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The Responses of Patuxent River Upper Trophic Levels to Nutrient and Trace Element Induced Changes in the Lower Food Web

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ABSTRACT: As a result of human activities, coastal waters can be exposed to multiple stressors that affect primary producers and their interactions with higher trophic levels. Mesocosm experiments were conducted during spring and summer 1996–1998 to investigate the responses of natural populations of primary producers to multiple stressors and the potential for these responses to be transmitted to higher trophic levels (i.e., copepods, bivalves, anemones, and fish). The effects of two stressors, elevated nutrient and trace element loadings, were examined individually and in combination. Nutrient additions had a positive effect on biomass, productivity, and abundance of primary producers (Breitburg et al. 1999; Riedel et al. 2003). Growth or abundance of consumers increased with nutrient additions, but the magnitude of the response was reduced relative to that of their prey. Responses to trace element additions varied seasonally and among taxa. The responses of zooplankton and bivalves to stressor additions were affected by the biomass and changes in species composition of phytoplankton assemblages. The presence of fish predators did not alter zooplankton responses to stressor additions. These results suggest that the extent to which nutrient and trace element effects are transmitted from primary producers to higher trophic levels depends on the capacity of consumers to respond to stressor-induced changes in abundance and species composition of prey, on the absolute abundance of prey, and on the ability of predators to feed on alternative prey. The magnitude of the effects of stressors on estuarine food webs may depend on seasonal variability in species composition of phytoplankton assemblages, whether sensitive species dominate, and whether these species are important prey for secondary consumers. Because spatial and temporal patterns in nutrient and trace element loadings to the estuary can affect species composition of primary producers, it is critically important to examine the magnitude, timing, and spatial relationships of loadings of multiple stressors to coastal waters in order to understand the impacts of these stressors on higher trophic levels.

Introduction

Over the past century, estuarine systems have been increasingly affected by stressors such as nutrients and contaminants originating from anthropogenic activity (Boynton et al. 1995; Nixon 1988; Riedel et al. 2000; Cloern 2001). The Maryland coastal plain, in which much of the Patuxent River is located, is currently experiencing one of the highest rates of urbanization on the eastern seaboard of the U.S., with some counties growing by more than 30% in the last decade (U.S. Census Bureau 2000). As population increases, the frequency and severity of nutrient and contaminant loadings can increase. Management actions can counteract this tendency; after loading were reduced by the nutrient reduction strategies that were implemented in the Patuxent River watershed, phosphorus and nitrogen concentrations in some regions of the river decreased significantly (Patuxent Tributary Team Report 1998).

Biomass, abundance, and species composition of phytoplankton in estuaries can be strongly affected by seasonal patterns of nutrient concentrations or nutrient ratios that modify interactive effects of nutrients and trace elements (Sanders 1979; Breitburg et al. 1999), and by factors such as loading rates and the complexing capacity of the system that can influence bioavailability of contaminants (Sanders and Riedel 1993; Donat and Bruland 1995; Lores and Pennock 1999). The responses of higher trophic levels to elevated nutrients, trace elements, and their interactive effects in estuaries are less well understood than the responses of primary producers. This is especially true in estuaries where trace element concentrations are generally not toxic to consumers. In such cases, the effects of nutrients and trace elements are transmitted by food web interactions. Stressor-induced increases and reductions in primary producer populations may lead to changes in abundance or growth of

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TABLE 1. Mesocosm organism treatments (bivalves = clams and oysters, see text for details).

Mesocosm Experiment (yr)	Complexity Level	Complexity Treatment	35-μm Screened River Water	Mesozooplankton + Microzooplankton	Fish	Bivalves	Anemones	Muddy Sediment in Trays	Sandy Sediment in Trays
Experiment 1 (1996)	1	Phytoplankton	X						
	2	Zooplankton	X	X					
	3	Fish	X	X	X				
	4	Sediment	X	X	X			X	
	5	Benthos	X	X	X	X	X	X	
Experiment 2 (1997–1998)	1	Phytoplankton	X						X
	2	Zooplankton	X	X					X
	3	Fish	X	X	X				X
	4	Sediment	X	X	X	X			X
	5	Benthos	X	X	X	X	X		X

consumers, but these responses may be dampened relative to the magnitude of the response of their prey (e.g., Nixon 1986; Oviatt et al. 1993; Breitburg et al. 1999). Where the responses of primary producer populations result in changes in size-class ratios or species composition, higher trophic level responses may depend on characteristics of the consumers such as diet breadth, prey preferences, and the ability to switch among prey types.

