs was a caging study in Narragansett Bay, Rhode Island (USA) showing that mussels suffered no predation during hypoxia (Altieri & Witman 2006).

Study organisms

The thin-shelled clam *Macoma balthica* was the experimental prey species. *M. balthica* is a deposit and facultative suspension feeder that is the biomass-dominant macrofaunal species in mud habitats of Chesapeake Bay, comprising over 85% of the biomass in some habitats (Holland et al. 1977). Its shell length is typically <40 mm, and it contributes greatly to energy flow and benthic–pelagic coupling (Baird & Ulanowicz 1989). *M. balthica* is tolerant of hypoxia, with an LT (lethal time) 50% of 15 d under near-anoxic conditions (Henriksson 1969). In response to hypoxia, *M. balthica* extends its siphons into the water column to reach normoxic waters within 24 h (Seitz et al. 2003) and migrates upward in the sediment within 72 h (Brafield 1963, Long et al. 2008). As *M. balthica* avoids predation by burying down to 40 cm in the sediment (Hines & Comtois 1985), a decrease in burial depth with hypoxia is likely to make this species more vulnerable to predation (Clark et al. 1999a,b, De Goeij et al. 2001, Seitz et al. 2001).

Predators of *Macoma balthica* in the York River include the blue crab *Callinectes sapidus* (Seitz et al. 2001). The blue crab is a key link in the food web (Fig. 1) (Baird & Ulanowicz 1989), with up to 55% of its diet consisting of clams (Hines et al. 1990). Three benthic piscine predators, the Atlantic croaker *Micropogonias undulatus*, spot *Leiostomus xanthurus* and hogchoker *Trinectes maculatus*, nip *M. balthica* siphons

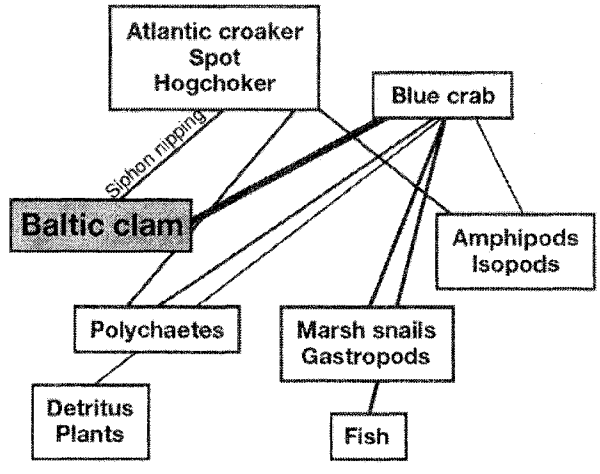

Fig. 1. *Macoma balthica*. Simplified food web showing important linkages for the Baltic clam in the Chesapeake Bay. Adapted from Lipcius et al. (2007)

(Fig. 1) (Hines et al. 1990, Pihl et al. 1992, Powers et al. 2005). Siphon nipping can force *M. balthica* to migrate vertically, making it more susceptible to other predators (e.g. birds; De Goeij et al. 2001). These predators, however, have low tolerances for hypoxia (Das & Stickle 1993) and generally avoid hypoxic areas (Pihl et al. 1991, Bell & Eggleston 2005). In the present study, we quantify the effects of hypoxia on the rate of predation in a soft-sediment community using a manipulative caging experiment to test the hypotheses that hypoxia increases (supporting PSMs) or decreases predation (supporting CSMs) in the York River system.

MATERIALS AND METHODS

We conducted this study in the York River, a tributary of Chesapeake Bay (Fig. 2), which is one of the largest eutrophic estuaries in the world and which suffers from seasonal hypoxia (Officer et al. 1984, Kemp et al. 2005). Hypoxia in the York River is episodic and primarily tidally driven; it tends to develop during neap tides, lasts about a week, and then dissipates when the spring tides mix oxygen-rich waters down from the surface (Haas 1977, Kuo & Neilson 1987).

At our field sites, hypoxic waters regularly develop in deeper areas during the summer (Pihl et al. 1991). In 2005, we haphazardly chose 4 replicate sites in both shallow (3 to 4 m), and deep (10 to 12 m) water (Fig. 2); environmental factors such as sediment type (all sites were mud or sandy mud), temperature, and salinity were similar among all sites. At each site, SCUBA divers established three 50 × 50 cm plots marked with a PVC frame: (1) caged, (2) uncaged, and (3) partially caged. We transplanted 40 *Macoma balthica* (shell lengths 10 to 35 mm), collected from the York River and marked with red permanent ink, into each plot. This resulted in a density of 160 m^{-2}, which is within the natural range (Seitz et al. 2005). We placed a full cage made from galvanized steel hardware cloth (1 cm mesh) over each plot for a minimum of 24 h to allow the clams to acclimate and bury (Seitz et al. 2001). After acclimation, we removed the cage on the uncaged plot, and replaced the cage on the partially caged plot with a partial cage. The partial cage had a 25 × 25 cm hole in the center of the top and a 25 × 7 cm hole in each of the sides. The partial cages allowed predator access but may have excluded larger piscine predators. The cages were 14 cm high and were inserted 7 cm into the sediment so the side holes were flush with the sediment surface.

