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Top-down Versus Bottom-up Limitation in Benthic Infaunal Communities: Direct and Indirect Effects

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ABSTRACT: Top-down effects of predators and bottom-up effects related to resource availability can be important in determining community structure and function through both direct and indirect processes. Their relative influence may vary among habitats. We examined the effects of nutrient enhancement and predation in southeastern North Carolina to determine relative effects on benthic macrofaunal communities. Short-term nutrient additions and predator exclusions were conducted in two estuaries to examine main and interactive effects on benthic microalgae and infauna. This experimental approach was complemented by comparisons of microalgal biomass, infaunal abundance and composition, predator abundance and predator exclusion among four estuarine systems that varied in background nutrient levels. In the short-term experiments, nutrient enhancement induced increased microalgal biomass but had limited effects on abundances or sizes of infauna. Predator exclusion increased the density of sedentary and near-surface dwelling fauna, but we did not observe interactions between predation and responses to nutrient additions, as might be predicted from a simple cascade model. General patterns of abundance were explained to a larger extent by interannual and among-estuary patterns. These results indicate a lack of simple trophic cascade responses for this community over a short time scale and little evidence for local interactive effects. The lack of interactive effects may reflect the opportunistic nature of the dominant infaunal species and potentially different time and spatial scales for the effects of predation and resource controls.

Introduction

Bottom-up (resource) and top-down (predator) controls in aquatic systems have direct, indirect and interactive effects. Nutrient enhancement can increase microalgal biomass and productivity in freshwater lakes (Edmonson 1970; Schelske 1979; Wetzel 1979; McQueen et al. 1989; Power 1992), freshwater rivers and streams (Power 1992; Deegan et al. 1997), and estuarine and nearshore marine planktonic systems (Marsh 1989; Beukema 1991; Nixon 1995; Pitta et al. 1998; Downing et al. 1999). Predation can directly regulate abundances of plants and animals at lower trophic levels (Schoener 1989; Rudstam et al. 1993) or have a variety of indirect effects through trophic cascades in a food web (Hairston et al. 1960; Carpenter et al. 1985; Carpenter and Kitchell 1988; Kneib 1988; Posey and Hines 1991; Rudstam et al. 1993; Menge 1995; Deegan et al. 1997; Heck et al. 2000).

The relative importance of bottom-up and top-down factors in structuring communities and regulating populations continues to be debated (Hunter and Price 1992; Power 1992; Strong 1992; Osenberg and Mittelbach 1996; Michelli 1999). Resource availability may set upper limits to population or biomass, but predation may regulate realized levels locally (Gutierrez et al. 1994). Productivity also may influence relative effects (Proulx and Mazumder 1998), with predator limitation possibly being more important in productive habitats where a more complex consumer guild can be supported (Oksanen et al. 1981; Osenberg and Mittelbach 1996). Top-down and bottom-up factors can act in opposing ways for intermediate trophic levels. Increases in plant productivity tend to drive increases in abundance and productivity of herbivores (Beukema 1991; Power 1992; Strong 1992; Wooten 1992; Sarda et al. 1996; Pitta et al. 1998). Predation can mask such responses by preventing abundance or biomass increases (Onuf et al. 1977; Wooton 1992; Sarda et al. 1996; Pitta et al. 1998; Menge et al 1999), effectively uncoupling bottom-up effects on producers from abundance responses at higher trophic levels. In lakes, zooplankton abundance and biomass may increase in response

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to phytoplankton blooms when predators are absent (Rudstam et al. 1993), but show no significant response when zooplanktivorous fish are present (Carpenter et al. 1985; McQueen et al. 1989).

The relative importance of top-down and bottom-up controls in marine and estuarine sedimentary systems is less well understood compared to lake habitats, due in part to the more open nature of these systems, complex trophic structure, and a diversity of production sources. The importance of predation in limiting abundances of certain marine soft-sediment fauna has been well-demonstrated, including infaunal increases with predator exclusion and seasonal changes in infauna with predator abundance changes (Peterson 1979; Levinton 1982; Wilson 1990). Nutrient enhancement (nitrogen and phosphorus) has been associated with increased benthic microalgal productivity and biomass under sufficient light conditions (Admiraal 1977; Colijn 1982; Dauer et al. 1982; Wiltse et al. 1984; Graneli and Sundback 1985; Howarth 1988; Posey et al. 1995, 1999; Becker 1996).

The proximate effects of bottom-up influences on macroinfauna are less certain. Abundances and growth rates of certain infauna increase with increased nutrient or organic inputs (e.g., sewage effluent or macroalgal decay) (Levinton and Bianchi 1981; Dauer et al. 1982; Tsutsumi 1990; Tsutsumi et al. 1990; Wolfrath 1992; Posey et al. 1999) and changes in trophic structure, including a loss of deep-burrowing taxa and a decrease in diversity, have been recorded from organically enriched or nutrient enhanced areas (Weston 1990; Simboura et al. 1995). There have been few field experimental studies that have examined relative effects of bottom-up limitation on infauna. These have indicated variable responses of macrofauna to nutrient enhancement, with increased growth and abundances in some instances (Dauer et al. 1982; Beukema 1991; Posey et al. 1995, 1999) but no detectable responses in other instances (Wiltse et al. 1984). Trophic interactions provide one possible explanation for variability in responses to bottom-up controls. Predators may crop infauna or microalgae to an extent that biomass responses to nutrient additions are not detectable. In this case, factors determining the effectiveness of predator controls may be crucial in understanding faunal responses to resource variations (Power 1992; Hauxwell et al. 1998).

Objectives and Methological Approach

We examined the relative influence of selected bottom-up and top-down factors on the composition of benthic infaunal communities. Ideally, such a study should include the full complexity of the estuarine community, including production from detrital pathways (bacteria and fungal contributions), benthic and planktonic microalgae, and higher plants; various intermediate consumers including protozoa, meiofauna, and macrofauna; and the several levels of epibenthic predators that may be resident or transient within the community. Such a study should also ideally involve broad-scale manipulations of both top-down and bottom-up factors, with appropriate controls, over a multi-year period to examine population trends. As a first approach to the complex issue of top-down and bottom-up effects we concentrated on a mid-intertidal benthic community, with a component food chain(s) represented by nutrients—benthic microalgae—benthic macroinfauna—transient epibenthic predators, experimentally examining short-term responses supported by correlative observations of ambient patterns. We concentrated on benthic microalgae as producers because of their demonstrated importance in the shallow water and intertidal systems of the southeastern United States (Cahoon and Cooke 1992; Cahoon 1999). Life history information and taxonomic considerations make benthic macrofauna most tractable for prediction of responses. We had an a priori prediction that resource availability would control benthic primary production (Cahoon 1999) with an upward cascading effect on infauna in the absence of predators. When predators are present they would control abundances of infauna with a downward trophic cascade effect (herbivory release) on benthic microalgae.

We used two basic approaches to understand infaunal responses to resource availability and predator controls. The first approach was to experimentally enhance local nutrient levels in the presence and absence of predators. Because epibenthic predators lower abundances of benthic grazers, we predicted maximal microalgal biomass increases when nutrients are added and epibenthic predators have access. Most near-surface taxa should respond to a release from predation in exclusions, likewise those taxa that can at least facultatively consume benthic microalgae should show strongest responses in treatments with nutrient additions combined with predator exclusion. Responses to nutrient additions would be best tested using obligate grazers. While several infauna in the mid intertidal habitats studied here utilize benthic microalgae during at least juvenile stages (Pettibone 1971; Mazurkiewicz 1975), there are insufficient data available to classify taxa as obligate grazers. Benthic microalgae constitute a significant component of the overall production in this and other mid-intertidal systems (Haines and Montague 1979; Asmus and Asmus 1985; Cahoon 1999) and increases in this potential food resource should result in faster growth and greater survival of juveniles for even facultative grazers if food resources are limiting (Thompson and Nichols 1988).

