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Benthic community responses to nutrient enrichment and predator exclusion: Influence of background nutrient concentrations and interactive effects

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Abstract

Potential community effects of nutrient enhancement are a topic of theoretical interest and increasing management concern in coastal marine systems. While increased nutrient levels may lead to increased microalgal production and biomass, studies have provided variable evidence regarding the existence of upward cascade effects on macrofauna. In benthic marine communities, limitation by predation or factors preventing recruitment response may contribute to weak coupling between resource availability and macrobenthos abundances. We conducted blocked nutrient addition and predator exclusion experiments in the intertidal of two estuaries that varied in background nutrient concentrations (Cape Fear and White Oak, southeastern North Carolina). Benthic community comparisons were also made among these and two other North Carolina estuaries to examine correlations in distribution patterns. Cape Fear, which had the highest background nitrogen and phosphorus concentrations, also had highest ambient benthic microalgal biomass. There was no significant response of microalgal biomass to local nutrient additions in Cape Fear and only one macrofaunal taxon during one season exhibited abundance responses to nutrient additions. White Oak, with lower background nutrient levels, was characterized by significant microalgal responses to nutrient additions and significant macrofauna abundance responses for 50% of the species examined during summer experiments. However, all of these macrofauna declined in abundance with nutrient enhancement while biomass remained constant or significantly increased with nutrient additions. This suggests a complex response of macrofauna to nutrient additions in this estuary with greater biomass per individual but a corresponding decline in abundances. Top-down/bottom-up interactive effects were observed for haustoriid amphipods, which were uncommon or absent when predators had access, but exhibited strong biomass responses to nutrient enhancement when predators were excluded. These results support a growing body of literature that indicates the importance of background conditions in regulating benthic community responses to nutrient enhancement. However, responses may be complex with biomass per individual rather than densities being the primary response variable for some taxa and predator moderation of responses occurring for some taxa but not others.
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1. Introduction

The impacts of resource enhancement (bottom-up effects) and trophic controls (top-down or predation effects) have been a major focus of research in aquatic

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systems for the past several decades (e.g. Edmonson, 1970; Beukema, 1991; Power, 1992; Deegan et al., 1997; Pitta et al., 1998; Downing et al., 1999; Menge et al., 1999). With population pressures and related human impacts to coastal systems, potential responses of coastal communities to increased nutrient loading or removal of top predators through fishery activities is becoming an increasingly acute management issue (Nixon, 1995; Michelli, 1999; Jackson et al., 2001). The potential severe consequences of such trophic perturbations are apparent in coral reef (Hughes, 1994), oyster (Breitburg et al., 2000; Mann, 2000), and developed bay and sound systems (Ulanowicz and Tuttle, 1992; Jackson et al., 2001). Despite the long-term scientific and growing management interests in responses to nutrient enhancement and variations in predator controls, there continues to be considerable debate about the actual impacts of these factors or their potential mechanisms of effect (Michelli, 1999; Posey et al., 2002).

When extreme, eutrophication in coastal systems can have dramatic impacts through developing hypoxic conditions (Shalovenkov, 2000; Elliot and de Jonge, 2002) and possible blooms of undesirable taxa (e.g. toxic microalgae; Burkholder and Glasgow, 1997; Burkholder et al., 1999). The benthic macrofaunal community can similarly exhibit dramatic changes under such severe stress, with domination by capitelid polychaetes and other opportunistic species being a sufficiently common response that it is included in many indices of community health (Hyland et al., 2004). However, the impact of more moderate increases in nutrient inputs is less certain. Moderate increases in nitrogen, and sometimes phosphorus, levels in coastal areas are often associated with increased microalgal biomass and occasionally changes in microalgal species composition (Graneli and Sundback, 1985; Howarth, 1988; Becker, 1996; Cahoon, 1999; Hagberg and Tumberg, 2000). Benthic macrofauna may experience food limitation on a periodic basis (Woodin, 1999; Estes and Peterson, 2000). However, impacts of nutrient enhancement and consequent food enhancement on macrofauna vary from altered abundances for selected species in certain studies (Dauer et al., 1982; Levin, 1986; Hauxwell et al., 1998; Beukema, 1991; Posey et al., 1995, 1999, 2002; Sarda et al., 1996; Dauer et al., 2000; Kihslinger and Woodin, 2000; Worm et al., 2000) to no or minimally detectable changes in community composition in other cases (Wiltse et al., 1984; Posey et al., 2002; Owens, 2003).

In freshwater lake and stream communities with relatively simple food web structure, predation may be an important factor modifying grazer/herbivore response to increased primary production (Carpenter et al., 1985; McQueen et al., 1989; Power, 1992; Osenberg and Mittelbach, 1996). Predation can keep numbers of herbivores sufficiently low that they are not able to exhibit numerical responses to increased food availability (Power, 1992; Osenberg and Mittelbach, 1996). Predation is well-demonstrated to be an important determinant of macrofaunal abundance patterns in shallow-water coastal communities (Peterson, 1979; Kneib, 1988; Wilson, 1990) and can control numbers of certain near-surface taxa (Posey, 1990; Posey et al., 1995, 1999). However, relatively few studies have directly tested whether predation may prevent numerical responses of grazers to increased resource availability, mostly with variable results (Wootin, 1992; Hauxwell et al., 1998; Michelli, 1999; Heck et al., 2000; Moon and Stiling, 2002; Silliman and Bertness, 2002; Valentine, 2003). Complex food webs with diverse food resources, recruitment limitation, and disturbance may all contribute to weak coupling between increases in a specific resource type and responses at intermediate or higher trophic levels. In a previous study we examined the potential importance and interactive effects of predation and nutrient enhancement (benthic microalgal enhancement) on benthic communities in 4 small tidal creek estuaries (Posey et al., 2002). That study showed few differences in responses of benthic microalgae to nutrient enhancement among tidal creeks with differing nutrient concentrations and indicated few benthic macrofaunal responses to enhanced microalgal biomass. Although several taxa exhibited increased abundances when predators were excluded, there was no evidence for interactions among top-down and bottom-up controls in which benthic grazers responded to nutrient enhancement and increased microalgal biomass when released from predation (Posey et al., 1999, 2002). However, the tidal creek systems we examined in that study exhibited minimal (<50%) variation in background nutrient conditions across the estuaries studied, were small interconnected systems with similar fauna dominating each, and were disturbed through local human activity and development. We also examined primarily numerical responses and did not measure potentially important biomass responses for macrofauna.

In this study we examine benthic community responses to local nutrient enhancement and varying predator access using manipulative experiments across several estuarine systems. We conducted these studies in systems that vary 2–3× in background nutrient loading,

that are not connected by adjoining sounds, and that are not subject to proximal development activity and disturbance that may alter local faunal response patterns. We predicted that: (1) nutrient enhancement would have no detectable impact on benthic microalgal responses in the estuary with greatest nutrient loading but would affect microalgal biomass in estuaries with lower background nitrogen and phosphorus concentrations; (2) deposit feeding and grazing macrofauna will be enhanced by nutrient additions (and microalgal increases) in the estuary with lower background nutrient levels; and (3) there will be an interactive effect of predator exclusion and nutrient addition such that responses to nutrient addition are greatest when predators are excluded.

2. Methodology

To address the issue of main and interactive impacts of predator exclusion and nutrient enhancement, our primary approach was to conduct blocked experimental manipulations of nutrient additions and predator exclusion in two river systems that vary in background nutrient loading. This was complemented by a comparison of microalgal biomass and benthic community composition among these and two other coastal river systems. In any study of trophic interactions and the effects of varying resource levels, it is ideal to examine all trophic levels (bacterial, fungal, microalgal, macrophyte, benthic, planktonic, and all nektonic components) in all connected subhabitats simultaneously, and over broad spatial scales over several years with both press and perturbation experiments. However, such a comprehensive approach is logistically daunting. This study focuses on the spatially dominant system that we previously explored in small tidal creek estuaries (Posey et al., 1999, 2002), examining microalgal production and benthic macrofaunal community and biomass responses to nutrient enhancement and predator exclusion/access in unvegetated soft substrates. Benthic macrofauna are well-demonstrated as indicators of community responses (Wilson, 1990; Estes and Peterson, 2000; U.S. EPA, 2002), benthic microalgae can be the dominant source of primary production in southeastern shallow water systems (Nearhoof, 1994; Cahoon, 1999), and they can be an important food source for surface deposit feeders (e.g. Levin, 1986; Owens, 2003).