We left the plots undisturbed for approximately 28 d before they were re-sampled with a suction apparatus to a depth of 40 cm (Eggleston et al. 1992). We counted and measured marked *Macoma balthica*, and calculated percent recovery for each plot. We identified unmarked ambient bivalves in each of the plots to species. The experiment was performed once in June, under normoxic conditions, and once in the period from August to September, under episodic hypoxic conditions. Two sites, one shallow and one deep, were unexpectedly destroyed during the experiment.

We used a continuous water-quality recorder (DataSonde 3, Hydrolab) to record bottom DO, tem-

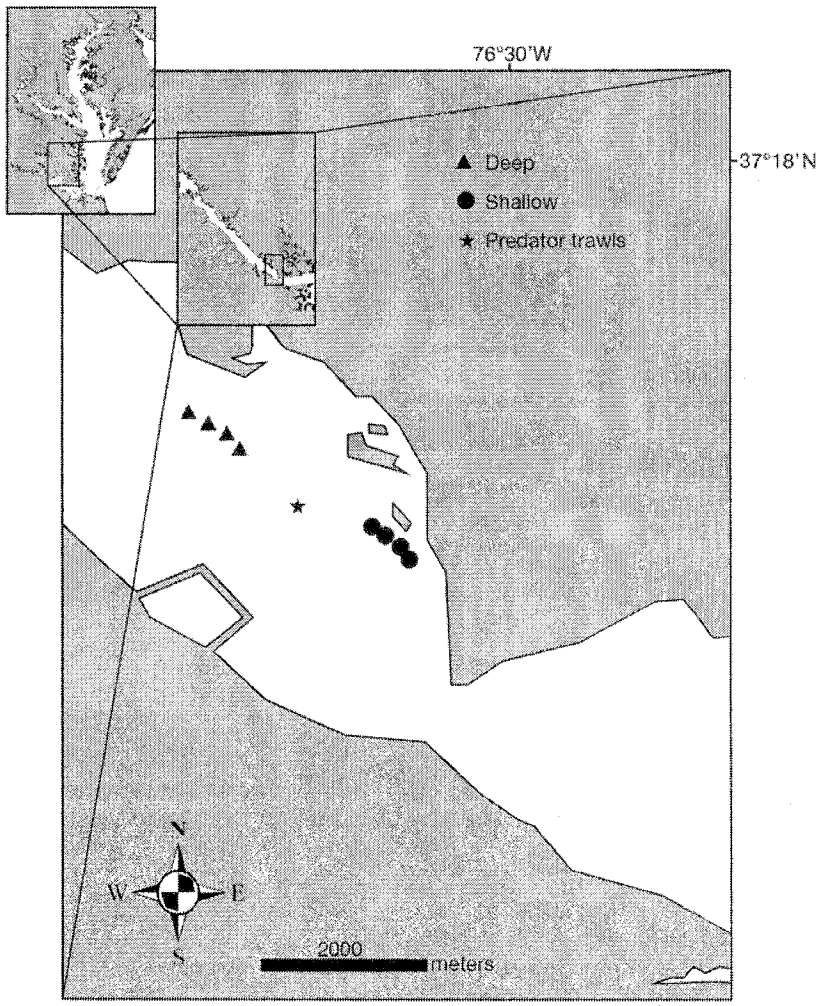

Fig. 2. Chesapeake Bay (left inset), the York River (middle inset), and our study sites at Gloucester Point (large frame)

perature, and salinity every 5 min. The recorder was placed at the most downriver deep site (Fig. 2) and was downloaded and serviced weekly. We used it for all but the first week of the June experiment and during 1 wk of the August experiment, after which it was permanently damaged. Once, during the course of the experiments, we applied a linear correction factor to the raw DO data when there was significant drift in the readings after deployment. DO measurements were smoothed by applying a running 5-point average (Fig. 3). Spot measurements (Fig. 3) were made every 3 to 4 d at each of the sites using a DO probe (YSI Model 85, Yellow Springs Instruments).