In order to exclude predators locally, we used exclusion cages. Experiments were limited to 4 wk because of the increased likelihood of caging artifacts with increased duration (Virnstein 1978; Peterson 1979) and the potential for resource changes associated with presence or cleaning of algal growth on cages (material falling onto the substrate). The experimental component examined short-term trophic responses. This is an appropriate time scale to address part of the broader question of trophic interactions in soft-sediment communities because many infauna exhibit rapid biomass, aggregative or population responses to changing resources or predation pressure (Dauer et al. 1982; Wilson 1991; Posey et al. 1995), including local changes over similar time scales as examined here. Nutrient inputs, microalgal production, predation pressures and recruitment also may vary seasonally in temperate estuaries and over much shorter timescales associated with runoff events (Mallin et al. 1998).

The second approach was to compare infaunal abundances in the presence and absence of predation across 4 estuarine systems that vary in ambient nutrient inputs. Although differences among estuarine systems may be expected in any study, we a priori predicted specific patterns of faunal abundance relative to nutrient and microalgal patterns if top-down and bottom-up factors were interacting. We predicted that microalgal biomass (planktonic + benthic) would be greater in those estuaries that have higher nutrient levels. These among-estuary differences include broader variations in both benthic and planktonic resource biomass than experimental manipulations, though they also include variations in covariate physical factors. Abundance of infaunal groups that consume microalgae should correlate with microalgal levels where predators are excluded, but no numerical response may be apparent where predators have access.

Methods

Study Areas

All studies were conducted in the mid-intertidal region of 4 coastal creek estuaries along the southeastern coast of North Carolina: Pages Creek, Howe Creek, Bradley Creek, and Hewletts Creek (Fig. 1). Each estuary is predominantly intertidal (> 50%) and each is an independent watershed with salinities ranging from freshwater at the head to full marine (35‰) at the mouth 3–5 km downstream. These estuaries are similar in size but differ in watershed development with consequent differences in nutrient loadings and productivity (Table 1; Mallin et al. 1998; Mallin et al. 2000). Relative annual ranks for nitrate and chl *a* were consistent for 1994–1997 (Mallin et al. 1998), with highest levels in Hewletts Creek and lowest in Pages (Table 1). Extreme levels for some creeks indicate varying responses to runoff events. Nutrient inputs are primarily from suburban and urban stormwater runoff.

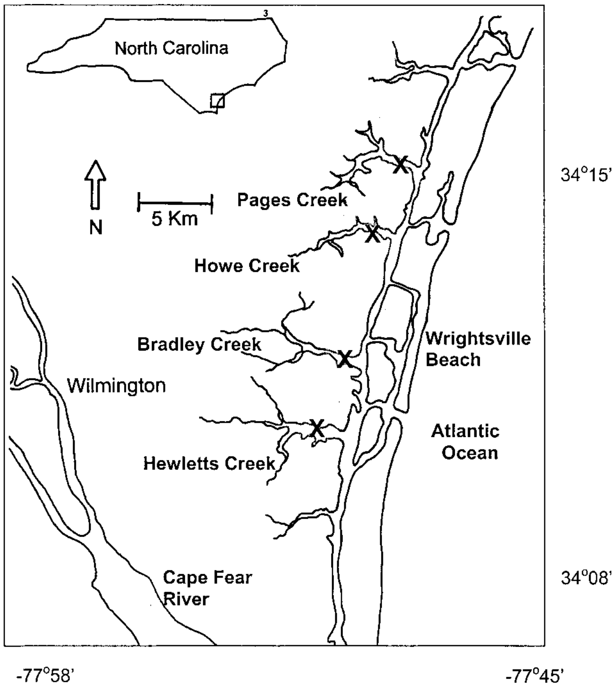

Fig. 1. Location of study creeks along the southeastern coast of North Carolina, USA. The town of Wrightsville Beach is indicated for reference.

Experimental Nutrient Additions

Blocked nutrient addition-predator exclusion experiments were conducted in Pages Creek and Bradley Creek during June 1995, June 1996 and February–March 1997. Summer is a period of high predator abundance and rapid infaunal growth in southeastern North Carolina, while winter is a period of low predator abundance. Each experiment lasted 4 wk. This duration was chosen as a compromise to reduce cage artifacts that may result from cumulative effects of current disruption and shading over time but allowing enough time for detection of density responses as evidenced in previous studies in these systems. Six experimental treatments were used representing a complete factorial design of the 2 nutrient treatments (nutrients added, no nutrients added) and 3 predator exclusion treatments (predator exclusion, no pred-

TABLE 1. Landscape, average water column nutrient conditions, and water column chlorophyll and nutrient levels during June 1995 and June 1996 for Pages, Bradley, Hewletts and Howe Creeks (area and population data from Mallin et al. 2000). Average water column nutrient and chl *a* values represent monthly means (and extremes) for 1994–1997 from 3–4 stations per creek (Mallin et al 1998). June 1995 and June 1996 values are means (and extremes) from mid estuary and lower estuary stations.

	Creek			
Parameter	Bradley	Hewletts	Howe	Pages
area (ha)	2,448	2,393	1,210	1,230
human population	13,657	13,000	3,937	4,185
average chl *a* (μg/l)	5.25 (54.6)	11.9 (203.8)	9.4 (88.4)	2.8 (40.7)
average nitrate (μM-N)	2.20 (10.61)	6.18 (41.54)	1.64 (26.52)	1.31 (7.59)
orthophosphate (μM-P)	0.18 (0.51)	0.21 (0.87)	0.21 (2.26)	0.22 (0.85)
June 1995 chl *a* (μg/l)	11.6 (11.9)	5.6 (7.9)	23.4 (61)	4.1 (9.3)
June 1995 nitrate (μM-N)	0.79 (1.43)	1.93 (15.7)	1.02 (2.64)	0.33 (0.64)
June 1995 orthophosphate (μM-P)	0.05 (0.71)	0.08 (0.16)	0.25 (0.32)	0.02 (0.26)
June 1996 chl *a* (μg/l)	5.4 (8.5)	20.4 (35.0)	13.8 (22.0)	10.2 (17.7)
June 1996 nitrate (μM-N)	3.93 (13.6)	4.21 (8.0)	0.44 (4.21)	0.33 (2.43)
June 1996 orthophosphate (μM-P)	0.26 (0.71)	0.19 (0.32)	0.13 (0.61)	0.18 (0.45)

ator exclusion-open plot, cage control-partial cage). Seven sets, each containing one replicate 1 m × 1 m plot of each treatment, were placed in each creek during each time period (moving locations between periods). This design blocked for small-scale heterogeneity that is characteristic of many tideflat areas. Plots were spaced at least 2 m apart with sets placed at least 10 m apart.

Nutrient addition was in the form of 56 g solid fertilizer spikes with an atomic N:P of 16:10 contained within an inert gypsum matrix (Posey et al. 1999). The spikes were used to provide gradual nutrient release and they provide similar nutrient elevations to repeated additions of nutrients in aqueous solution over a 4 week period (Posey et al. 1995), without the disturbance effects of solution additions. Four spikes were placed in each nutrient enriched plot 20 cm from each of the four plot sides in a diamond pattern (45° offset from the cage corners, flush with the substrate). Predators were excluded by placing a 1 m × 1 m × 12.5 cm high hardware cloth cage over the plot (Posey et al. 1999). Each cage had 1 cm mesh and was soaked for 7 days in seawater before placement in the field. Partial cages were used to mimic some of the physical effects of a cage that may produce experimental artifacts (e.g., shading and flow disruption) and were 1 m^2 made of 4 sides with a partial roof over 2 sides. Previous studies have indicated few to no significant caging artifacts with this design (Posey et al. 1995, 1999). Observations at high tide indicated mummichogs, pinfish, spot and small crabs foraged within the partial cages.