We conducted experimental manipulations in two southeastern North Carolina river systems, the Cape Fear River estuary and the White Oak River estuary, and comparative sampling in two additional estuaries, the New River and the Newport River estuaries (Fig. 1). These estuaries are all located within the southeastern coastal region of North Carolina. This region is characterized by small sounds and direct connections between the estuaries and adjacent coastal waters, thus creating relatively independent systems. This is in contrast to the Pamlico and Albemarle Sound complex in northern North Carolina where rivers empty into a large, interconnected sound, possibly leading to stronger linkages among estuaries. These four estuaries were chosen because they provide a range of background nutrient levels and inputs much greater than in our previous study of small tidal creek estuaries, with Cape Fear having >2× average nitrogen and phosphorus loading compared to any of the other estuaries. NO_2+ NO_3 concentrations, averaged over January/February and June/July, for Cape Fear, Newport, New and White Oak Rivers are 0.47 mg/l, 0.025 mg/l, 0.023 mg/l and 0.013 mg/l, respectively (North Carolina Division of Water Quality, 1997–1999 statistics). Phosphorus levels for the same estuaries are 0.094, 0.029, 0.047, and 0.022 mg/l, respectively (NCDWQ, 1997–1999 statistics). Two sites were sampled in the lower mesohaline (20–25‰) region of each estuary. Each site was dominated by fine sands (<5% silt/clays), was mid-intertidal, and was located on unvegetated tideflat adjacent to fringing *Spartina alterniflora* marsh (5–7 m from the sampling areas).

Blocked nutrient addition/predator exclusion experiments were conducted at the two mid-intertidal sites in Cape Fear and the two sites in White Oak during

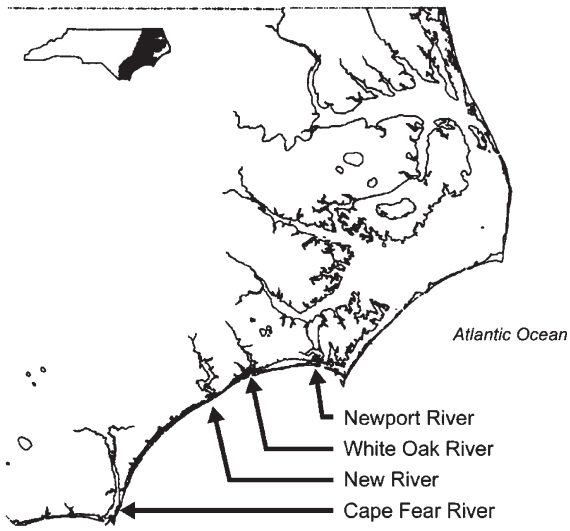

Fig. 1. Cape Fear River, New River, White Oak River and Newport River estuaries. Experimental manipulations were conducted within the Cape Fear and White Oak estuaries.

summer 2000 (June/July) and winter 2001 (February/March). Summer is a period of high predator abundance and rapid infaunal growth in southeastern North Carolina while winter is a period of lower predator abundance (Mallin et al., 2000), slower microalgal growth (Freeman, 1989; Cahoon, 1999), but higher abundances of certain infaunal taxa (e.g. amphipods; Fox and Ruppert, 1985; Posey et al., 2002). Each experiment lasted 4 weeks. This duration was chosen as a compromise to reduce potential cage artifacts that may result from cumulative effects of current disruption and shading over time but allowing sufficient time for biomass and density responses. This interval has been shown to be sufficient to allow detectable responses to both nutrient enhancement and predator exclusion in previous studies in southeastern North Carolina (Posey et al., 1995, 1999). Six experimental treatments were used, representing a blocked design of two nutrient treatments (nutrients added; nutrients not added) and three predator exclusion treatments (predator exclusion/full cage, no predator exclusion/open plot, and cage artifact control/partial cages). Treatments were placed in sets containing one replicate of each; with nine replicate sets per site, two sites per estuary. Each treatment plot was 1 m × 1 m in size and was placed at least 3 m from the nearest adjacent treatment plot. This design allowed us to block for potential small-scale heterogeneity on the tideflats.

Predators were excluded using a 1 m × 1 m × 12 cm high hardware cloth cage placed over the plot. The cages had 1 cm mesh and the wire was soaked for at least 7 days prior to deployment in the field. Because cage structures may have unintended effects resulting from current disruption or shading (Virnstein, 1978), partial cages were used to provide potential physical effects without excluding predators. Partial cages were 1 m^2 with 4 sides and a partial roof over 2 sides. Our previous work has indicated few to no significant caging artifacts with this design (Posey et al., 2002) and we have observed mummichogs, pinfish, spot and small blue crabs foraging within the partial structures. No predators were observed within exclusion cages.

Nutrients were added in the nutrient addition treatments using 56 g solid fertilizer spikes with an atomic N/P ratio of 16:10 contained within an inert gypsum matrix (Posey et al., 2002). Spikes were used to provide a gradual release of nutrients, and prior work indicates they provide similar nutrient elevation as measured with repeated addition of nutrients over the plot in aqueous form (at low tide) but without the associated disturbance effects (Posey et al., 1995). Five spikes were placed in each addition plot in a diamond pattern, four placed 20 cm from the sides and 45° offset from the cage corners and one placed in the center of the plot. Each spike was pushed into the sediment until the top of the spike was flush with the surrounding surface, ~7.5 cm deep.

Macrofauna and benthic microalgae were sampled in each plot at the end of 4 weeks, with both river systems being sampled within 4 days of each other. Plots were only sampled if all cages were fully in place (a few cages, 0–2 per site/date combination, were burrowed under by crabs during experiments). Macrofauna were sampled with two 10 cm diameter × 15 cm deep cores, each taken between and 15 cm distant from each of 2 fertilizer stakes. Cores were preserved in 10% formalin with rose bengal dye added and were subsequently sieved through a 0.5 mm screen. Our previous work in this region has indicated this experimental duration and sieve size combination is sufficient to observe initial numerical responses (including recruitment) within experimental plots (Posey et al., 1999; Owens, 2003). Retained organisms were transferred to 50% isoproponal for sorting and identification. After identification and enumeration, biomass was estimated for higher taxonomic groups (polychaetes, crustaceans, bivalves, other taxa combined including forms such as nemertea, gastropods and oligochaetes). Individual species were often represented by only one or two small individuals per sample, making species-level biomass measures unreliable. Samples were dried at 70 °C for 20 h and then weighed. Samples were subsequently ashed at 500 °C for 5 h and biomass determined by weight loss. Four 2.5 cm diameter × 3 cm deep cores were taken from each plot for analysis of chlorophyll *a* as a measure of microalgal biomass. These cores were placed on ice in the field and frozen at −4 °C upon return to the laboratory. Cores were later thawed and chlorophyll *a* biomass was determined by the double extraction and spectrophotometric procedure of Whitney and Darley (1979), except that 24 h of acetone extraction was replaced by acetone extraction with sonication for 30 s. All chlorophyll *a* was contained within the top 2 cm of sediment at these sites (Becker, 1996).

In addition to sampling of experimental plots in summer 2000 and winter 2001, macrofauna were sampled from open, unmanipulated plots in all 4 estuarine systems during summers 2000 and 2001 as well as winters 2000 and 2001. Sampling for all rivers within a given season/year combination was completed within a 1 week period. Benthic microalgae were sampled in summer 2000 in all 4 estuarine systems. Sampling was conducted at 2 sites in each estuary as described above.