We calculated predation based on the recovery of marked *Macoma balthica*. Recovery in the caged plots averaged 87% in June and 85% in August. Marked undamaged shells of *M. balthica* were counted as recovered for the purpose of calculating predation, because they represented non-predatory mortality. The predation rate was calculated using:

$$S = Ne^{-pt}$$

where S is the number of recovered clams, N is the initial number, p is the instantaneous predation rate per day, and t is the time elapsed. The rate of predation, p, was calculated for both the uncaged and partially caged plots in each site. The recovery of clams in the

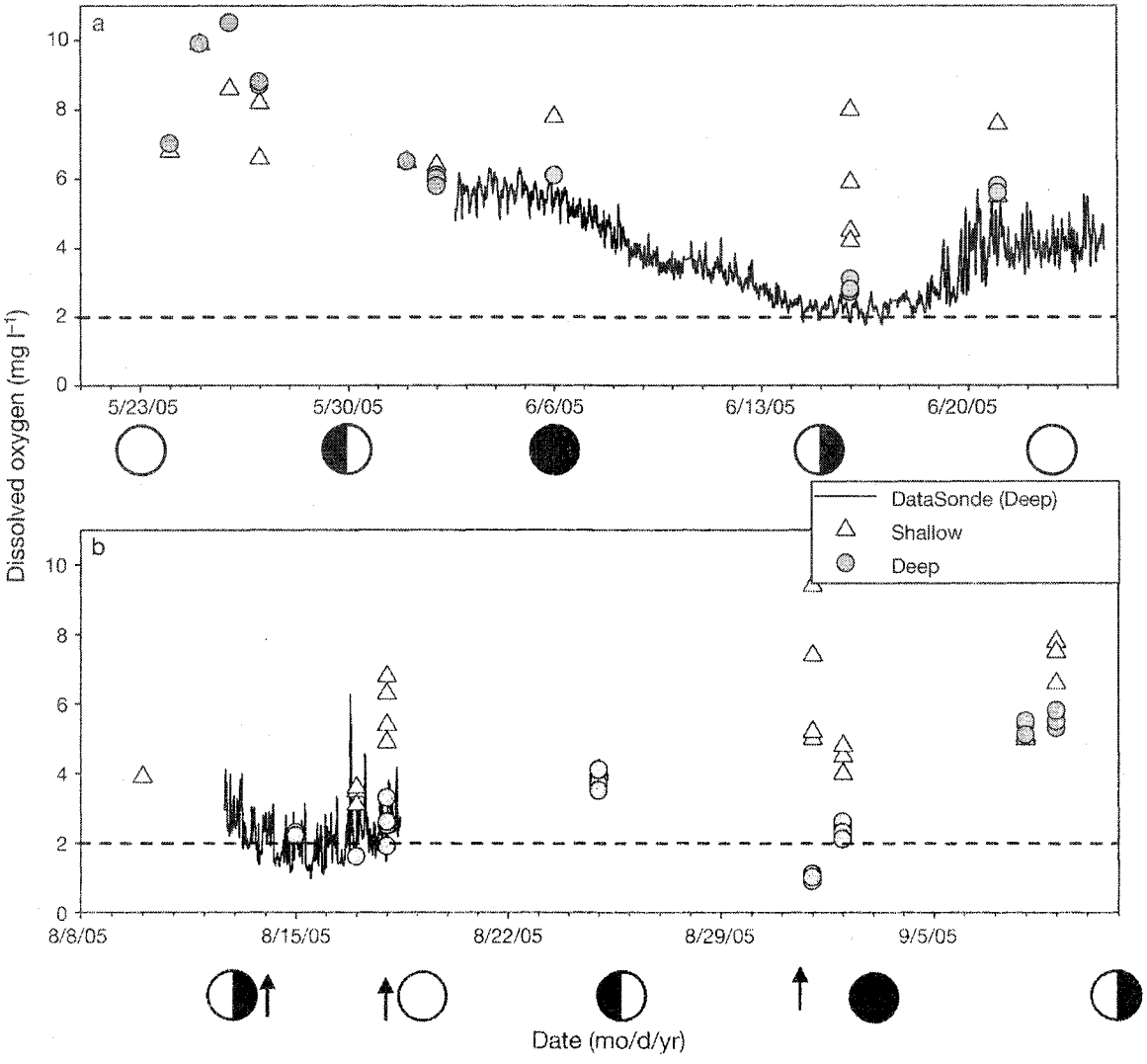

Fig. 3. Dissolved oxygen concentrations observed at study sites in the York River during the (a) June and (b) August experiments. Readings under dashed line at 2 mg l^{-1} are considered nominally hypoxic. Lines represent continuously recorded DataSonde measurements taken at deep site 1. YSI Model 85 measurements at: deep (⊗); and shallow sites (△). (○, ●): lunar phase; (↑): hypoxia