Macrofauna, microalgae, and porewater nutrients were sampled in each plot at the end of 4 weeks. Macrofauna were sampled with two 10 cm diameter × 15 cm deep cores, each taken 10 cm from a fertilizer spike. Cores were preserved in 10% formalin with rose bengal dye added and were subsequently sieved through a 0.5 mm screen and all retained organisms transferred to 50% isopropanal for later sorting and identification. Four 2.5 cm diameter × 3 cm deep cores were taken from each plot for analysis of chl *a* as a measure of microalgal biomass during summer 1995 and summer 1996 (not in winter 1997 because of logistical limitations). These cores were placed on ice in the field and frozen at −4°C upon return to the laboratory. Cores were later thawed and chl *a* biomass determined by the double extraction and spectrophotometric procedure of Whitney and Darley (1979), except that the 24 h acetone extraction was replaced by acetone extraction with sonication for 30 s. All chl *a* was contained within the top 2 cm of sediment (Becker 1996). Porewater was collected at low tide from temporary wells in each plot during summers 1995 and 1996 and was analyzed for total nitrogen and total phosphorus following Valderama (1981) on a Technicon autoanalyzer. Orthophosphate was measured in porewater using the colorimetric methods of Strickland and Parsons (1972). Benthic chlorophyll and porewater nutrients were compared among treatments and creeks using Analysis of Variance (ANOVA; see below for full model description). Data met assumptions of normality and non-heterogeneity of variances without transformation.

Over 200 infaunal species were identified from the benthic samples, with greater than 97% of the individuals collected represented by only 31 taxa. ANOVA was used to test specific hypotheses for functional group responses while multivariate approaches were used to examine year/creek/treatment groupings based on faunal abundance and community composition patterns. Since analysis of individual species' patterns would entail many multiple tests, direct comparisons of infaunal abundances between treatments were based on functional groupings. This is appropriate since initial predictions concerning responses to nutrient additions and exclusion centered on life history, feeding type, and predator susceptibility. Although assigning species to specific guilds can be problematic because of insufficient life history information and variations in feeding and movement behaviors (Fauchald and Jumars 1979), guild-level analyses have proven useful for summarizing patterns across groups of species that share certain general life history characteristics (Rhoads and Young 1970; Woodin 1976; Posey 1987, 1990; Wilson 1991; Roth and Wilson 1998; McGrady-Steed and Morin 2000). Fauna were classified into feeding groups as being deposit feeders, filter feeders, grazers (taxa demonstrated to prey on benthic microalgae), and others (infaunal predators and unknown feeding modes). Our a priori predictions were that grazers should be most sensitive to microalgal enhancement, at least when predators were excluded, with responses also likely from surface deposit feeders. Vulnerability to epibenthic predators is more dependent on position relative to the sediment surface than feeding type, so infauna were also classified as being near-surface burrowers (living predominantly within 1 cm of the sediment surface), deep burrowers, sedentary or tube dwelling fauna, or as unknown. Classifications for functional groupings were based on Fauchald and Jumars (1979), Posey et al. (1998), Gaston (1987), Flint and Rabalais (1980), Mazurkiewicz (1975), Pettibone (1971), Dauer (1997), Bianchi and Rice (1988), and field and laboratory observations.

Initially, densities of each functional group were compared among the main effects of nutrient addition (+ or −), predator exclusion (exclusion, cage control, open plots), creek (Pages or Bradley) and year using an Analysis of Variance model that also included all 2-way and 3-way interactions for all variables. Analyses were blocked for differences among experimental sets. Densities were $\log(x + 1)$ transformed to homogenize variances (Sokal and Rohlf 1981, all variances were non-heterogeneous after transformation, F-max test). However, this initial analysis of the data indicated strong differences in faunal composition among years and strong interactions ($p < 0.001$) between years and creeks, years and exclusion effects, and years and nutrient effects for all groups except deep burrowers. Analyses were then conducted separately for each year for all groups except deep burrowers using nutrient addition, exclusion and creek as main effects, blocking for experimental sets (including 3-way and 2-way interactions).

Patterns of abundance for individual taxa comprising at least 1% of the fauna collected in any time period for either creek were compared across samples using principal components analysis. Because principal components like other ordination analyses may be susceptible to variations in rare taxa, we restricted these analyses to taxa that were common in at least one treatment block and thus can reasonably be expected to contribute significantly to general community trophic interactions (species not included were generally represented by less than 10 individuals). This analysis summarized major abundance patterns and a biplot of the first 2 principal components (representing > 35% of the total variation) was used to identify major sample groupings (De'ath 1999). Sample clusters were identified using Wards Minimum Variance Cluster Analysis ($p < 0.05$, SAS Institute 1990). This approach assessed individual species' responses without collapsing taxa into functional groups.

COMPARISONS AMONG ESTUARINE SYSTEMS

During June–July 1995 and June–July 1996, benthic communities and selected water quality characteristics were compared across all 4 creeks (winter sampling could not be done in Howe and Hewletts Creeks because of logistical constraints). Benthic infaunal densities were recorded from 1 m × 1 m open plots, predator exclusion plots, and cage control plots in each of the 4 creeks. These were constructed and placed as described previously, except there were no nutrient additions in these plots. Seven replicates of each plot type were established in each creek, with plots arranged in 7 sets containing one replicate of each treatment and placed in areas of similar substrate type, tidal inundation and salinity. Infauna were sampled at the end of 4 weeks in the same manner as described before. Abundances of major functional guilds (see above) were compared by year using ANOVA with predator treatment and creek as main effects. Abundances were $\log(x + 1)$ transformed to correct heterogeneity of variances. Principal components analysis was used as described before to summarize patterns of abundance for the community defined at the species level across years, creeks, and exclusion treatments.

Sizes of three numerically dominant infaunal species, the polychaetes *Streblospio benedicti, Laeonereis culveri* and *Aricidea* sp., were measured using an ocular micrometer. Total length was measured for *Streblospio*; however, both *Aricidea* and *Laeonereis* fragmented during collection and processing, so lengths were recorded for the thoracic segments for these groups. Measurements were made only from exclusion treatments in all creeks, including both nutrient and non-nutrient exclusions in Pages and Bradley Creeks, to prevent size-selective predation biases. Measurements were recorded only for undamaged animals for *Streblospio* and for specimens that contained both undamaged thoracic and anterior abdominal segments for the other two

TABLE 2. Benthic chl *a* and sediment porewater nutrient levels in nutrient addition/predator exclusion experiments. Numbers indicate mean and (SE). F-values and significance levels are from analysis of variance comparing either year, creek, nutrient or predator exclusion treatments. All interactions were non-significant. NA = not available.

	Year		Creek		Nutrient		Predator		
Parameter	Su 95	Su 96	Bradley	Pages	Addition	No Addition	Exclusion	Open	Partial
Benthic Chl *a* (mg chl*a*/m^2)	28.1 (1.4)	52.7 (1.9)	42.4 (2.5)	38.2 (1.8)	43.0 (2.2)	37.2 (2.0)	37.4 (2.8)	40.1 (2.6)	42.9 (2.6)
	$F = 122.01$, $p < 0.0001$		$F = 4.82$, $p < 0.03$		$F = 5.22$, $p < 0.025$		$F = 1.47$, NS		
Porewater P (μM P)	32.6 (3.0)	34.0 (3.6)	38.5 (3.9)	28.7 (3.6)	40.1 (4.3)	25.9 (2.4)	39.8 (3.7)	23.2 (2.8)	NA
	$F = 0.07$, NS		$F = 4.39$, $p < 0.05$		$F = 8.65$, $p < 0.005$		$F= 16.31$, $p < 0.0002$		
Porewater N (μM N)	233 (50.1)	115 (25.4)	202 (46.1)	104 (17.9)	202 (42.7)	91.4 (16.1)	201 (38.0)	72.9 (12.2)	NA
	$F = 5.68$, $p < 0.03$		$F = 2.39$, NS		$F = 5.31$, $p < 0.03$		$F = 3.21$, NS		

species. Because of sieving damage, this reduced the number of individuals that could be measured and sizes are only reported for those combinations where at least 8 individuals could be sized.