Initial analysis indicated strong interactive effects between responses of benthic macrofauna to experimental treatments and estuarine system (Cape Fear and White Oak had differing dominant fauna) as well as differing responses dependent on season of experiment (winter versus summer experiments). As a result, analyses of faunal responses to nutrient and predator manipulation experiments were conducted separately for each estuarine system and each of the 2 seasons. The experimental design allowed a direct test of main treatment effects as well as predicted interactions between nutrient additions and predator exclusion. A two-way Analysis of Variance (ANOVA) was used to determine main and interactive effects of nutrient treatments (addition, no addition) and predator exclusion treatments (exclusion, open plot, partial cage control) on abundances of numerically dominant fauna (all fauna comprising at least 3% of the total individuals for an estuary/season combination). A two-way ANOVA was also used to determine treatment effects on biomass of major taxonomic groups. Both abundance and biomass data were log (10) transformed before analyses to meet assumptions of non-heterogeneity of variances. The impacts of the main effects of nutrient addition (2 levels: addition and no addition) and predator exclusion (exclusion, open plots, partial cages) on benthic chlorophyll *a* also were compared separately for each river system and season using a two-way ANOVA with interaction. Chlorophyll *a* data met assumptions of normality and non-heterogeneity of variances without transformation. Benthic macrofaunal community composition, including both dominant and rarer taxa, was compared among treatment/season combinations for each estuarine system using the multivariate approaches of Multidimensional Scaling (MDS) combined with Analysis of Similarity (ANOSIM) to compare treatment and season sample groupings (PRIMER statistical package, Clarke and Warwick, 2001). MDS and ANOSIM compare relative species composition based on the Bray–Curtis similarity matrix (Clarke and Warwick, 2001). Data were square-root transformed before analysis. Comparison of benthic communities in open plots among the four estuaries and four sampling periods were also conducted using MDS and ANOSIM.

3. Results

Among estuarine patterns in benthic microalgal biomass paralleled historical patterns in nitrogen and phosphorus concentrations. The Cape Fear system had the highest benthic microalgal biomass, averaging 350–375 mg/m^2 in winter with higher levels in summer (>400 mg/m^2, though variable among the different treatments used) (Fig. 2). These levels differed from and were 3× greater than those in the three other estuaries studied. There was no significant difference in average benthic microalgal biomass among White Oak, New and Newport River sites. There was no significant effect of either exclusion or nutrient addition treatments on microalgal biomass in the Cape Fear estuary. However, there was a significant ($p<0.05$), though small, increase in benthic

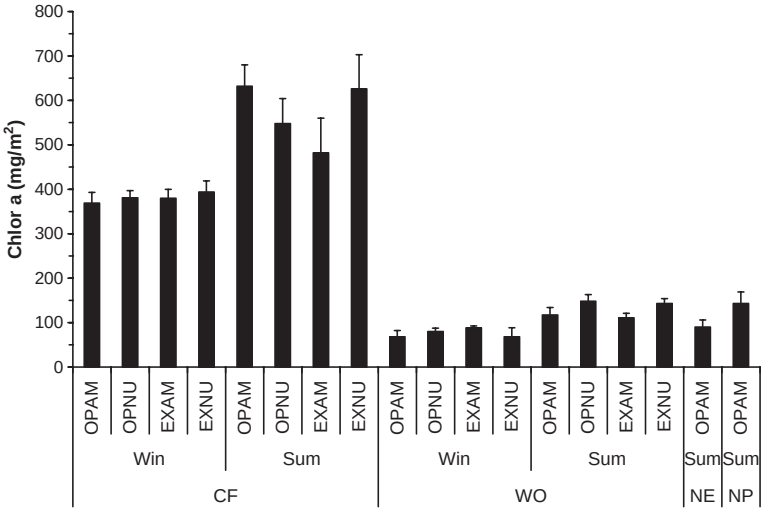

Fig. 2. Chlorophyll *a* (microalgal) biomass within winter 2001 and summer 2000 experimental plots in the Cape Fear (CF) and White Oak (WO) estuaries and within summer 2000 open plots in the New (NE) and Newport (NP) estuaries. Numbers indicate mean biomass (+1 S.E.). OPAM: open plot, ambient nutrient conditions; OPNU: open plot, nutrients addition; EXAM: predator exclusion, ambient nutrient conditions; EXNU: predator exclusion, nutrients added.

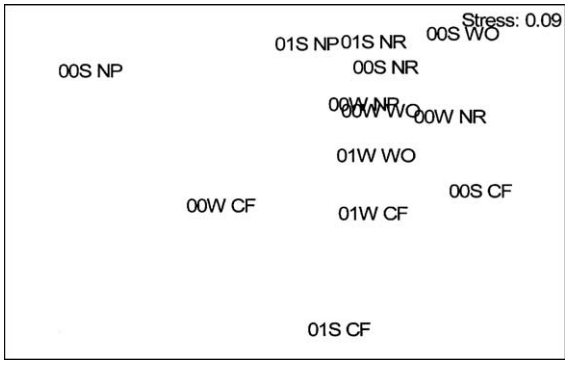

Fig. 3. MDS biplot of faunal similarity in open plots among the four estuarine systems during summer and winter sampling. Point designations are given as sample year (00=2000; 01=2001), season (W=winter; S=summer), and estuary (CF=Cape Fear, WO=White Oak, NR=New River, NP=Newport).

microalgal biomass with nutrient addition in White Oak experiments (Fig. 2). Predator exclusion was not associated with a consistent change in benthic microalgal biomass and there were no interactive effects between nutrient addition and predator exclusion treatments.

For overall ambient community assessment, the strongest among-estuary pattern for benthic communities was a difference between Cape Fear and the other three estuaries (Fig. 3). ANOSIM indicated a marginally significant difference in community structure between Cape Fear benthos and that of the other estuaries (Cape Fear vs. New River, $p<0.055$; Cape Fear versus White Oak and Cape Fear versus New River, $p<0.085$). The White Oak, New and Newport benthic communities did not group distinctly from each other. Not surprisingly, there was a separation among summer and winter samples for White Oak, New and Newport and, distinctly, among winter and summer samples for Cape Fear (Fig. 3; seasonal effect, $p<0.055$, ANOSIM).

There were seasonal variations in treatment effects for experimental manipulations in Cape Fear. The numerically dominant taxonomic group in Cape Fear was polychaetes (*Eteone lactea*, *Maranzellaria viridis*, *Mediomastus* spp., *Parandalia*, *Polydora ligni* and *Streblospio benedicti*) with oligochaetes, haustoriid amphipods, and the bivalve *Mulinea lateralis* as subdominants (Table 1). Most of these taxa are considered opportunistic and are characteristic of eutrophic estuaries along the mid-Atlantic and southeast coasts (Fauchald and Jumars, 1979; Dauer et al., 1982, 2000; Levin, 1986; Marsh and Tenore, 1990; Beukema, 1991; Levin et al., 1996). During winter experiments, only two taxa exhibited significant responses to predator

Table 1
Mean density (S.E.) of common macroinfauna in exclusion and nutrient treatments in the Cape Fear estuary

Taxa	Exclusion	Exclusion partial	Open	Exclusion effect	Nutrient		Nutrient effect	Exclusion * nutrient interaction
					+Nutrients	No added nutrient		
Winter								
Eteone lactea (P)	0.85(0.27)	0.57(0.31)	0.80(0.20)	ns	1.04(0.28)	0.51(0.14)	ns	ns
Haustoriidae (C)	0.30(0.13)	0.11(0.07)	0.35(0.12)	ns	0.19(0.08)	0.32(0.10)	ns	ns
Maranzellaria viridis (P)	3.03(0.67)	3.66(0.59)	5.29(0.79)	ns	3.60(0.55)	4.62(0.63)	ns	ns
Mediomastus spp. (P)	3.06(0.92)	2.60(0.75)	4.98(0.95)	ns	2.38(0.58)	4.80(0.81)	ns	ns
Mulinea lateralis (B)	4.73(0.95)	2.80(0.53)	3.35(0.51)	ns	2.81(0.46)	4.18(0.60)	ns	ns
Oligochaeta	60.52(12.77)[a]	63.57(12.65)[a]	28.51(5.93)[b]	5.27**	52.52(9.12)	44.43(7.83)	ns	ns
Parandalia (P)	3.79(0.47)	3.31(0.67)	4.92(0.70)	ns	3.54(0.47)	4.58(0.57)	ns	ns
Polydora ligni (P)	6.24(1.29)	5.97(0.83)	4.00(0.66)	ns	5.63(0.73)	4.89(0.74)	ns	3.47*
Streblospio benedicti (P)	38.39(4.94)[a]	42.74(4.29)[a]	25.82(4.11)[b]	6.73**	40.04(3.80)	29.94(3.56)	5.39*	ns
Summer								
Eteone lactea (P)	3.79(0.59)[a]	2.33(0.45)[ab]	1.44(0.19)[b]	7.13**	2.20(0.30)	2.33(0.35)	ns	ns
Haustoriidae (C)	1.00(0.30)[a]	1.07(0.37)[a]	4.87(1.07)[b]	5.54**	2.64(0.75)	3.23(0.87)	ns	ns
Maranzellaria viridis (P)	0.14(0.07)	0.15(0.07)	0.02(0.02)	ns	0.09(0.04)	0.07(0.03)	ns	ns
Mediomastus spp. (P)	17.59(6.01)[a]	2.63(0.75)[b]	2.56(0.43)[b]	4.96**	4.98(1.88)	8.00(2.81)	ns	ns
Mulinea lateralis (B)	0.90(0.21)	1.11(0.23)	0.60(0.10)	ns	0.82(0.13)	0.79(0.14)	ns	ns
Oligochaeta	1.10(0.48)	0.89(0.26)	0.40(0.13)	ns	0.56(0.14)	0.84(0.27)	ns	3.16*
Parandalia (P)	1.48(0.34)[ab]	0.93(0.23)[a]	1.84(0.24)[b]	3.24*	1.51(0.22)	1.54(0.24)	ns	ns
Polydora ligni (P)	0.10(0.06)	0.04(0.04)	0.11(0.05)	ns	0.11(0.05)	0.07(0.03)	ns	ns
Streblospio benedicti (P)	55.48(13.11)[a]	19.33(2.00)[b]	14.73(2.24)[b]	10.66****	22.40(3.50)	30.52(7.04)	ns	ns