caged plot was used as the initial number, N, thus accounting for sampling error (i.e. non-recovered clams). The rate of non-predatory mortality was calculated with the same equation using the recovery of dead, marked, whole *M. balthica* shells in the partially caged plot as 1–S and the recovery in the caged plots as N. In sites where the caged plots could not be used, the mean recovery from caged plots within that depth and time period was used as N instead. This happened only twice, once because a failure of the suction sampler resulted in a lost sample, and once because a blue crab had been inadvertently included in the cage, as indicated by a high abundance of marked shell fragments due to predation and a low recovery of live *M. balthica* (13%).

Predation and ambient bivalve densities were analyzed with an ANOVA with Time period (pre- or post-onset of hypoxia), Depth (deep or shallow), and Plot (uncaged or partially caged) as factors and Site (nested within Depth and Time) as a blocking factor. Non-predatory mortality was analyzed with a 2-way ANOVA with Time and Depth as factors. Where a significant interaction effect was observed, a Student-Newman-Keuls (SNK) post-hoc multiple comparison test was performed. The assumption of homogeneity of variance was verified using Levine's test for all ANOVA-type analyses. In all cases, this assumption was met.

Predators were sampled by the Virginia Institute of Marine Science (VIMS) Juvenile Finfish and Blue Crab Trawl Survey, which takes monthly trawls at sites in the Virginia portion of the Chesapeake Bay and its tributaries. The survey uses a 9 m semi-balloon otter trawl (38.1 mm stretch-mesh body, 6.35 mm mesh cod-end liner). Each month, one 5 min trawl was performed at the sampling site (Fig. 2). All animals were identified to species, counted, and measured.

RESULTS

In June, before hypoxia, DO in deep and shallow sites was normoxic (>2 mg l^{-1}) for most of the experimental period (Fig. 3a). DO did not differ between deep and shallow sites (1-way ANOVA: $F_{1,32} = 0.87$; $p = 0.357$; $N = 34$; Deep = 6.1 ± 0.58 [SE] mg l^{-1}; Shallow = 6.8 ± 0.35 mg l^{-1}). During August, the shallow zone remained normoxic, but the deep zone experienced several hypoxic episodes (Fig. 3b). DO in the deep sites was significantly lower than in the shallow sites ($F_{1,56} = 25.98$; $p < 0.0005$; $N = 58$; Deep = 3.0 ± 0.30 mg l^{-1}, Shallow = 5.1 ± 0.28 mg l^{-1}). During both time periods, the deep sites were about 1°C cooler than the shallow sites and 1 psu more saline, as expected due to the stratification of the system.

Recovery rates of marked *Macoma balthica* were generally lowest in open plots, intermediate in partial cages, and highest in full cages. Predation rates differed significantly by the interaction between Time period (pre- or post-onset of hypoxia) and Depth (Table 1). Predation was significantly higher at the deep sites after hypoxia than in the shallow sites after hypoxia (Fig. 4a) (SNK: $p < 0.05$) or in the deep sites before hypoxia ($p < 0.01$). There was a non-significant trend ($p < 0.1$) for higher predation at the shallow sites after hypoxia as compared to before. A significant interaction existed between Plot (uncaged and partially caged) and Time (Table 1), with uncaged plots having significantly higher predation rates than partially caged plots in August (Fig. 4b) ($p < 0.01$), but not in June. No major fouling occurred on the cages over the course of the experiment.

Ambient clams were significantly less dense in the deep sites than in the shallow sites (Fig. 4c) (ANOVA: $F_{1,21} = 25.90$, $p < 0.0005$, $N = 44$), and less dense in August than in June ($F_{1,21} = 13.23$, $p = 0.002$). Non-predatory mortality was 0.055 ± 0.014 [SE] d^{-1} and did not differ by Depth (2-way ANOVA: $F_{1,10} = 0.00$, $p = 0.974$, $N = 14$), Time ($F_{1,10} = 1.04$, $p = 0.332$), or interaction ($F_{1,10} = 2.08$, $p = 0.180$).