Abundances of potential predators, including benthic-feeding fish and certain decapods, were assessed for each creek for each year using a standard bag seine. Seine hauls were conducted June and July of 1995 and 1996 at sites approximately 50 m from the location of caging experiments. The seine was 12.3 m long × 1.2 m tall with 3.2 mm Delta mesh in the wings. The bag was 1.8 m long with 1.6 mm Delta mesh. Three seines were pulled on two replicate days in each creek during each sampling period. All organisms caught were identified to lowest possible taxon, usually species.

Field parameters were measured at each site using either a YSI 6920 Multiparameter Water Quality Meter and Probe (sonde) or a Solomat 803PS Multiparameter sonde coupled with a Solomat 803 datalogger. Individual probes within the instruments measured water temperature, pH, dissolved oxygen, salinity, and conductivity. The instruments were calibrated prior to and after each sampling trip. For water column N, P, and chlorophyll, samples were collected monthly, at or near high tide. For nitrate+nitrite (hereafter referred to as nitrate) and orthophosphate, triplicate acid-washed 125 ml bottles were placed c. 10 cm below the water surface, filled, capped, and stored on ice until processing. In the laboratory the triplicate samples were filtered simultaneously through 1.0 μm glass fiber filters using a manifold with three funnels. The pooled filtrate was stored frozen until analysis using a Technicon AutoAnalyzer following EPA protocols (EPA 1997).

The analytical method used to measure chl *a* is described in Welschmeyer (1994) and EPA (1997). Chl *a* concentrations were determined directly from the 1.0 μm glass fiber filters used for filtering samples for nitrate and orthophosphate analyses. All filters were wrapped individually in aluminum foil, placed in an airtight container containing desiccant, and stored in a freezer until analysis. During the analytical process, the glass filters were separately immersed in 10 ml of a 90% acetone solution for 24 h. Each acetone solution was then analyzed for chl *a* concentrations using a Turner AU-10 fluorometer.

Results

Nutrient Addition Experiments

Nutrient additions significantly enhanced both benthic chl *a* levels and porewater nutrients, with no significant interactions ($p > 0.05$) among nutrient addition effects and creek, year or exclusion treatments (Table 2). The observed 20% greater benthic chl *a* concentration in nutrient addition plots is likely a conservative estimate of actual effects (Table 2; see Discussion). Concurrent pigment analysis indicated that primarily benthic Chlorophyta were enhanced within nutrient addition experiments (as indicated by pigment ratios from HPLC analysis) (Becker 1996). Porewater phosphorus was 55% greater and porewater nitrogen 120% greater in nutrient addition plots compared to non-addition plots (no significant interactive effects). Creek differences reflected previous observations of higher nutrient and chl *a* concentrations within Bradley Creek. Surprisingly, there was no significant effect of predator exclusion on benthic chl *a* concentrations. Our a priori hypothesis was that benthic chl *a* would be greatest in open plots where predators had access and grazer numbers were lower. The greatest variability in chl *a* levels was interannual, with an almost 2-fold difference in benthic chl *a* levels between years (Table 2).

Thirty-one taxa comprised over 97% of the individuals collected and these taxa dominated guild abundance patterns (Table 3). Polychaetes were the most numerous fauna, especially *Streblospio benedicti, Tharyx,* syllids, *Laeonereis* and *Aricidea,* with the clam *Gemma gemma,* oligochaetes, and flatworms also representing numerically important subdominants. As indicated before, total fauna, deposit feeders, grazers, sedentary-tube builders and

TABLE 3. Dominant infauna and guild classifications. G = grazers, D = deposit feeders, F = filter feeders, O = other (predators), DB = deep burrowers, NS = near surface burrowers, ST = sedentary/tube dwellers.

Taxa	Overall Mean Abundance* (no./cm^2)	Feeding Guild	Motility/Living Position Guild
Polychaetes			
Aricidea spp.	0.059 (0.004)	G	DB
Armandia maculata	0.017 (0.003)	D	NS
Capitella spp.	0.003 (0.0004)	D	DB
Hemipodus roseus	0.003 (0.0004)	O	DB
Laeonereis culveri	0.083 (0.008)	G	NS
Leitoscoloplos robustus	0.02 (0.002)	G	DB
Lumbrineris sp.	0.016 (0.001)	G	DB
Mediomastus spp.	0.021 (0.002)	D	DB
Nereis falsa	0.032 (0.005)	G	NS
Nereis succinea	0.01 (0.001)	G	NS
Notomastus sp.	0.002 (0.0003)	D	DB
Polydora socialis	0.002 (0.002)	D	ST
Prionospio heterobranchia	0.009 (0.001)	D	ST
Spiophanes bombyx	0.001 (0.0008)	D	ST
Streblospio benedicti	0.260 (0.021)	D	ST
Syllid spp.	0.095 (0.012)	O	NS
Tharyx (annulosus)	0.168 (0.012)	D	NS
Terrebelid sp.	0.011 (0.002)	D	ST
Bivalves			
Gemma gemma	0.059 (0.005)	F	ST
Solen viridis#	0.0008 (0.0002)	F	ST
Tagelus plebeius#	0.018 (0.001)	F	ST
Tellina aequistriata#	0.011 (0.002)	F/D	ST
Gastropods			
Acetocina caniculata	0.002 (0.0004)	G	NS
Ilyanassa obsoleta	0.008 (0.001)	D	NS
Saccoglossus	0.004 (0.0004)	D	DB
Diptera larva	0.005 (0.0008)	G	NS
Idotea	0.002 (0.0004)	G	NS
Oligochaeta	0.023 (0.002)	D	DB
Nematostella	0.011 (0.002)	O	ST
Phoronida	0.009 (0.002)	F	ST
Turbularia	0.083 (0.014)	O	DB

* n = 288, 1 SE indicated in parentheses; # predominantly juveniles.

near-surface burrowers exhibited differences between experimental periods and interactive effects between sampling period (especially winter vs. summer) and other treatments (Table 4).

Among the 3 living position guilds, both sedentary tube builders and near-surface fauna exhibited strong positive responses to predator exclusion during summer 1995 and summer 1996 (Fig. 2; Tables 4 and 5). There were no significant differences between no cage (open) and partial cage treatments for 11 of the 14 instances where predator exclusion effects were apparent (Table 5), indicating minimal cage artifacts. There were only 3 instances with partial cage effects, 2 occurred in winter and may represent algal trapping artifacts at this time (drift macroalgal is moderate in winter but absent in summer). There was only one instance of an intermediate effect in summer (1995; near-surface), with abundances within partials 81% of controls and 66% of exclusions. There was no evidence of changes in sediment grain size within cages and a previous study also indicated no detectable change for a similar caging design (Posey et al. 1999). Both sedentary fauna and near-surface fauna had significantly higher abundances within predator exclusion treatments relative to no cage treatments during summers. There was no significant difference among predator exclusion treatments during winter 1997 for sedentary fauna, but there was a significant density increase within partial cage treatments relative to controls for near-surface taxa. There was only a marginal effect of predator exclusion on deep-burrowing fauna, with slightly higher abundances in open plots than exclusions during winter 1997. Feeding guilds exhibited a mixed pattern. Both deposit feeders and grazers exhibited higher abundances within exclusion cages during the two summer periods, but both also exhibited significantly lower abundances within exclusion cages relative to no-cage treatments during winter 1997 (Fig. 2). Total faunal density reflected that of the numerically dominant guilds, with predator exclusion effects during summer but not during winter.

There was relatively little faunal response to nutrient additions at the temporal and spatial scale of these manipulations. Grazers and near-surface fauna exhibited higher abundances with addition of nutrients during summer 1995 (Fig. 3; Tables 4 and 5). No taxon exhibited significant responses to nutrient additions during 1996, possibly related to higher background benthic chl *a* and water column nutrient levels in 1996 compared to 1995 (Tables 1 and 2). Responses to nutrient additions were mixed during winter 1997 experiments. Deposit feeders and sedentary organisms were less dense with nutrient addition during winter, but only in no-cage treatments (possibly reflecting interactions with drift algae), while densities of near-surface fauna were greater with nutrient addition. Interactions between nutrient additions and exclusion treatments were observed during winter 1997 for grazers, deposit feeders, and sedentary tube builders. In all cases these involved significant reduction in density with nutrient additions in open plots and no significant effects for exclusion or partial cage treatments (based on analysis of nutrient effects by treatment). Differences between creeks were also observed for several groups, with generally higher abundances in Pages Creek than Bradley Creek (Table 5).