Where main effects of exclusion treatments, nutrient enrichment treatments or interactive effects are significant, *F*-values from ANOVA are indicated. ns=not significant, *$p<0.05$, **$p<0.01$, ****$p<0.0001$. For exclusion treatments, treatments with the same letter superscript do not differ significantly (SNK post hoc test, $p<0.05$) (P=polychaete, C=crustacean, B=bivalve).

exclusion treatments, *S. benedicti* and oligochaeta, and both showed similar increases in both partial and full cages relative to controls. This likely reflects an artifact of the cage structure (both partial and full) snagging drift *Enteromorpha* spp. that was present in late winter and early spring. The only response to nutrient additions during winter was enhancement of *S. benedicti*. Interactive effects were absent for all taxa except for a weak effect on *Polydora*. No main effect of nutrient addition was detected when *Polydora* abundances were analyzed separately by exclusion treatment type.

Predator abundances within most southeastern estuaries are greater in summer and previous work we have conducted indicates a similar pattern for the Cape Fear estuary (Posey et al., 2005). Predator exclusion effects reflected this seasonality. During summer experiments in Cape Fear, three taxa were enhanced within predator exclusion experiments relative to partial cage controls and open plots (*S. benedicti*, *Mediomastus* spp., and *E. lactea*) (Table 1). Surprisingly, Haustoriidae showed a decline in exclusion treatments relative to partial cages and controls, possibly reflecting impacts of enhanced polychaete numbers, and *Parandalia* exhibited mixed patterns. There were no significant effects of nutrient addition on any of the dominant taxa, though a weak interactive effect was observed for oligochaetes. Oligochaetes did not have a significant response to nutrient addition when nutrient effects were analyzed separately by exclusion treatment type.

MDS indicated the strongest pattern for the Cape Fear system was the result of seasonal differences in faunal composition (Fig. 4a). Differences were also apparent among predator exclusion treatments for summer ($p<0.04$; ANOSIM), but no distinction was observed among nutrient enhancement treatments.

In contrast to Cape Fear, nutrient addition effects were seasonally much stronger in White Oak. White Oak was dominated by a more mixed macrofaunal assemblage than Cape Fear, including 6 polychaetes (*Aricidea* sp., *Heteromastus filiformis*, *Hypereteone heteropoda*, *Mediomastus* spp., *Nereis falsa*, and *S. benedicti*), 2 bivalves (*Gemma gemma* and *Tellina aequistriata*), 1 gastropod (*Hydrobia*), and oligochaetes. During winter, only one taxa (*Hydrobia*) exhibited significant responses to exclusion treatments (Table 2), though this was primarily due to increased numbers in partial cages and may represent an artifact of trapped drift algae as described above. Two taxa exhibited increased density with increased nutrients, *Hydrobia* and *Streblospio*. Summer responses to nutrient enhancement were more widespread. Two taxa were significantly enhanced by predator exclusion relative to partial

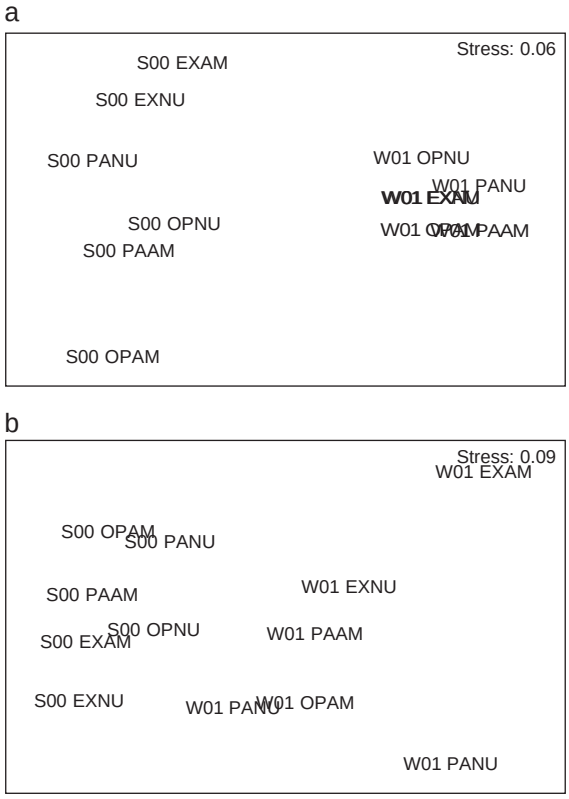

Fig. 4. MDS biplot of faunal similarity among treatments during 2 seasons of experiments in the Cape Fear (a) and White Oak (b) estuaries. Point designations are given as season (S = summer; W = winter), year (00 = 2000; 01 = 2001), and treatment (OPAM: open plot, ambient nutrient conditions; OPNU: open plot, nutrients addition; PAAM: partial cage, ambient nutrient conditions; PANU: partial cage, nutrients added, EXAM: predator exclusion, ambient nutrient conditions; EXNU: predator exclusion, nutrients added).

cage or open plot treatments (*Hypereteone* and *Streblospio*; Table 2). Five of the 10 numerically dominant taxa responded to nutrient additions (*Gemma*, *Hypereteone*, *Mediomastus*, *Nereis*, and *Streblospio*). However, in contrast to our *a priori* expectations, all 5 taxa were less abundant within nutrient addition experiments compared to non-addition plots (Table 2). MDS indicated seasonal differences as the dominant overall pattern, with nutrient addition and predator exclusion effects not being strong (Fig. 4b).