Predator density and composition changed between the June and August experiments (Fig. 5). In May and early June, predator density was low and dominated by blue crab *Callinectes sapidus*, Atlantic croaker *Micropogonias undulatus*, and hogchoker *Trinectes maculatus*. In August and September, the predator assemblage was dominated by spot *Leiostomus xanthurus* and *T. maculatus*, which resulted in a near doubling of the predator abundance from early June to early August. *C. sapidus* were also abundant in September. There were no clear trends in the size of piscine predators; the mean length of *M. undulatus* was 238 mm and the monthly means varied from 205 mm in September to 278 mm in June. Mean length

Table 1. Fully crossed 3-way ANOVA table for predation rates with Depth (deep and shallow), Time (pre- or post-onset of hypoxia), and Cage (partial and uncaged) as main factors, and Site (nested within Depth and Time) as a blocking factor

Source of variation	df	SS	F	p
Depth	1	0.00171	2.86	0.122
Time	1	0.01514	25.22	0.001
Cage	1	0.01239	20.65	0.001
Depth × Time	1	0.00303	5.06	0.048
Depth × Cage	1	0.00102	1.69	0.222
Time × Cage	1	0.00778	12.97	0.005
Depth × Time × Cage	1	0.00081	1.36	0.271
Site (Depth Time)	10	0.00686	1.14	0.419
Error	10	0.00600		

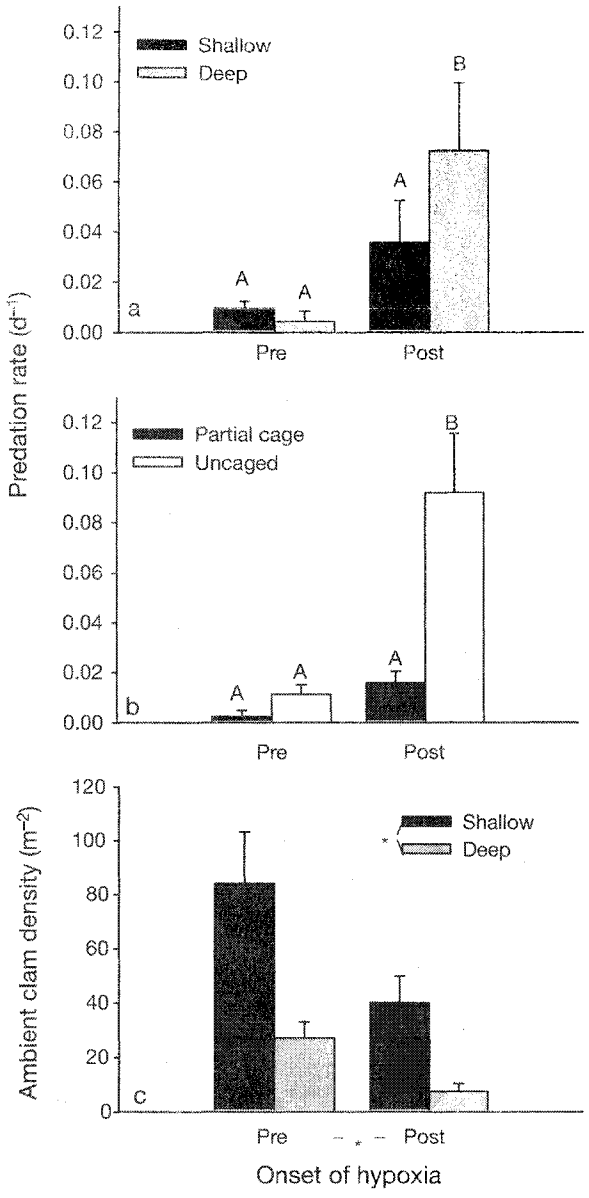

Fig. 4. (a) Predation rate (N = 10) and (b) caging artifacts (expressed as a mortality rate; N = 10) at each site during each experiment. Bars with different letters above them differ at the 0.05 level (Student-Newman-Keuls). (c) Ambient bivalve densities at both depths during each experiment. Levels within a factor marked with an asterisk differ at the 0.05 level (ANOVA: N = 28). Error bars are +1 SE

of *T. maculatus* was 109 and varied from 92 mm in August to 123 mm in May and September. *L. xanthurus* were only abundant in late summer and had a mean length of 116 mm. *C. sapidus* increased slightly in size between May (mean carapace width = 51 ± 11 [SE] mm) and September (75 ± 13 mm).