Principal components analyses of community-wide responses emphasized the seasonal and creek

TABLE 4. Mean abundance (no. cm^{-2} [1 SE]) of functional groups among exclusion treatments and nutrient treatments by year and creek.

Group	Creek	Year	Excl	Exclusion Treatment		Nutrient Treatment	
				Partial	Open	Nutrients Added	Control
Filter Feeding:							
	Bradley	1995	0.03 (0.004)	0.03 (0.005)	0.04 (0.01)	0.03 (0.005)	0.03 (0.006)
		1996	0.14 (0.05)	0.18 (0.03)	0.12 (0.03)	0.15 (0.03)	0.15 (0.03)
		1997	0.23 (0.03)	0.13 (0.03)	0.13 (0.03)	0.16 (0.03)	0.18 (0.03)
	Pages	1995	0.05 (0.01)	0.07 (0.01)	0.06 (0.01)	0.05 (0.01)	0.07 (0.01)
		1996	0.21 (0.03)	0.17 (0.03)	0.16 (0.04)	0.17 (0.03)	0.19 (0.03)
		1997	0.21 (0.04)	0.20 (0.02)	0.13 (0.02)	0.19 (0.03)	0.16 (0.02)
Deposit Feeding:							
	Bradley	1995	0.65 (0.06)	0.37 (0.04)	0.36 (0.05)	0.44 (0.05)	0.45 (0.05)
		1996	0.93 (0.15)	0.77 (0.08)	0.68 (0.08)	0.85 (0.10)	0.72 (0.05)
		1997	0.15 (0.07)	0.11 (0.02)	0.53 (0.15)	0.10 (0.01)	0.47 (0.12)
	Pages	1995	1.01 (0.21)	0.49 (0.07)	0.30 (0.04)	0.63 (0.14)	0.55 (0.09)
		1996	1.70 (0.14)	0.47 (0.06)	0.39 (0.03)	0.84 (0.14)	0.85 (0.17)
		1997	0.24 (0.02)	0.29 (0.03)	0.60 (0.12)	0.27 (0.02)	0.48 (0.09)
Grazers:							
	Bradley	1995	0.16 (0.02)	0.13 (0.02)	0.11 (0.01)	0.15 (0.01)	0.12 (0.02)
		1996	0.31 (0.06)	0.22 (0.03)	0.22 (0.03)	0.24 (0.04)	0.24 (0.02)
		1997	0.08 (0.01)	0.10 (0.02)	0.11 (0.02)	0.09 (0.01)	0.10 (0.02)
	Pages	1995	0.43 (0.06)	0.34 (0.03)	0.24 (0.02)	0.38 (0.04)	0.29 (0.03)
		1996	0.82 (0.06)	0.38 (0.04)	0.32 (0.03)	0.51 (0.06)	0.49 (0.06)
		1997	0.07 (0.01)	0.11 (0.02)	0.18 (0.04)	0.09 (0.01)	0.15 (0.03)
Sedentary/Tube Building:	Bradley	1995	0.36 (0.05)	0.20 (0.03)	0.16 (0.02)	0.22 (0.03)	0.24 (0.03)
		1996	0.44 (0.13)	0.37 (0.05)	0.31 (0.05)	0.40 (0.08)	0.34 (0.03)
		1997	0.38 (0.07)	0.25 (0.03)	0.52 (0.10)	0.28 (0.03)	0.53 (0.08)
	Pages	1995	0.89 (0.17)	0.42 (0.06)	0.25 (0.04)	0.51 (0.11)	0.51 (0.09)
		1996	1.52 (0.16)	0.41 (0.05)	0.36 (0.05)	0.69 (0.11)	0.83 (0.18)
		1997	0.34 (0.05)	0.40 (0.04)	0.40 (0.05)	0.36 (0.03)	0.40 (0.04)
Deep Burrowers:							
	Bradley	1995	0.12 (0.02)	0.11 (0.02)	0.13 (0.02)	0.13 (0.01)	0.12 (0.02)
		1996	0.13 (0.04)	0.14 (0.02)	0.16 (0.03)	0.16 (0.03)	0.12 (0.01)
		1997	0.07 (0.01)	0.09 (0.02)	0.14 (0.03)	0.08 (0.01)	0.13 (0.03)
	Pages	1995	0.19 (0.02)	0.18 (0.01)	0.18 (0.01)	0.19 (0.01)	0.17 (0.01)
		1996	0.27 (0.02)	0.24 (0.02)	0.24 (0.03)	0.26 (0.02)	0.24 (0.02)
		1997	0.07 (0.01)	0.11 (0.01)	0.21 (0.04)	0.09 (0.01)	0.17 (0.03)
Near Surface:							
	Bradley	1995	0.38 (0.03)	0.23 (0.02)	0.22 (0.03)	0.29 (0.02)	0.25 (0.03)
		1996	0.82 (0.10)	0.67 (0.08)	0.56 (0.05)	0.69 (0.08)	0.66 (0.05)
		1997	1.03 (0.09)	0.92 (0.11)	0.52 (0.10)	0.97 (0.08)	0.65 (0.10)
	Pages	1995	0.41 (0.10)	0.30 (0.03)	0.18 (0.02)	0.36 (0.06)	0.23 (0.03)
		1996	0.99 (0.10)	0.42 (0.06)	0.31 (0.03)	0.61 (0.10)	0.51 (0.07)
		1997	1.08 (0.15)	1.59 (0.18)	0.96 (0.17)	1.46 (0.14)	0.98 (0.14)

differences observed with guild comparisons (Fig. 4). The first principal component axis was dominated primarily by seasonal differences, with the winter 1997 treatments (A group) clustering separately from all other samples (Fig. 4). The second principal component included aspects of separation between the two summer periods, separation of creeks, and some predator exclusion effects (separation of full cage versus partial and open treatments). Distinct clusters included the 1995 samples from Bradley Creek, a mix of 1995 Pages Creek and 1996 Bradley Creek samples, 1996 nonexclusion treatments Pages Creek samples, and the 1996 exclusion treatments for Pages Creek (indicating exclusion effects for this creek system). There was no indication of a separation between nutrient addition and non-addition treatments.

Comparisons Among Estuarine Systems

In 1995, Pages Creek had lowest water column chl *a* levels and lowest levels of nitrate and phosphate (Table 1). Chl *a* levels were highest in Howe Creek with intermediate levels in Bradley and Hewletts. In 1996, relative chl *a* levels changed among

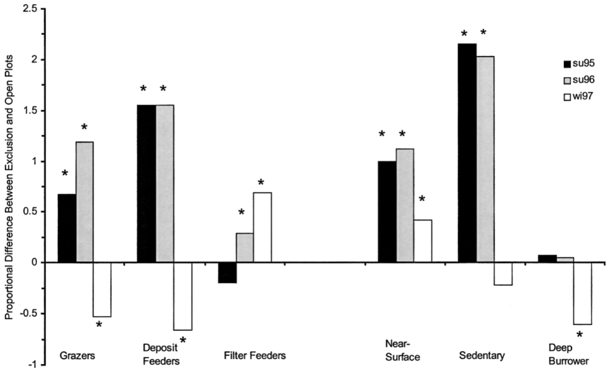

Fig. 2. Proportional difference between exclusion and noncage (open) treatments in Bradley and Pages Creek. Numbers represent the average difference among treatments standardized to open treatment densities ({exclusion − open}/open). Means and SE for each treatment/date combination are given in Table 4. Significant differences between exclusion and open treatments are indicated by * (see Table 5 for full ANOVA results).

the estuaries, without strong relation to changes in either phosphate or nitrate levels. Chl *a* is a measure of biomass and not actual productivity and may have a variety of predicted relationships with nutrient levels depending on loss rates and nutrient flux.