The surprising decline in abundance of five taxa with nutrient additions in the summer White Oak experiments may reflect tradeoffs between biomass and numerical responses. Bivalves exhibited a trend toward higher biomass in nutrient addition treatments relative to non-addition treatments during both winter and summer experiments (Fig. 5, Table 3). Even though numbers of *Gemma* were lower within nutrient addition

Table 2
Mean density (S.E.) of common macroinfauna in exclusion and nutrient treatments in the White Oak estuary

Taxa	Exclusion	Exclusion partial	Open	Exclusion effect	Nutrient		Nutrient effect	Exclusion * nutrient interaction
					+Nutrients	No added nutrient		
Winter								
Aricidea spp. (P)	3.00(0.45)	2.71(0.87)	3.27(0.37)	ns	3.70(0.38)	1.54(0.21)	ns	ns
Gemma gemma (B)	0.50(0.22)	3.00(1.05)	1.45(0.32)	ns	1.70(0.41)	5.48(0.58)	ns	ns
Heteromastus filiformis (P)	0.83(0.65)	0.71(0.47)	0.45(0.19)	ns	0.65(0.30)	1.81(0.25)	ns	ns
Hydrobia	0.33(0.21)[b]	3.86(2.89)[a]	1.18(0.34)[ab]	4.05*	2.04(0.94)	0.03(0.03)	6.55*	3.39*
Hypereteone heteropoda (P)	0	1.14(0.14)	0.06(0.04)	ns	0.09(0.06)	2.22(0.31)	ns	ns
Mediomastus spp. (P)	0.67(0.49)	0.14(0.14)	1.70(0.35)	ns	1.30(0.37)	0.04(0.03)	ns	ns
Nereis falsa (P)	1.33(0.49)	2.00(0.72)	0.91(0.20)	ns	1.04(0.24)	1.45(0.33)	ns	ns
Oligochaeta	2.17(0.70)	2.57(1.51)	2.06(0.51)	ns	2.26(0.65)	0.15(0.07)	ns	ns
Streblospio benedicti (P)	11.50(4.67)	15.00(3.94)	13.67(1.71)	ns	16.91(2.19)	34.16(7.54)	9.15**	ns
Tellina aequistriata (B)	2.17(1.05)	1.86(0.67)	2.76(0.46)	ns	2.65(0.57)	0.48(0.12)	ns	ns
Summer								
Aricidea spp. (P)	1.60(0.22)	1.30(0.29)	1.74(0.26)	ns	1.60(0.22)	1.54(0.21)	ns	ns
Gemma gemma (B)	5.50(0.81)	4.55(0.62)	3.87(0.46)	ns	3.64(0.40)	5.48(0.58)	5.98*	ns
Heteromastus filiformis (P)	1.20(0.28)	1.65(0.32)	1.91(0.30)	ns	1.43(0.25)	1.81(0.25)	ns	ns
Hydrobia	0.05(0.05)	0	0.04(0.03)	ns	0.03(0.02)	0.03(0.03)	ns	ns
Hypereteone heteropoda (P)	2.93(0.49)[a]	1.28(0.21)[b]	1.65(0.24)[b]	5.18**	1.61(0.23)	2.22(0.31)	4.05*	ns
Mediomastus spp. (P)	0.05(0.03)	0.03(0.03)	0	ns	0	0.04(0.03)	3.97*	ns
Nereis falsa (P)	1.40(0.33)	1.35(0.49)	0.83(0.18)	ns	0.87(0.19)	1.45(0.33)	3.66*	ns
Oligochaeta	0.08(0.06)	0.23(0.11)	0.17(0.07)	ns	0.16(0.06)	0.15(0.07)	ns	ns
Streblospio benedicti (P)	64.7(10.94)[a]	7.78(2.82)[b]	5.78(0.90)[b]	71.12****	13.76(2.64)	34.16(7.54)	7.08**	3.84*
Tellina aequistriata (B)	0.60(0.16)	0.38(0.15)	0.46(0.15)	ns	0.48(0.13)	0.48(0.12)	ns	ns

Where main effects of exclusion treatments, nutrient enrichment treatments or interactive effects are significant, *F*-values from ANOVA are indicated. ns = not significant, *$p<0.05$, **$p<0.01$, ****$p<0.0001$. For exclusion treatments, treatments with the same letter superscript do not differ significantly (SNK post hoc test, $p<0.05$) (P = polychaete, C = crustacean, B = bivalve).

experiments, absolute biomass showed a trend towards greater biomass with nutrient addition, suggesting fewer but larger clams in plots with nutrient addition. Crustaceans (mainly haustoriid amphipods) were not numerically dominant and did not show a numerical response to nutrient addition, but they did exhibit

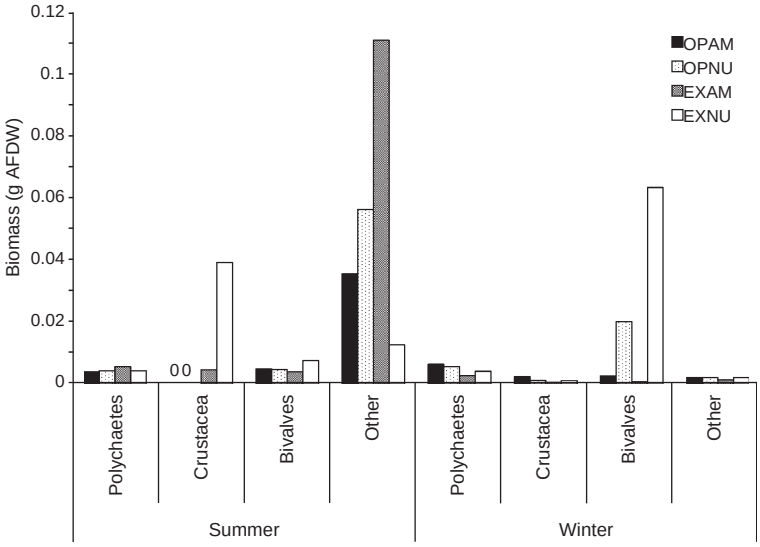

Fig. 5. Macrofauna biomass, given as ash free dry weight per plot, in summer and winter experiments in the White Oak estuary. OPAM: open plot, ambient nutrient conditions; OPNU: open plot, nutrients addition; EXAM: predator exclusion, ambient nutrient conditions; EXNU: predator exclusion, nutrients added.

Table 3
ANOVA on biomass for major taxonomic groups during summer and winter experiments in the White Oak and Cape Fear estuaries

River	Season	Taxa	Nutrient	Exclusion	Nutriens × exclusion
White Oak	Summer	Polychaetes	0.82 ns	1.42 ns	1.46 ns
		Bivalves	2.63 (0.1)	1.30 ns	0.54 ns
		Crustaceans	37.05 (0.03)	–	–
		Other	1.80 ns	0.69 ns	0.27 ns
	Winter	Polychaetes	0.40 ns	2.63 (0.09)	0.54 ns
		Bivalves	4.31 (0.053)	0.60 ns	0.52 ns
		Crustaceans	2.32 ns	0.68 ns	0.57 ns
		Other	0.01 ns	0.14 ns	0.27 ns
Cape Fear	Summer	Polychaetes	0.02 ns	11.22 (0.002)	0.01 ns
		Bivalves	0.11 ns	0.80 ns	2.42 ns
		Crustaceans	0.20 ns	1.75 ns	0.01 ns
		Other	0.05 ns	1.73 ns	0.28 ns
	Winter	Polychaetes	0.51 ns	0.01 ns	0.01 ns
		Bivalves	5.73 (0.02)	3.13 (0.08)	2.52 ns
		Crustaceans	4.16 (0.046)	0.10 ns	0.65 ns
		Other	3.87 (0.054)	2.82 (0.098)	0.01 ns

Shown are *F*-values (*p* value) for main effects of nutrient enhancement and predator exclusion treatments as well as 2-way interaction.

significantly greater biomass with nutrient additions in predator exclusion treatments during summer. This response indicates an interactive effect of release from predation pressure and potential response to nutrient additions for this taxonomic group, whose partial epifaunal habit may make it more susceptible to fish predation than other infauna. Polychaetes exhibited a numerical decline in summer nutrient addition plots relative to controls, but they exhibited no difference in overall biomass. This again suggests fewer but larger individuals with nutrient addition, with potential consequences for reproductive ability given the non-linear relationship between biomass and egg production among certain polychaete species (Levin and Creed, 1986; Gremare, 1994; Owens, 2003).

In Cape Fear, polychaetes had greater biomass in summer predator exclusion experiments whether or not nutrient addition occurred, paralleling numerical responses (Fig. 6, Table 3). Greater biomass of bivalves occurred in non-exclusion, non-nutrient addition plots during winter while crustaceans and other taxa (primarily oligochaetes) showed significant declines in biomass with nutrient additions during winter experiments (Table 3, Fig. 6)—a pattern opposite to the White Oak site.