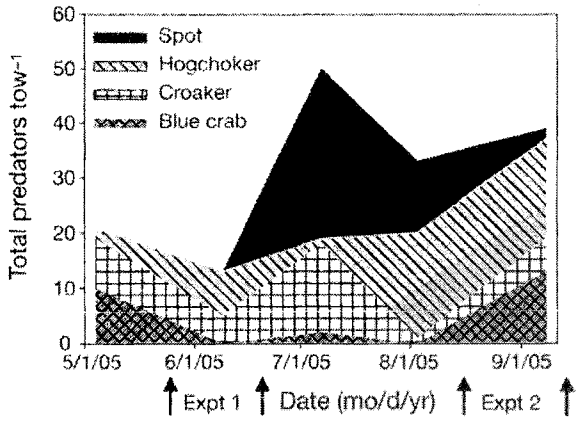

Fig. 5. Cumulative monthly predator density from the VIMS Juvenile Finfish and Blue Crab Trawl Survey. Only epibenthic predator species are shown. (↑): beginning and end of Expt 1 (June, prior to hypoxia), and Expt 2 (August, during hypoxia)

DISCUSSION

Patterns of dissolved oxygen concentrations in the summer of 2005 were similar to those observed during strong hypoxic years in the York River (Pihl et al. 1991). Our time series of DO corresponded well with the tidal regime, with a twice daily cycling of about ±0.5 mg l^{-1} around a daily mean, as well as a longer cycle that correlated with the neap–spring tidal cycle (Haas 1977). Although there were hypoxic excursions lasting only 1 to 2 h during our nominally normoxic experiment, this duration of hypoxia is not long enough to cause behavioral changes in *Macoma balthica*; in laboratory experiments *M. balthica* extended their siphons after about 24 h of exposure to hypoxia (Seitz et al. 2003), and vertically migrated after 48 to 72 h (Long et al. 2008). In contrast, during the August experiment, there were at least 2 hypoxic episodes at the deep sites, one around 17 August, and one around 1 September. During the first episode, DO dropped to less than 1.2 mg l^{-1} and lasted at least 4 d, which is long enough for *M. balthica* to exhibit behavioral responses to hypoxia. During the second episode, severe hypoxia occurred, as the DO dropped below 1 mg l^{-1}.

In our experiment, predation varied with time period, depth, and DO. The increase in predation in the shallow areas from June to August can be explained by the increase in predator abundance observed over this period. The higher predation rates in August in deep areas (with episodic hypoxia) compared to both the rates in deep areas in June (with normoxia) and in shallow areas in June and August (with normoxia), is counter to expectations based on laboratory and field studies where predators have much lower tolerances

for hypoxia than *Macoma balthica* (Henriksson 1969, Bell & Eggleston 2005) and feed at a lower rate under hypoxic conditions (Seitz et al. 2003). Studies with ultrasonically tagged crabs indicate that crabs in hypoxic areas do not feed after relaxation of the hypoxic events (Bell et al. 2003a,b), however, it is possible that other, unstressed crabs from outside the hypoxic area may be able to invade and feed immediately after relaxation of hypoxia.

We suggest that the pattern of higher predation in deep zones during hypoxia derives from the predators' optimal foraging behavior. In June, there is no hypoxia to stress either the predators or the prey. At that time, the prey populations are denser in the shallow zones (Fig. 6a), probably because of the annual hypoxic conditions that occur in deeper areas and cause mortality of infauna there (e.g. Powers et al. 2005). Lower densities in the deep zone would increase searching time of the predators; thus, they preferentially forage in the shallow areas (Clark et al. 1999a,b). For example, blue crabs forage with tactile probing and will leave an area if few prey items are detected, but will continue to search in an area if multiple prey are encountered (Clark et al. 1999a,b). Throughout the summer, predation reduces prey densities in the shallows (Holland et al. 1977). When hypoxia develops, the prey species in the deep zone become stressed and exhibit behaviors that make them easier to find and thus more vulnerable to predation (e.g. clams extending siphons and reducing burial depths; Seitz et al. 2003, Long et al. 2008). Therefore, during periods of episodic hypoxia, although prey densities in the deep areas are lower than those in shallow areas, a predator's searching time is much lower due to the increased susceptibility of prey to encounters, and predators can exploit the prey in this area at a higher rate (Fig. 6b). These results therefore support PSMs rather than CSMs, whereby prey are more stressed than predators, allowing predators to increase the rate of predation.