There were higher infaunal densities in 1996 compared to 1995 and significant differences in abundances among creeks for most functional guilds (Table 6; Fig. 5). In both years all guilds had higher density in Pages Creek or Pages and Bradley Creeks and lowest density in Hewletts or Howe Creeks, with the exception of deep burrowers in 1996 which were lowest in Bradley Creek. The only interactions between predator exclusion and creek occurred in 1996, with separate by-creek analysis of exclusion effects indicating significant differences among caging treatments in Pages and Hewletts Creeks and no significant treatment effects in Bradley or Howe Creeks for sedentary and tube dwellers and deposit feeders. Highest average predator abundances during 1996 were also observed within Pages and Hewletts Creeks (Fig. 6; see below).

Significant predator exclusion effects were observed for near-surface burrowers, sedentary organisms, and deposit feeders in both 1995 and 1996 though effects for sedentary and deposit feeding guilds in 1996 were apparent only for Hewletts and Pages Creeks (Table 6; Fig. 7). Unlike the nutrient addition-exclusion experiments, there was some evidence of cage artifacts in this experiment, with partial cages having densities intermediate to those of full cages and open treatments in 6 of 7 instances where treatment effects occurred. There was no significant difference between partial cages and open plots in 6 of 7 contrasts. Most of the intermediate effect was due to patterns in Hewletts Creek, where partial cages had intermediate densities, and was not apparent in Bradley or Pages Creeks (Fig. 2). In all cases where treatment effects occurred, abundances were highest in predator exclusion treatments relative to no cage treatments. Deep burrowing taxa did not exhibit numerical responses to predator exclusion.

The primary benthic predators were pinfish (*Lagodon rhomboides*), spot (*Leiostomus xanthurus*), flatfish (*Paralichthys* spp.), blue crabs (*Callinectes sapidus*) and mummichogs (*Fundulus* spp.), with pinfish and spot comprising over 90% of the benthivorous fish by number (Fig. 6). As with microalgae and infauna, predator densities were greater in 1996 compared to 1995.

Principal components analysis emphasized the differences observed among years and creeks for functional guilds (Fig. 8). Howe and Hewletts Creeks clustered together for each year as did Pages and Bradley Creeks. For each creek pair, 1996 formed separate groupings from 1995 samples, reflecting higher densities in 1996. There was no separation of predator exclusion (caging) treatments.

Size for selected taxa was not larger with nutrient addition or in creeks with higher microalgal biomass (Table 7). *Streblopsio benedicti* was present in all creeks in both years. The only trend in mean sizes involved slightly greater length in non-nutrient vs. nutrient treatments for *Streblospio* in Pages Creek for 1995, and greater size in 1996 compared to 1995 for Pages Creek non-nutrient and Bradley Creek samples (both non-significant, ANOVA). *Laeonereis* and *Aricidea* showed no strong size differences between years. There was no evidence for increased size with nutrient additions for any of the taxa measured.

Discussion

The benthic community studied here did not exhibit simple trophic cascades in either the sense of alternating trophic control (Hairston et al. 1960; Osenberg and Mittelbach 1996) or strong top-down effects at all trophic levels (Menge et al. 1986) and there appeared to be weak coupling between the producer and herbivore levels over the time and spatial scales examined. Predator exclusion effects were strong for infauna during both summers, consistent with other studies (Peterson 1979; Levinton 1982; Sarda et al. 1998), but were not important for microalgal biomass. Microalgal biomass responded to nutrient enhancement, but there was only limited infaunal response to nutrient additions with or without predator exclusion. There were few interactive effects between predator exclusion and nutrient addition treatments.

TABLE 5. Direct and interactive effects of nutrient additions and predator exclusion on abundances of major functional groups. Significance levels are from Analysis of Variance and values are from F-tests. For predator exclusion effects, treatments with the same number superscript do not differ significantly ($p > 0.05$, SNK test). F = full cage, P = partial cage, N = no cage. +n = nutrient addition, Con = no nutrients added. PA = Pages Creek, BR = Bradley Creek.

Taxa	Year	Nutr. Addit.	Pred. Excl.	Creek	Nutr. × Excl.	Excl. × Creek	Nutr. × Creek
Total fauna	sum 1995	ns	13.84**** $F^1 > P^2 = N^2$	14.62*** PA > BR	ns	ns	ns
	sum 1996	ns	9.11*** $F^1 > P^2 = N^2$		ns	ns	ns
	win 1997	ns	ns	9.38** PA > BR	ns	ns	ns
Feeding Guild:							
Filter Feeders	combined	ns	ns	5.27* PA > BR	ns	ns	ns
Deposit feeders	sum 1995	ns	14.38**** $F^1 > P^2 = N^2$	ns	ns	ns	ns
	sum 1996	ns	15.62**** $F^1 > P^2 = N^2$	ns	ns	6.27**	ns
	win 1997	23.82***[a] F, P: ns No cage: con > +n****	25.90**** $N^1 > P^2 = F^2$	37.38**** PA > BR	27.11****[a]	ns	ns
Grazers	sum 1995	8.05** +n > con	4.57* $F^1 > P^2 = N^2$	85.32**** PA > BR	ns	ns	ns
	sum 1996	ns	12.89**** $F^1 > P^2 = N^2$	38.57**** PA > BR	ns	ns	ns
	win 1997	ns[a] F,P: ns No cage: con > +n****	7.73** $N^1 = P^1 > F^2$	ns	21.43****[a]	ns	ns
Living Position Guild:							
Sedentary/ tube builders	sum 1995	ns	14.54**** $F^1 > P^2 = N^2$	16.09*** PA > BR	ns	ns	ns
	sum 1996	ns	12.51**** $F^1 > P^2 = N^2$	15.83*** PA > BR	ns	7.55**	ns
	win 1997	6.85*[a] F,P: ns No cage: con > + n****	ns	ns	10.12***[a]	ns	ns
Deep Burrowers	combined	ns	4.43* N > P = F	39.46*** PA > BR	ns	ns	ns
Near surface	sum 1995	7.19** +n > con	9.80*** $F^1 > P^2 > N^3$	ns	ns	ns	ns
	sum 1996	ns	11.69*** $F^1 > P^2 = N^2$	ns	ns	ns	ns
	win 1997	21.13**** +n > con	13.38**** $P^1 = F^1 > N^2$	13.39**** PA > BR	ns	4.35*	ns

* $0.01 < p < 0.05$; ** $0.001 < p < 0.01$; *** $0.0001 < p < 0.001$; **** $p < 0.0001$.

[a] Comparison of nutrient treatments made separately for each exclusion treatment because of strong interactive effects.

Benthic microalgal responses at the scales examined in these experiments were not transmitted to the infaunal trophic level. This is consistent with Micheli (1999), who suggested that for marine planktonic systems increased nutrients may enhance phytoplankton and carnivory may depress herbivores, but there is weak coupling between phytoplankton and herbivore trophic levels. We propose that for the system we studied responses are due to the open nature of the community and the opportunistic feeding strategies of the dominant infauna. Use of a variety of food resources and opportunistic life histories would mitigate against tight coupling between population and community responses and specific food resources.