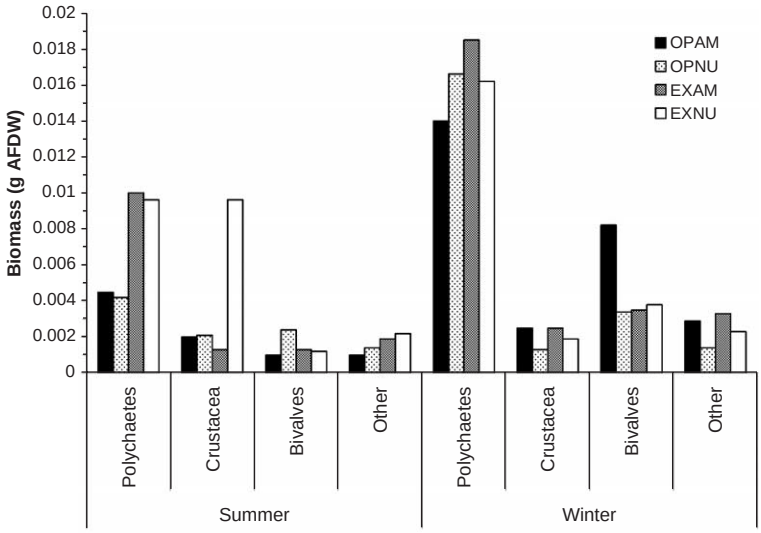

Fig. 6. Macrofauna biomass, given as mean ash free dry weight per plot, in summer and winter experiments in the Cape Fear estuary. OPAM: open plot, ambient nutrient conditions; OPNU: open plot, nutrients addition; EXAM: predator exclusion, ambient nutrient conditions; EXNU: predator exclusion, nutrients added.

4. Discussion

We predicted that: (a) strongest effects of nutrient addition should occur in the estuarine system with lowest background nutrient loading (in this case the White Oak), (b) that nutrient addition should result in increased numbers of grazing or deposit feeding taxa, and (c) responses should be greatest in predator exclusion experiments where intermediate trophic levels achieve a release from predator control. We did observe greater responses to nutrient enhancement in White Oak, but our other two predictions were not met in a simple manner. Although numerical responses occurred among 50% of the dominant taxa in White Oak, these all involved lower numbers with nutrient addition. Biomass patterns suggested the response to nutrient enhancement was complex, with lower numbers but larger biomass per individual such that total biomass was unchanged or greater with nutrient addition even with an opposing pattern for actual abundances. One unexpected and confounding factor was a difference in species composition between Cape Fear and the other 3 estuaries. Differences in exact species composition is a potential problem in any across-estuaries comparison and the estuaries in this study were chosen based on differing background conditions. However, we do not believe the differences in responses to nutrient/predation manipulations are artifacts of differing species, i.e. differential responses were not due to species present in Cape Fear being non-responsive to nutrient addition while those present in White Oak were sensitive to nutrient changes, because patterns held for those species that were in common (e.g. *Streblospio*, *Mediomastus*, oligochaeta) as well as among ecologically similar but taxonomically distinct species.

Cape Fear is characterized by higher historical nutrient levels than the other estuarine systems examined (Mallin et al., 1999). Cape Fear drains a watershed containing extensive farming areas, several small municipalities, and abundant animal husbandry operations (Mallin et al., 1999, 2000). Given the high microalgal biomass observed in the mid-intertidal Cape Fear sites in this study, indicative of a persistent eutrophic condition, it is not surprising that added nutrients in our experimental plots had little impact on faunal abundances. Lower biomass of macrofauna during certain seasons with nutrient addition in Cape Fear is suggestive that additional nutrients may have a detrimental effect. Such an inhibition may result from local hypoxic conditions when the plots were inundated. Visual observation of the plots indicated a golden sheen throughout the site (consistent with high microalgal biomass), but also dark areas suggestive of local hypoxia wherever small pieces of debris (e.g. sticks or leaf blades) or small depressions occurred on the sediment surface. In contrast, benthic microalgal biomass was much lower in the other estuarine systems examined, consistent with lower nutrient availability (Thayer, 1971; Fisher et al., 1992; Mallin, 1994; Cahoon, 1999; Glasgow and Burkholder, 2000), and microalgal biomass did exhibit a significant response to nutrient addition in both open and exclusion plots.

Benthic macrofauna may respond to increased resource availability in several ways and a variety of factors may moderate those responses. Nutrient enhancement can be associated with increased benthic microalgal food resources, especially Chlorophyta and certain benthic diatoms (Becker, 1996; Posey et al., 2002; Owens, 2003). A variety of common benthic grazers and detritivores are known to consume benthic microalgae, at least as juveniles (Pettibone, 1971; Mazurkiewicz, 1975; Stocks and Grassle, 2001; Owens, 2003), and certain taxa may demonstrate increases in reproductive potential (Bridges and Heppell, 1996; Owens, 2003). Benthic macrofauna may respond to this increased resource availability through greater abundances if survival is enhanced, if there is immigration into enriched plots from surrounding areas, or if there is greater in situ reproduction (such as with amphipods or oligochaetes that have direct development with no larval dispersal). Increased densities have been observed in large-scale comparisons of estuarine systems that vary in background nutrient levels (Beukema, 1991; Woodin, 1999; Dauer et al., 2000; Worm et al., 2000), as well as in experimental manipulations of nutrients (Dauer et al., 1982; Posey et al., 2002). However, the patterns have been mixed, especially for smaller-scale manipulative studies (Wiltse et al., 1984; Tsutsumi et al., 1990; Posey et al., 2002). Benthic macrofauna may also respond to increased food resources by growing larger (Gremare et al., 1988; Tsutsumi et al., 1990; Gremare, 1994; Levin, 1986). This may have population-level consequences, especially since the relationship between size and reproductive capacity may increase non-linearly. However, increased local reproduction may not be evidenced in small plots because of dispersal to surrounding areas. In this study we found evidence for biomass (size) responses for a variety of taxa with nutrient addition in White Oak. However, in our summer experiments increased organism size was coupled with reduced numbers for most taxonomic groups, with total numbers declining for 50% of dominant taxa but total biomass remaining constant or increasing with nutrient addition

for the corresponding higher taxonomic groups. Trade-offs between size and number are well demonstrated for resource-limited systems. However, reduction of numbers as a result of food limitation is not thought to be a common occurrence in soft-substrate communities (Peterson, 1979; Wilson, 1990). Another possible explanation for a trade-off between numbers and size is aggressive interactions among smaller and larger individuals. Several of the common taxa observed in White Oak (e.g. *Streblospio*, *Polydora*, *Nereis*, and *Aricidea*) are known to aggressively interact with both conspecifics as well as other species utilizing the near-surface benthic habitat (Commito, 1982; Levin, 1982; Posey, 1990). If nutrient additions allow some individuals to grow more rapidly, they may begin to inhibit others (Commito, 1982; Levin, 1982; Posey, 1990), leading to locally decreased abundances. One test of this hypothesis would be to examine size distributions of target taxa in nutrient addition and non-addition plots at intervals through the experiment.

Work in freshwater systems has indicated the potential importance of top-down factors in moderating responses to resource availability at intermediate trophic levels (Osenberg and Mittelbach, 1996; Power, 1992). However, the potential existence of such interactive effects in marine systems has been disputed except for limited instances (Michelli, 1999; Heck et al., 2000; Jackson et al., 2001). In this study, we did observe evidence for predator suppression of responses to resource enhancement for amphipods in both Cape Fear and White Oak during summer experiments. In White Oak during summer, amphipods were absent when predators had access regardless of nutrient treatments but exhibited a several-fold increase in nutrient addition plots relative to non-addition plots when predators were excluded. Amphipods show strong seasonal declines with the arrival of predatory fish in mid-spring (Fox and Ruppert, 1985; Posey et al., 2005) and may be particularly susceptible to predator suppression relative to infaunal polychaetes or oligochaetes. However, no other groups showed such a dramatic top-down: bottom-up interactive effect. This may be partially explained by the weak predation effects demonstrated in White Oak during both seasons or in Cape Fear during winter. Predator exclusion had a clear effect on faunal abundances for only 2 taxa in White Oak over both seasons and did not significantly affect biomass for any taxa in White Oak. However, one of the taxa responding to predator exclusion in White Oak was *Streblospio*, which is known to be strongly affected by predation (Posey et al., 1999), yet still did not exhibit interactive responses. Differing pathways for predation and nutrient enhancement effects may also be inhibiting top-down/bottom-up interactions. Predation primarily affected abundances in this study while the major impact of nutrient enhancement was to increase growth (size). On the local scale of our experimental plots, such differences in organism/population impacts from nutrient additions and predator exclusion may be expressed as independent responses.