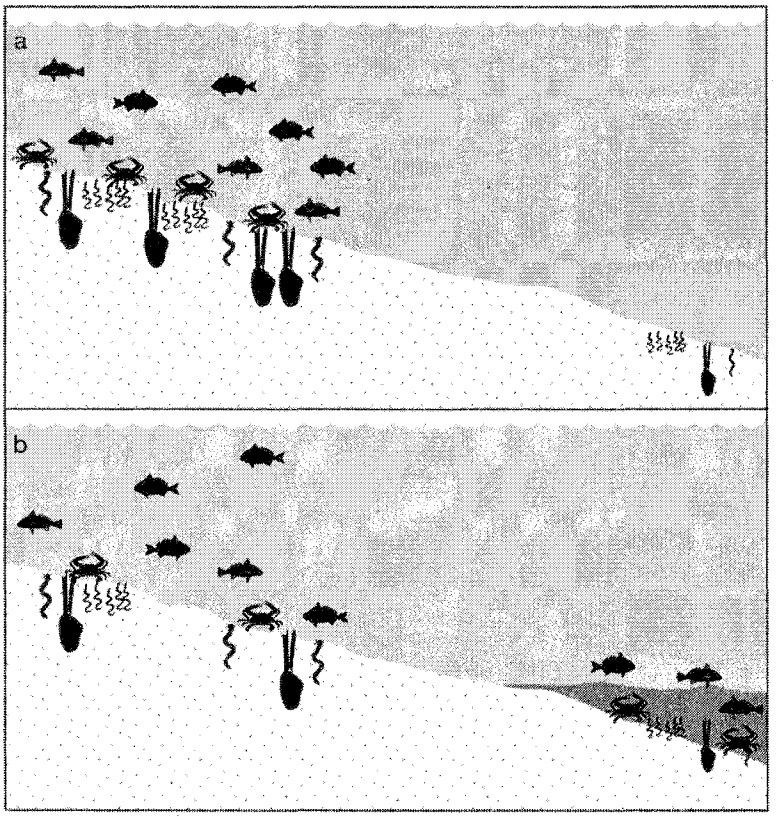

Fig. 6. Predator and prey behavior (a) before and (b) after onset of hypoxia (includes episodes of hypoxia). Stippling: sediment; light gray shading: normoxic water column; dark gray shading: extent of hypoxic water. Infaunal clams and polychaetes are pictured with relative position in relation to the sediment–water interface. (a) Before hypoxia, predators feed in shallow areas where prey are more abundant. (b) During hypoxia, prey species migrate vertically and become more vulnerable to epibenthic predators. Predators move in to feed either during a hypoxic episode or after relaxation before the prey rebury

In our experiments, we could not distinguish whether predation occurred during hypoxia or shortly after each hypoxic episode because of the episodic nature of hypoxia in this system and the length of our experiments. Two distinct hypoxic episodes occurred during August, and the predators could have been foraging at any time during the 28 d experiment. Because most predators avoid hypoxic areas, foraging probably occurred soon after hypoxia but before the prey recovered (Pihl et al. 1992); however, our data do not rule out the alternative of predation during hypoxia (Rahel & Nutzman 1994, Nestlerode & Diaz 1998). Our results indicate that hypoxia is the driving force of the enhanced predation and prey mortality in the deep zone, regardless of when that predation takes place.

Caging artifacts differed by time period, but not by depth. Partial cages may have provided limited protection against predation, explaining the lower predatory mortality in the partially caged plot as compared to the uncaged plot. Some predators, especially large fish such as Atlantic croaker *Micropogonias undulatus* with lengths > 15 cm, may not have been able to access the clams in the partial cages, feeding only in the uncaged plots. Blue crab *Callinectes sapidus* had access to partial

cages, as we found molted exoskeletons in the partial cage plots, and blue crabs were at high densities during late August and early September during our hypoxic experiments. The major change in the predator assemblage between June and August was the increase in the densities, but not the sizes, of all predators, especially fish predators. The temporal patterns in predator density may thus explain the greater caging artifacts in August, when more fish predators would be feeding preferentially in uncaged plots instead of partially caged plots. Caging artifacts did not differ between deep and shallow areas, indicating that our conclusions regarding depth differences were robust.

The results of the caging artifacts indicate that future experiments in this system may have increased power by dispensing with the partial cage treatment. Partial cages either had no effect, or provided a partial refuge from predation, indicating that it is not necessary to control for caging in this system. Using a non-blocked design would also increase statistical power, though it would increase the logistical difficulties of relocating multiple plots in zero-visibility diving conditions.

Based on our finding that predation rates were higher during periods of episodic hypoxia than under normoxic conditions, a shift in our concept of hypoxia's effects on trophic dynamics and energy flow is necessary. Previously, it had been assumed that a CSM applies to this system because benthic infauna suffer mortality during hypoxia and predators avoid hypoxic areas; it has been concluded that the majority of the mortality in hypoxic areas is caused by hypoxic stress rather than by predation (Sagasti et al. 2001, Powers et al. 2005). Under this assumption, the energy from animals that die directly from hypoxic stress would enter the microbial loop, rather than being transferred to predators. Thus, hypoxia would have a net negative effect on energy transfer to higher trophic levels and fishery species (Baird et al. 2004, Altieri & Witman 2006).