Another possible explanation for the lack of response of infauna to nutrient additions is the short-term duration of these experiments. Experimental exclusions were limited in duration because of the likelihood of increasing cage artifacts over time, limiting the overall time for response in these experiments. Other studies in this system (Posey et al. 1995) indicate that this duration is sufficient to allow detection of increased survival and growth of recruits and immigration (aggregative response) that would be expected from food enhancement if food is limiting. There also was no evidence for effects on size and biomass of selected taxa, which should respond at more rapid rates than density. Among-creek comparisons were not subject to the

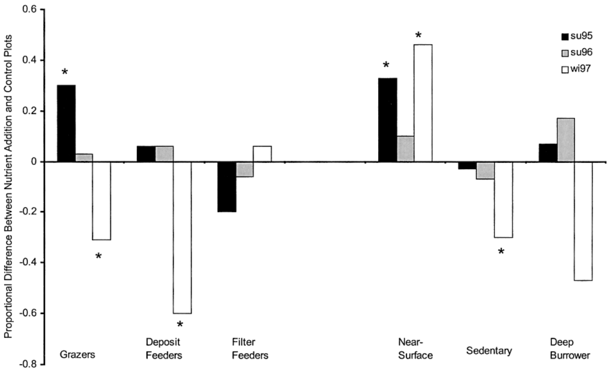

Fig. 3. Proportional difference between nutrient addition and nonaddition (control) treatments. Numbers represent the average difference among treatments standardized to control densities ({+nutrients − control}/control). Means and SE for each treatment/date combination are given in Table 4. Significant differences between nutrient addition and open treatments are indicated by * (see Table 5 for full ANOVA results).

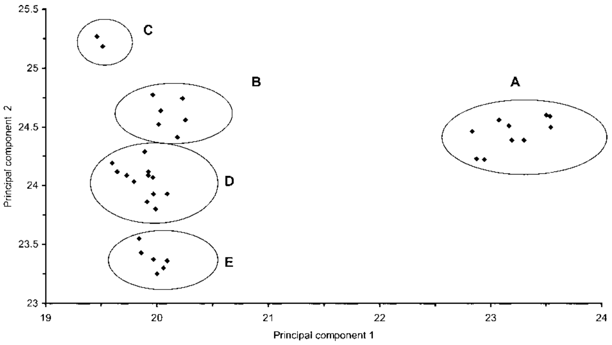

Fig. 4. Biplot of 1st and 2nd principal components for abundances of common taxa. Clusters are identified from subsequent cluster analysis of individual samples. A = all winter 1997 samples; B = 1996 Pages Creek, non exclusion samples, C = 1996 Pages Creek exclusion samples, D = 1995 Pages Creek and 1996 Bradley Creek samples, and E = 1995 Bradley Creek samples.

TABLE 6. Differences in abundance of major guilds between creeks and predator exclusion treatments during summers 1995 and 1996. PA = Pages Creek, BR = Bradley Creek, HO = Howe Creek, HE = Hewletts Creek. F = full exclusion, P = partial cage, N = no exclusion (open plot). Values are F-tests from ANOVA. Treatments or creeks with the same number superscript do not differ significantly ($p > 0.05$, SNK test).

Taxa	Year	Creek	Exclusion	Creek × Exclusion
Total fauna	1995	17.31**** PA^1 BR^{12} HO^2 HE^3	9.27*** F^{1}P^{12} N^2	ns
	1996	9.28**** PA^1 BR^{12} HE^2 HO^3	6.99**^{a} HO, BR: ns HE, PA: F^1 P^{12} N^2	4.4**^{a}
Feeding Guilds:				
Filter feeders	1995	4.98** PA^1 HO^2 BR^2 HE^3	ns	ns
	1996	14.90**** PA^1 BR^1 HO^2 HE^2	ns	ns
Deposit feeders	1995	15.67**** PA^1 BR^1 HO^2 HE^3	16.54**** F^1 P^2 N^3	ns
	1996	5.13** BR^1 PA^1 HE^{12} HO^2	7.81**^{a} HO, BR: ns HE, PA: F^1 P^2 N^2	5.07***^{a}
Grazers	1995	29.25**** PA^1 BR^2 HO^2 HE^3	ns	ns
	1996	8.25*** PA^1 HE^2 BR^{23} HO^3	ns	ns
Living Position Guilds:				
Near-surface burrowers	1995	15.38**** BR^1 PA^1 HO^2 HE	6.75** F^1 P^{12} N^2	ns
	1996	8.59**** BR^1 PA^1 HE^1 HO^2	4.14* F^1 P^{12} N^2	ns
Sedentary/tube dwellers	1995	21.95**** PA^1 BR^2 HO^2 HE^3	11.08**** F^1 P^2 N^3	ns
	1996	11.87**** PA^1 BR^2 HO^3 HE^3	7.15**^{a} HO, BR: ns HE, PA: F^1 P^{12} N^2	5.24***^{a}
Deep burrowers	1995	**** PA^1 BR^2 HE^3 HO^3	ns	ns
	1996	8.47**** PA^1 HE^1 HO^{12} BR^2	ns	ns

* $0.01 < p < 0.05$; ** $0.001 < p < 0.01$; *** $0.0001 < p < 0.001$; **** $p < 0.0001$.

[a] Comparison of exclusion effects made separately for each creek because of strong interactions.

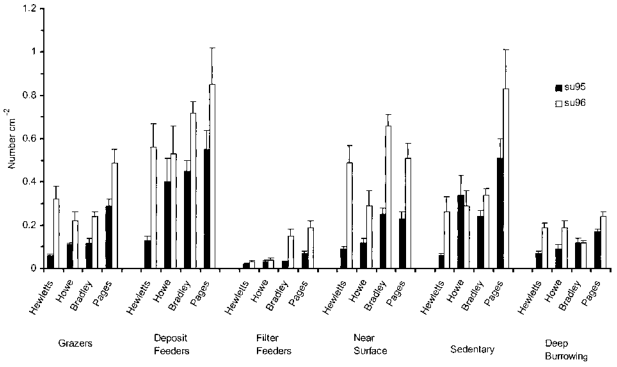

Fig. 5. Abundances of major functional groups across the 4 estuarine systems during June 1995 and June 1996. Bars represent mean per cm^2 per creek and lines above bars indicate 1 SE.

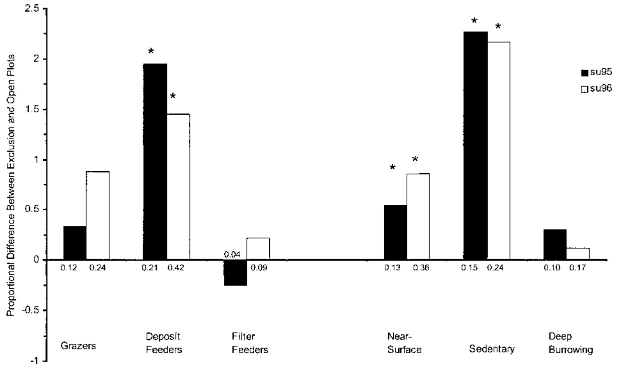

Fig. 7. Proportional difference between exclusion and noncage (open) treatments across the four creek systems. Numbers represent the average difference among treatments standardized to open treatment densities ({exclusion − open}/open). Mean density in open treatments (#/cm^{-2}) is indicated below bars. Significant differences between nutrient addition and open treatments are indicated by * (see Table 6 for full ANOVA results).

time limits of manipulations and they also did not provide evidence consistent with strong upward trophic cascades (macrofaunal densities were greatest in the estuary with lowest microalgal biomass and nutrient levels). Power analyses indicate that we should have been able to detect changes within 60–80% of the mean (depending on the group), so more subtle effects may not have been detected, especially for near-surface, deposit-feeding and grazing groups (Fig. 2).

Sensitivity of microalgae to nutrient enhancement in our experiments is consistent with other studies of both benthic microalgae (McClelland and Valiela 1998; Cahoon 1999) and estuarine/marine phytoplankton (Howarth 1988; Beukema 1991; Mallin et al. 1991; Mallin 1994; Pitta et al. 1998; Micheli 1999; Frouin 2000; Hagberg and Tumberg 2000). The average overall increase of approximately 20% is likely a conservative estimate of actual effects since laboratory studies of timescale of benthic microalgal response to continual nutrient inputs indicates that biomass may peak within 1–2 weeks and then decline (Haggerthy unpublished data; Cahoon 1999, possibly reflecting other limiting nutrients or species replacement), and there may be declines over time in nutrient inputs for our study due to dissolution of stakes and assimilation. Greater differences in microalgal biomass were observed among estuaries, with both benthic and water column chlorophyll measures historically greater in creek systems that had highest N and P concentrations and lowest in the system with lower nutrient concentrations.