In any study utilizing cages for exclusion of predators, one must consider potential artifacts due to the caging approach. The mesh used in this experiment was chosen, based on our previous observations, to be the smallest that could be used without extensive fouling and reduced flow effects to the underlying plots. However, it may have allowed access by small predators such as grass shrimp or juvenile mummichogs (e.g. Posey and Hines, 1991). If smaller predators were more numerous in White Oak, that may have led to lower predator exclusion effects compared to Cape Fear as well as larger infauna surviving to the end of the experiment. However, casual seine and trap sampling for epibenthic predators at both White Oak and Cape Fear sites did not indicate higher abundances of grass shrimp or small fish in White Oak and the intertidal positioning of cages would have prevented small predators from being resident in the cage plots. Moreover, nutrient addition and non-addition exclusion cages would have the same accessibility to small predators so the differences in these treatments are not likely due to exclusion artifacts, unless there was some mechanism for preferential attraction. While we cannot exclude the possibility of this artifact, we did not see any evidence that it occurred and there has been no evidence for increased abundances or foraging by smaller predators within similar cage structures in our previous studies in this region (Posey et al., 1995, 1999).

We observed significant, though seasonally varying, effects of both predation and resource enhancement. As expected, resource enhancement effects were most pronounced in the system with lower background nutrient levels. However, predation primarily affected abundances while nutrient enhancement was associated with a complex response involving both numbers (lower in summer, White Oak experiments) and biomass increases. Only one taxa, haustoriid amphipods, showed clear interactive effects between predator exclusion and nutrient enhancement. In summary, these results emphasize the varying impacts of top-down versus bottom-up factors as well as the need to measure a variety of both population and size/biomass distribution responses in the context of landscape when examining the impacts of these potential controlling influences. The results of

this study also emphasize the potential importance of moderate and local nutrient increases on benthic communities. Coastal eutrophication is receiving increased attention for its environmental impacts. However, much of the attention has focused on impacts of resulting hypoxia and anoxia. We must also recognize that there may be differential effects on benthic species at much lower levels of nutrient inputs and over small spatial scales. Furthermore, these effects may be accentuated by reductions in fish and crustaceans predators for certain fauna.

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References

Becker, M.E., 1996. The effect of nutrient loading on benthic microalgae biomass and taxonomic composition. MS Thesis, University of North Carolina at Wilmington. 29pp.

Beukema, J.J., 1991. Changes in composition of bottom fauna of a tidal-flat area during a period of eutrophication. Mar. Biol. 111, 293–301.

Breitburg, D.L., Coen, L.D., Luckenbach, M.W., Mann, R., Posey, M., Wesson, J.A., 2000. Oyster reef restoration: convergence of harvest and conservation strategies. J. Shellfish Res. 19, 371–377.

Bridges, T.S., Heppell, S., 1996. Fitness consequences of maternal effects in *Streblospio benedicti* (Annelida: Polychaeta). Am. Zool. 36, 132–146.

Burkholder, J.M., Glasgow Jr., H.B., 1997. *Pfiesteria piscicida* and other *Pfiesteria*-like dinoflagellates: behavior, impacts, and environmental controls. Limnol. Oceanogr. 42, 1052–1075.

Burkholder, J.M., Mallin, M.A., Glasgow Jr., H.B., 1999. Fish kills, bottom water hypoxia, and the toxic *Pfiesteria* complex in the Neuse River and Estuary. Mar. Ecol. Prog. Ser. 179, 301–310.

Cahoon, L.B., 1999. The role of benthic microalgae in neritic ecosystems. Oceanogr. Mar. Biol.: Annu. Rev. 37, 47–86.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. BioScience 35, 634–639.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edition. PRIMER-E, Plymouth.

Commito, J.A., 1982. The importance of predation by infaunal polychaetes in controlling the structure of a soft-bottom community in Maine, USA. Mar. Biol. 68, 77.

Dauer, M.W., Ewing, R.E., Tourtelloutte, G.K., Harlan, W.T., Sourbeer, J.W., Baker, H.R., 1982. Predation, resource limitation and the structure of the lower Chesapeake Bay. Benthic studies of lower Chesapeake Bay I. Int. Rev. Gesamten Hydrobiol. 67, 477–489.

Dauer, D.M., Weisberg, S.B., Ranasinghe, J.A., 2000. Relationship between benthic community condition, water quality, sediment quality, nutrient loads and land use patterns in Chesapeake Bay. Estuaries 23, 80–96.

Deegan, L.A., Peterson, B.H., Golder, H., McIver, C.C., Miller, M.C., 1997. Effects of fish density and river fertilization on algal standing stock, invertebrate communities, and fish production in an Artic river. Can. J. Fish. Aquat. Sci. 54, 269–283.

Downing, J.A., Osenberg, C.W., Sarnelle, O., 1999. Meta-analysis of marine nutrient-enrichment experiments: variation in the magnitude of nutrient enrichment. Ecology 80, 1157–1167.

Edmonson, W.T., 1970. Phosphorus, nitrogen and algae in lake Washington after diversion of sewage. Science 169, 373.

Elliot, M., de Jonge, V.N., 2002. The management of nutrients and potential eutrophication in estuaries and other restricted water bodies. Hydrobiologia 475, 513–524.

Estes, J.A., Peterson, C.H., 2000. Marine ecological research in seashore and seafloor systems: accomplishments and future directions. Mar. Ecol. Prog. Ser. 195, 281–289.

Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol., Annu. Rev. 17, 193–284.

Fisher, T.R., Peele, E.R., Ammerman, J.W., Harding Jr., L.W., 1992. Nutrient limitation of phytoplankton in Chesapeake Bay. Mar. Ecol. Prog. Ser. 82, 51–63.

Fox, R.S., Ruppert, E.E., 1985. Shallow-water Marine Benthic Macroinvertebrates of South Carolina. University of South Carolina Press, Columbia. 329 pp.

Freeman, D.D. 1989. The distribution and trophic significance of benthic microalgae in Masonboro Sound, North Carolina. MS Thesis, University of North Carolina at Wilmington. 122 pp.

Glasgow Jr., H.B., Burkholder, J.M., 2000. Water quality trends and management implications from a five-year study of a eutrophic estuary. Ecol. Appl. 10, 1024–1046.

Graneli, E., Sundback, K., 1985. The response of phytoplankton and microbenthic algal assemblages to nutrient enrichment in shallow coastal waters, southwest Sweden. J. Exp. Mar. Biol. Ecol. 85, 253–268.

Gremare, A., 1994. What describes the fecundity of *Capitella* sp. I better: macro- or micronutrient availability? Mar. Biol. 119, 367–374.

Gremare, A., Marsh, A.G., Tenore, K.R., 1988. Short-term reproductive responses of *Capitella* sp. I (Annelida: Polychaeta) fed on different diets. J. Exp. Mar. Biol. Ecol. 123, 147–162.

Hagberg, J., Tumberg, B.G., 2000. Studies on the covariation between physical factors and the long-term variation of the marine soft-bottom macrofauna of western Sweden. Estuar. Coast. Shelf Sci. 50, 373–385.

Hauxwell, J., McClelland, J., Behr, P.J., Valiela, I., 1998. Relative importance of grazing and nutrient controls of macroalgal biomass in three shallow estuaries. Estuaries 21, 347–360.

Heck Jr., K.L., Pennock, J.R., Valentine, J.F., Coen, L.D., Sklenar, S. A., 2000. Effects of nutrient enrichment and small predator density on seagrass ecosystems: an experimental assessment. Limnol. Oceanogr. 45, 1041–1057.

Howarth, R.W., 1988. Nutrient limitation of net primary production in marine ecosystems. Ann. Rev. Ecolog. Syst. 19, 89–110.

Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265, 1547–1551.

Hyland, J.L., Balthus, W.L., Posey, M., Hackney, C.T., Alphin, T., 2004. Soft-bottom macrobenthos of North Carolina estuaries. Estuaries 27, 501–514.

Jackson, J.B.C., Jirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.A., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–637.

Kihslinger, R.L., Woodin, S.A., 2000. Food patches and a surface deposit feeding spionid polychaete. Mar. Ecol. Prog. Ser. 201, 233–239.