Temporal and spatial patterns of nutrient and trace element loadings in estuarine systems are complex, and the bioavailability and toxicity of trace elements are affected by geochemical processes, as well as anthropogenic activities. The ecological effects of nutrient and trace element inputs may vary with precipitation rate, salinity, sediment type, and land use (Malone et al. 1988; Hall and Anderson 1995; Riedel et al. 2000). In the Patuxent River, inputs of trace elements such as arsenic, cadmium, nickel, and lead from terrestrial sources can be two to five times higher in winter than in summer, as a consequence of increased precipitation during this time (Riedel et al. 2000), while trace element fluxes from the sediment are affected by oxygen concentrations and the activity of benthic infauna (Riedel et al. 1997). Speciation of trace elements can be controlled by biomass and species composition of phytoplankton, which in turn mediate trophic transfer rates and control trace element availability to higher trophic levels (Sanders and Riedel 1993; Donat and Bruland 1995). Because of the potential for interactions among stressors such as nutrients and trace elements, it is important to examine their effects on the lower food web as multiple, rather than individual stressors, and to examine the responses of higher trophic levels in a context that includes seasonal, geochemical, and biological influences.

We describe results of a study that was designed to examine the potential for direct effects of multiple stressors (nutrients and trace elements) on phytoplankton assemblages to be transmitted through the food web to higher trophic levels. We examine how the magnitude and direction of the responses of higher trophic levels reflect the responses of primary producers. Our study focuses on the mesohaline Patuxent River, a tributary of Chesapeake Bay, but addresses an issue of general concern about coastal systems that are strongly influenced by human activities.

Methods

To examine the individual and interactive effects of nutrients and trace elements, as well as potential seasonal patterns of these effects, we conducted two mesocosm experiments, one during spring and summer 1996 (Experiment 1) and one during spring and summer 1997 and spring 1998 (Experiment 2). Although the two experiments varied slightly in their methods (see below), their results are combined in this manuscript for analyses of seasonal effects of stressors. When considered together, the two experiments included 4 mesocosm runs conducted in spring and 4 in summer. Each mesocosm run used twenty 1-m^3 cylindrical mesocosms that were mixed by slowly rotating paddles (described in Breitburg et al. 1999) and each lasted 5 wk.

In each mesocosm run, the interactive effects of trophic complexity and stressor treatments were examined in a factorial design of two levels of nutrients × two levels of trace elements × five levels of system complexity (Breitburg et al. 1999). Table 1 illustrates how trophic complexity was manipulated. All 20 mesocosms were filled with 35-μm screened river water, which supplied phytoplankton and smaller microzooplankton. As appropriate, trophic complexity was then increased by lengthening and broadening the food web. Mesozooplankton and microzooplankton collected from the river were added to create the second level of complexity. Fish (juvenile mummichogs; *Fundulus heteroclitus*) were added to create the third. In Experiment 1 (1996), sediment (i.e.,

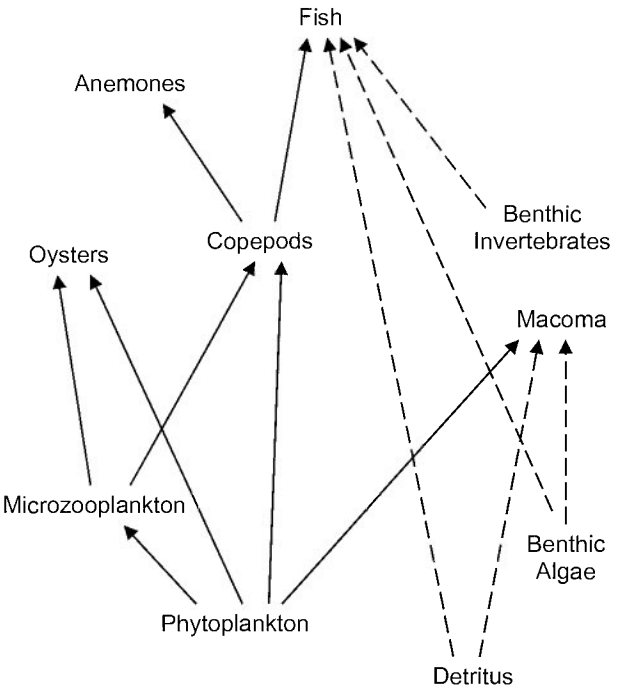

Fig. 1. Food web interactions between the major taxa in experiments. Dashed lines indicate interactions measured at a less frequent sampling interval and only indirectly as benthic respiration and photosynthesis.

muddy sand that was heat-treated to kill macrofauna) was added to create the fourth level so that sediment effects could be isolated from effects of benthos. Oysters (*Crassostrea virginica*), clams (*Macoma balthica*), and anemones (*Diadumene leucolena*) were added to create the fifth level of complexity. In Experiment 2 (1997 and 1998), trays of sandy sediment were included in all tanks, oysters and clams were added to create the fourth level, and anemones were added to create the fifth (Table 1). We made a change in sediment type to sand in Experiment 2 to reduce the confounding effects of nutrient release from sediments; the inclusion of sandy sediment in all mesocosm treatments allowed a more direct test of the effects of food web complexity on the responses to stressors. Figure 1 diagrams the dominant feeding interactions among organisms in the mesocosms.