Benthic infauna exhibited mixed responses to nutrient addition. At the small scale of nutrient enhancement experiments, only grazers and near-

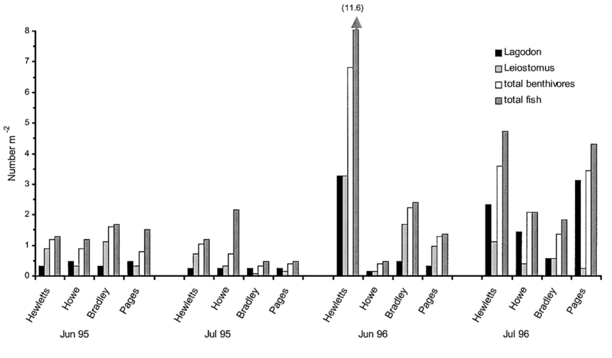

Fig. 6. Abundances of the 2 dominant benthic-feeding fish caught in seines (pinfish, *Lagodon rhomboides,* and spot, *Leiostomus xanthurus*), total benthivore abundance, and total fish abundance among the four estuarine systems in summer 1995 and summer 1996. Bars indicate mean per m^2.

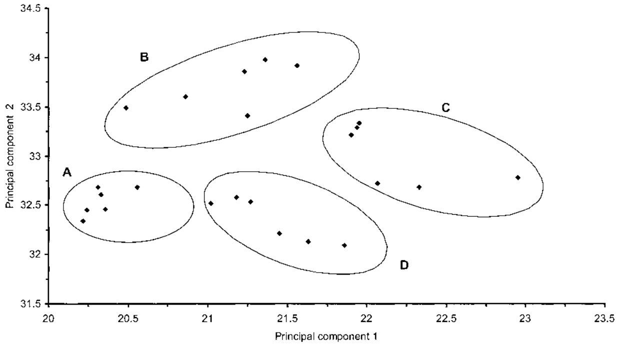

Fig. 8. Biplot of 1st and 2nd principal components for abundances of common taxa. Clusters are identified from subsequent cluster analysis of individual samples. A = all 1995 Hewletts and all 1995 Howe Creek samples, B = all 1996 Hewletts and all 1996 Howe Creek samples, C = all 1996 Pages and all 1996 Bradley Creek samples, and D = all 1995 Pages and all 1995 Bradley Creek samples. There was no differentiation among exclusion treatments for any year or creek.

TABLE 7. Sizes of selected infauna in exclusion treatments during 1995 and 1996. Numbers indicate mean total length (*Streblospio*) or thoracic length (*Laeonereis, Aricidea*) in mm. 1 SE is indicated in parentheses. N/A indicates fewer than 8 individuals could be measured.

Taxa	Year	Pages Cr.		Bradley Cr.		Hewletts Cr.	Howe Cr.
		+ Nutrients	No Nutrients	+ Nutrients	No Nutrients		
Streblospio	1995	3.3 (0.2)	4.0 (0.4)	3.3 (0.2)	3.3 (0.2)	2.9 (0.3)	3.8 (0.3)
	1996	3.8 (0.3)	3.8 (0.3)	3.7 (0.2)	3.7 (0.1)	3.2 (0.2)	3.2 (0.2)
Laeonereis	1995	1.5 (0.2)	1.5 (0.2)	1.4 (0.2)	1.0 (0.1)	N/A	N/A
	1996	1.1 (0.1)	1.4 (0.2)	1.2 (0.2)	1.1 (0.3)	N/A	N/A
Aricidea	1995	1.8 (0.2)	N/A	1.4 (0.1)	2.4 (0.3)	2.0 (0.1)	N/A
	1996	1.3 (0.1)	1.1 (0.1)	N/A	N/A	2.0 (0.4)	1.3 (0.2)

surface taxa exhibited significant responses to nutrient enhancement in summer. In both cases, responses were observed only in summer 1995 and were due primarily to increased density of *Aricidea* sp. and *Laeonereis culveri* with nutrient additions (Posey et al. 1999). Both of these polychaetes consume benthic Chlorophyta directly as either juveniles or adults (Pettibone 1971; Mazurkiewicz 1975; Fauchald and Jumars 1979) and benthic Chlorophyta were enhanced in our experiments (Becker 1996). The lack of a statistically significant response in summer 1996 may reflect the higher ambient levels of benthic chlorophyll and nutrients in 1996 compared to 1995, with differences in chlorophyll levels among years greater than small-scale enhancement effects. Greater nutrient and chlorophyll levels may be related to rainfall patterns, suburban fertilization activities, and consequent runoff during 1996 (Cahoon and Mallin unpublished data) and may have swamped manipulation effects. Patterns varied considerably in winter, with some taxa increasing with nutrient additions and other taxa less abundant with nutrient additions. Enhancement of certain taxa within open or partial treatments relative to exclusions in winter may reflect greater availability of drift macroalgae in these plots at this time. Regardless of the season, effects of experimental nutrient additions were of a much smaller magnitude than exclusion effects or among creek differences, consistent with other studies examining small-scale nutrient additions (Dauer et al. 1982; Wiltse et al. 1984; Posey et al. 1995; Hauxwell et al. 1998).

Previous studies at broader spatial scales or longer temporal scales have suggested community responses to moderate eutrophication includes species shifts from deep-burrowing to shallow-burrowing forms, increased abundance of selected taxa, and changes in sizes of certain taxa (Weston 1990; Whitehurst and Lindsay 1990; Tsutsumi et al. 1990; Beukema 1991; Sarda et al. 1996; Hauxwell et al. 1998; Hagberg and Tumberg 2000; Frouin 2000; Shalovenkov 2000). Densities of all infaunal groups in our study were lowest in the 2 estuaries with highest nutrient loading (Hewletts and Howe) and greatest in the estuary with the lowest nutrients (Pages). The experimental sites in each estuary were similar with respect to salinity, sediment grain size, distance from an inlet, and sedimentation characteristics. We suggest that the differences among the estuarine systems may reflect covariates associated with runoff (Mallin et al. 1998; Mallin et al. 2000), especially turbidity, sediments, and inputs from suburban development. Construction activity on Howe and Hewletts Creeks during 1995 and 1996 may have contributed to pulses in suspended sediments that may have negatively impacted certain groups. Differences among creek systems do not appear to be explained by differing predator abundances or relative predation effects among these creeks. Several of the groups exhibiting significant differences between creek systems did not respond significantly to predator exclusion. There were also few interactive effects between predator exclusion and creek and the magnitude of predation effects (as evidenced by difference between paired exclusion and controls within each set in each creek) also did not differ among creeks. The relative proportion of each predator type was also similar between creeks, suggesting that differences were not due to differences in type of predator present. Predation appeared to be more important in determining within-estuary abundance patterns than among estuary or among year variability.

The results of this study provide further support to the idea that marine benthic communities may not exhibit simple trophic cascades as observed in some other aquatic systems and that there may be weak coupling between local benthic production and densities of many consumers, at least over limited time scales. This may reflect the complexity of trophic interactions (Menge and Sutherland 1987), diversity of production sources, opportunism of taxa, and/or effects of other factors in limiting populations. There may also be aspects of scale dependency in effects, with bottom-up effects acting at longer time scales and over broader spatial scales than predator limitation. Density of benthic microalgae, infauna and fish were greater in all estuaries in 1996. Such among-year patterns may reflect bottom-up processes controlling broad-scale patterns, with increases at all trophic levels reflecting resource availability. In marine benthic systems there has long seemed to be a dichotomy in approaches. Experimental work, often requiring a smaller spatial scale, has emphasized the importance of predation (Peterson 1979; Wilson 1991). Broader ecosystem approaches, often involving large-scale comparisons, have often emphasized bottom-up processes (nutrient dynamics and productivity). Future work needs to concentrate on which factors may reduce transfer of effects upward or downward through the producer-macrofauna-predator web.

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