In our study, predation increased significantly during episodic hypoxia, whereas non-predatory mortality did not increase. In laboratory experiments, *Macoma balthica* can survive for more than 4 d under mild hypoxia (Henriksson 1969, Seitz et al. 2003), such as they experienced here, so we did not expect to see an increase in non-predatory mortality. As predation increased during periods with hypoxia and the majority of the biomass was passed up to higher trophic levels rather than into the microbial loop, episodic hypoxia can have a positive effect on trophic transfer to predators. This enhanced flow of secondary production likely depends on the prey species. Some species have evolved strong shells, such as *Mercenaria mercenaria*, or aggregative behavior, such as *Mytilus edulis* (Altieri & Witman 2006), in response to predators. Such species probably do not exhibit increased vulnerability during hypoxia, because behavioral changes during hypoxic conditions should not affect their primary defense (Vermeij 1987). In contrast, species such as *Macoma balthica* and *Mya arenaria* (Taylor & Eggleston 2000), which have evolved a deep burial depth in response to predators, are more likely to be more vulnerable to predators under hypoxia because they migrate to the sediment surface where they are easily detected.

These results also indicate that the spatial and temporal scales of hypoxic episodes determine trophic effects (Diaz & Rosenberg 1995, Eby & Crowder 2004), as observed in other consumer–prey interactions (Orrock et al. 2003). Our hypoxic sites were in close proximity (100s of meters) to shallow normoxic sites, where predators congregate during hypoxia (Lenihan et al. 2001, Eggleston et al. 2005). Predatory density and predation pressure can be elevated on the outside edge of hypoxic patches during hypoxic episodes (Lenihan et al. 2001). Similarly, reinvasion and predation by predators in hypoxic areas is likely to be most intense along the inside edge of hypoxic patches after hypoxia relaxes (Clark et al. 1999b, Eggleston et al. 2005). If a hypoxic patch is large (≫1000 m in diameter), predators may not be able to exploit vulnerable prey in central areas before the prey recover. Although our study allows inference regarding changes in predator–prey interactions during episodic hypoxia (<1 wk), it may also apply to systems where hypoxia lasts weeks or months. In the Rappahannock River of Chesapeake Bay, extended periods of hypoxia can be preceded by one or more short episodes of hypoxia (Llansó 1992), which would give predators a chance to prey upon much of the infaunal biomass. Furthermore, our study does not preclude active foraging by predators during hypoxia (Rahel & Nutzman 1994, Nestlerode & Diaz 1998). Ultimately, if hypoxia is severe enough, benthos within a hypoxic zone will be killed, either by physiological stress (Seitz et al. 2003, Powers et al. 2005, Altieri & Witman 2006) or by predation, and the relative importance of each is probably influenced by the duration and spatial extent of hypoxia.

Hypoxia has long been recognized as a severe environmental degradation that devastates benthic communities (Diaz & Rosenberg 1995). We demonstrate that, under certain conditions, decreases in the benthos can be primarily attributed to enhanced predation on stressed prey and not to mortality from hypoxic stress. Regardless of the proximal cause, this decrease in abundance and biomass may lead to a reduction in net annual benthic production. However, the impact on production in higher trophic levels in the short term is probably not as negative as has been thought previously, and may be positive. Indeed, there has been no observed decrease in fisheries yield in the Chesapeake

Bay attributable to hypoxia, despite an increase in the spatial and temporal extent of hypoxia over the past few decades (Kemp et al. 2005). Moreover, the yield of some fisheries in the Gulf of Mexico increased during 4 decades of increasing hypoxia, suggesting that any effects of hypoxia on the nekton are masked by compensatory forces (Chesney & Baltz 2001).

Though our findings demonstrate that the effects of periodic hypoxia may increase predation and thus transfer of secondary production to upper trophic levels, this does not imply that hypoxia and the associated eutrophication are insignificant. In the Neuse River, North Carolina (USA), habitat compression and the resulting increase in predator density can cause an increase in conspecific consumption in blue crabs (Eggleston et al. 2005), and this may have a greater effect on predator populations than does food limitation (Aumann et al. 2006). However, these studies do not account for increased availability of prey due to hypoxia.

The effect of a stressor on consumer–prey interactions sometimes can be predicted based on the relative tolerance of the species to that stressor (e.g. Altieri & Witman 2006), but, as in this study, this is not always the case (e.g. Thomson et al. 2002). In the York River system, subtle changes in prey behavior under hypoxic stress (e.g. reduced burial depth) have a substantial effect on trophic dynamics, as predation increases during hypoxia.

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