For each of the 5 levels of trophic complexity, there were 4 stressor treatments: controls, nutrient additions (+N), trace element additions (+T), and nutrients plus trace element additions (+N+T). Within individual mesocosm runs, the 20 stressor-complexity treatments were not replicated, but each of the two experiments (consisting of 4 mesocosm runs each) provided replication through time as randomized blocks. Temperatures during the earliest spring mesocosm run (April 1996 of Experiment 1) were substantially colder than in other mesocosm runs (Table 2), nutrient levels in filtered river water that served as input to controls were higher than most of the other +N treatments (Table 3), and the species composition of zooplankton assemblages differed dramatically (see below). The April 1996 mesocosm run is therefore not included in statistical analyses presented in this paper.

A continuous flow of Patuxent River water, nominally filtered to 1 μm using an in-line sand filter and large capacity filter cartridges, was maintained to each mesocosm with a resulting turnover of 10% d^{-1}. Nutrients (nitrate and phosphate at a ratio of 16:1; Table 3) and trace elements were continuously added to the filtered river water to maintain target loadings of nutrients and target concentrations of trace metals in relevant treatments (Breitburg et al. 1999). The target loadings for nutrients were increases of 1.3–1.6 times ambient nitrogen loadings, and the target concentrations of trace elements were increases of 2–5 times typical Patuxent River concentrations. Typical levels were calculated from 1984–1995 average loadings, and 1995–1996 ambient concentrations in the Patuxent River, for nutrients and trace elements, respectively (Hagy 1996; Riedel et al. 2000). We targeted nutrient loadings and trace element concentrations in the mesocosm experiments because the dynamics of the two stressors differ in aquatic systems; nutrients are quickly taken up by primary produc-

TABLE 2. Mean, maximum, and minimum temperature (°C ± SE) and salinity (‰ ± SE) recorded in mesocosms. * Not included in statistical analyses.

Date	Season	Mean Temperature	Maximum Temperature	Minimum Temperature	Salinity
April 1996*	Early spring	13.2 (0.1)	23.5	6.2	9.0 (0.2)
June 1996	Spring	23.0 (0.1)	28.8	16.3	7.5 (0.1)
July 1996	Summer	26.1 (0.0)	29.3	20.8	8.5 (0.1)
September 1996	Summer	23.6 (0.1)	29.6	19.4	10.8 (0.0)
June 1997	Spring	19.5 (0.1)	25.3	14.9	9.8 (0.0)
July 1997	Summer	27.1 (0.0)	33.6	23.0	11.6 (0.0)
September 1997	Summer	24.7 (0.1)	29.3	21.0	14.3 (0.0)
May 1998	Spring	17.5 (0.1)	22.8	13.9	7.0 (0.0)

TABLE 3. Nutrient loadings to mesocosm tanks ($\mu g\ l^{-1}\ d^{-1} \pm$ SE). Control = filtered river water with no added nutrients. Treat = filtered river water with NO_3^- and PO_4 added. * Not included in statistical analyses.

	$[NO_3^-]$		$[PO_4]$	
Mesocosm Run	Control	Treat	Control	Treat
April 1996*	3622.7 (287.2)	5222.7 (287.2)	38.7 (5.1)	138.7 (5.1)
June 1996	1953.3 (54.8)	3553.3 (54.8)	42.7 (4.7)	142.7 (4.7)
July 1996	1684.2 (48.6)	3284.2 (48.6)	93.4 (3.8)	193.4 (3.8)
September 1996	1650.0 (51.2)	3250.0 (51.2)	130.0 (2.5)	230.0 (2.5)
June 1997	2034.0 (79.1)	3634.0 (79.1)	21.4 (1.2)	121.4 (1.2)
July 1997	1507.4 (46.4)	3107.4 (46.4)	49.0 (1.7)	149.0 (1.7)
September 1997	1112.2 (37.4)	2712.0 (37.4)	68.4 (1.6)	168.4 (1.6)
May 1998	975.4 (49.1)	2575.4 (49.1)	12.0 (0.4)	112.0 (0.4)

ers while trace elements tend to reach equilibrium between solid and dissolved phases.

Although nickel and zinc were included in the suite of trace elements in Experiment 1, information from the literature suggested that effects of nickel and zinc would be minor at the concentrations we used, so these metals were not included in the Experiment 2 in 1997–1998. Experiments designed to test individual trace element effects in our mesocosms verified this and showed that phytoplankton were primarily responding to copper and arsenic (Riedel et al. 2003). In all cases, trace elements were added to achieve target trace element concentrations (Table 4) that were below lethal levels for the animals tested (Breitburg et al. 1999).