Kneib, R.T., 1988. Testing for indirect effects of predation in an intertidal soft-bottom community. Ecology 69, 1795–1805.

Levin, L.A., 1982. Interference interactions among tube-dwelling polychaetes in a dense infaunal assemblage. J. Exp. Mar. Biol. Ecol. 65, 107.

Levin, L., 1986. Effects of enrichment on reproduction in the opportunistic polychaete *Streblospio benedicti* (Webster): a mesocosm study. Biol. Bull. 171, 143–160.

Levin, L., Creed, E.L., 1986. Effect of temperature and food availability on reproductive responses of *Streblospio benedicti* (Polychaeta: Spionidae) with planktotrophic or lecithotrophic development. Mar. Biol. 92, 103–114.

Levin, L., Caswell, H., Bridges, T., DiBacco, C., Cabrera, D., Plaia, G., 1996. Demographic responses of estuarine polychaetes to pollutants: life table response experiments. Ecol. Appl. 6, 1296–1313.

Mallin, M.A., 1994. Phytoplankton ecology of North American estuaries. Estuaries 17, 561–574.

Mallin, M.A., Posey, M.H., Shank, G.C., McIver, M.R., Ensign, S.H., Alphin, T.D., 1999. Hurricane effects on water quality and benthos in the Cape Fear watershed: natural and anthropogenic impacts. Ecol. Appl. 9, 350–362.

Mallin, M., Burkholder, J., Cahoon, L., Posey, M., 2000. North and South Carolina coasts. Mar. Pollut. Bull. 41, 56–75.

Mann, R., 2000. Restoring the oyster reef communities in the Chesapeake Bay: a commentary. J. Shellfish Res. 19, 335–339.

Marsh, A.G., Tenore, K.R., 1990. The role of nutrition in regulating the population dynamics of opportunistic, surface deposit feeders in a mesohaline community. Limnol. Oceanogr. 35, 710–724.

Mazurkiewicz, M., 1975. Larval development and habits of *Laeonereis culveri* (Webster) (Polychaeta: Nereidae). Biol. Bull. 149, 186–204.

McQueen, D.J., Johannes, M.R.S., Post, J.R., Stewart, T.J., Lean, D.R. S., 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr. 59, 289–309.

Menge, B.A., Daley, B.A., Lubchenko, J., Sanford, E., Dahlhoff, E., Halpin, P.M., Hudson, G., Burnaford, J.L., 1999. Top-down and bottom-up regulation of New England rocky intertidal communities. Ecol. Monogr. 69, 297–330.

Michelli, F., 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. Science 285, 1396–1398.

Moon, D.C., Stiling, P., 2002. The influence of species identity and herbivore feeding mode on top-down and bottom-up effects in a salt marsh ecosystem. Oecologia 133, 243–253.

Nearhoof, J.E., 1994. The distribution and relative abundance of benthic microalgae and phytoplankton in North Carolina estuaries of varying depth and clarity. MS Thesis, University of North Carolina at Wilmington. 52 pp.

Nixon, S.W., 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. Ophelia 41, 199–220.

Osenberg, C.W., Mittelbach, G.G., 1996. The relative importance of resource limitation and predator limitation in food chains. In: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York, pp. 134–148.

Owens, M.Q., 2003. Growth, reproduction and survivorship responses to food enhancement for two species of estuarine polychaetes: *Streblospio benedicti* and *Laeonereis culveri*. MS Thesis, University of North Carolina at Wilmington. 63 pp.

Peterson, C.H., 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Livingston, R.J. (Ed.), Ecological Processes in Coastal and Marine Systems. Plenum Publishing Corp, pp. 233–261.

Pettibone, M.H., 1971. Revision of Some Species referred to *Leptonereis*, *Nicon*, and *Laeonereis* (Polychaetea: Nereidae). Smithsonian Institution Press, Washington, DC. 53 pp.

Pitta, P., Giannakourou, A., Divanauh, P., Kentouri, M., 1998. Planktonic food in marine mesocosms in the eastern Mediterranean: bottom-up or top-down regulation? Hydrobiologia 363, 97–105.

Posey, M.H., 1990. Functional approaches to soft-substrate communities: how useful are they? Rev. Aquat. Sci. 2/3, 343–356.

Posey, M.H., Hines, A.H., 1991. Complex predator–prey interactions within an estuarine benthic community. Ecology 72, 2155–2169.

Posey, M.H., Powell, C., Cahoon, L., Lindquist, D., 1995. Top-down vs. bottom-up control of benthic community composition on an intertidal tideflat. J. Exp. Mar. Biol. Ecol. 185, 19–31.

Posey, M.H., Alphin, T., Cahoon, L., Lindquist, D., Becker, M.E., 1999. Interactive effects of nutrient additions and predation on infaunal communities. Estuaries 22, 785–792.

Posey, M.H., Alphin, T., Cahoon, L.B., Lindquist, D.G., Mallin, M.A., Nevers, M.B., 2002. Top-down versus bottom-up limitation in benthic infaunal communities: direct and indirect effects. Estuaries 25, 999–1014.

Posey, M.H., Alphin, T.D., Harwell, H., Allen, B., 2005. Importance of low salinity areas for juvenile blue crabs, *Callinectes sapidus* Rathbun, in river-dominated estuaries of southeastern United States. J. Exp. Mar. Biol. Ecol. 319, 81–100.

Power, M.E., 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73, 733–746.

Sarda, R., Valiela, I., Foreman, K., 1996. Decadal shifts in a salt marsh macroinfaunal community in response to sustained long-term experimental nutrient enhancement. J. Exp. Mar. Biol. Ecol. 205, 63–81.

Shalovenkov, N., 2000. Scales of ecological processes and anthropogenic loads on the coastal ecosystems of the Black Sea. Estuar. Coast. Shelf Sci. 50, 11–16.

Silliman, B.R., Bertness, M.D., 2002. A trophic cascade regulates salt marsh primary production. Proc. Natl. Acad. Sci. 99, 10500–10505.

Stocks, K.I., Grassle, J.F., 2001. Effects of microalgae and food limitation on the recolonization of benthic microalgae into in situ saltmarsh–pond mesocosms. Mar. Ecol. Prog. Ser. 221, 93–104.

Thayer, G.W., 1971. Phytoplankton production and distribution of nutrients in a shallow unstratified estuarine system near Beaufort, NC. Chesap. Sci. 12, 240–253.

Tsutsumi, H., Fukunaga, S., Fujita, N., Sumida, M., 1990. Relationship between growth of *Capitella* sp. and organic enrichment of the sediment. Mar. Ecol. Prog. Ser. 63, 157–162.

Ulanowicz, R.E., Tuttle, J.H., 1992. The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. Estuaries 15, 298–306.

U.S. Environmental Protection Agency (EPA), 2002. Environmental Monitoring and Assessment Program, Research Strategy. 620/R-02/002. Environmental Protection Agency, Office of Research and Development, Washington, DC.

Valentine, J.F., 2003. Seagrass herbivory, new evidence of dynamical interactions between seagrasses and their consumers. Gulf Mex. Sci. 21, 122–123.

Virnstein, R.W., 1978. Predator caging experiments in soft sediment: caution advised. In: Wiley, M.L. (Ed.), Estuarine Interactions. Academic Press, New York, pp. 261–273.

Whitney, D.E., Darley, W.M., 1979. A method for the determination of chlorophyll *a* in samples containing degradation products. Limnol. Oceanogr. 24, 183–187.

Wilson, W.H., 1990. Competition and predation in marine soft-sediment communities. Ann. Rev. Ecolog. Syst. 21, 221–241.

Wiltse, W.I., Foreman, K.H., Teal, J.M., Valiela, I., 1984. Effects of predators and food resources on the macrobenthos of salt marsh creeks. J. Mar. Res. 42, 923–942.

Woodin, S.A., 1999. Shallow water benthic ecology: a North American perspective of sedimentary habitats. Aust. J. Ecol. 24, 291–301.

Wootin, J.T., 1992. Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. Ecology 73, 981–991.

Worm, B., Lotze, H.K., Sommer, U., 2000. Coastal food web structure, carbon storage, and nitrogen retention regulated by consumer pressure and nutrient loading. Limnol. Oceanogr. 45, 339–349.