The mesocosms were sampled twice weekly for salinity and pH, approximately weekly for nutrients and particulate carbon and nitrogen, and twice per run for trace element concentrations. Temperature was measured continuously. Phytoplankton samples were collected biweekly, preserved, and then weekly counts were conducted using inverted microscopy (Utermohl 1958). Total abundance was determined from the total number of phytoplankton cells greater than 3 μm (longest dimension) ml^{-1}. Phytoplankton cells greater than 3 μm were identified to the lowest taxonomic level possible (generally to species), and categorized by size (longest dimension) and by taxa. Phytoplankton carbon was estimated by applying volumetric conversion factors specific to each species. Phytoplankton biomass was estimated at the same time each day by in vivo fluorescence (IVF; Goldman et al. 1973; D'Elia et al. 1986). Chlorophyll *a* (chl *a*) concentrations were determined approximately weekly (Parsons et al. 1984). Phytoplankton productivity, measured as ^{14}C incorporation of samples incubated at saturating light intensities (Strickland and Parsons 1972), was estimated using 100 ml samples taken weekly from each mesocosm. Details of phytoplankton, bacterioplankton, and whole system productivity and metabolism are described in Riedel et al. (2003), Wiegner et al. (2003), and Breitburg et al. (1999).

Zooplankton

For all mesocosm runs, on the day before nutrients and trace elements were first added to mesocosm tanks, mesozooplankton were collected from the mesohaline portion of the Patuxent River by short duration plankton tows using a 0.5-m, 202-μm mesh plankton net with a solid cod-end. Zooplankton were held overnight in aquaria, then divided into aliquots and added to the appropriate mesocosms the next day. Added mesozooplankton consisted mostly of calanoid copepods, with *Acartia tonsa* composing the majority (> 99%) in all mesocosm runs analyzed for this paper. *A. tonsa* is the dominant calanoid in the mesohaline Patuxent River in late spring, summer, and fall. Densities in control tanks were similar to those seen in the Patuxent River during spring and summer 1997 and 1998 (Chesapeake Bay Program unpublished data). Starting densities in mesocosms ranged from 1.2 to 11.3 copepods l^{-1} and there were no significant differences in starting densities among the stressor or complexity treatments (randomized block ANOVA on rank transformed data: $p > 0.1$ for all comparisons), with the exception of the July 1997 mesocosm run ($p < 0.02$). In that mesocosm run, initial copepod abundances in trace element treatments (+T) were significantly higher than in control and +N treatments, but were not different from +N+T treatments ($p < 0.05$, SNK a posteriori test). Mean abundances in +T mesocosms for the entire run were not significantly higher than in controls or other treatments (see results). Microzooplankton (consisting mostly of tintinnids and rotifers) were collected using short tows with a 0.3-m, 35-μm mesh plankton net, and were handled in a similar manner as mesozooplankton.

Beginning the day following zooplankton additions to the mesocosms, mesozooplankton were generally sampled biweekly by pumping 50 l from each tank through a submerged 202-μm mesh

TABLE 4. Concentrations of dissolved trace elements measured in mesocosm tanks (μg l^{-1}). Control = average of control and +N tanks; Treat = average of +T and +T+N tanks. * Not included in statistical analyses.

	[As]		[Cu]		[Cd]		[Ni]		[Zn]	
Mesocosm Run	Control	Treat	Control	Treat	Control	Treat	Control	Treat	Control	Treat
April 1996*	0.39 (0.01)	8.24 (0.33)	0.95 (0.06)	4.70 (0.09)	0.04 (0.00)	0.79 (0.03)	1.21 (0.1)	5.44 (0.2)	3.30 (0.3)	8.05 (0.6)
June 1996	0.58 (0.02)	8.89 (0.94)	0.93 (0.06)	4.14 (0.14)	0.05 (0.01)	0.62 (0.04)	1.15 (0.1)	5.14 (0.2)	0.76 (0.1)	4.34 (1.5)
July 1996	0.85 (0.05)	4.35 (0.58)	0.70 (0.03)	3.32 (0.18)	0.02 (0.00)	0.61 (0.06)	0.71 (0.1)	4.16 (0.2)	0.38 (0.1)	1.23 (0.3)
Sept 1996	1.10 (0.10)	7.68 (0.66)	0.66 (0.06)	3.40 (0.11)	0.02 (0.00)	0.69 (0.03)	0.96 (0.0)	4.76 (0.1)	0.72 (0.1)	2.61 (0.2)
June 1997	0.31 (0.01)	11.46 (0.17)	1.06 (0.06)	5.48 (0.10)	0.07 (0.00)	0.18 (0.01)	na	na	na	na
July 1997	0.54 (0.02)	10.77 (0.21)	0.71 (0.02)	5.13 (0.10)	0.04 (0.00)	0.11 (0.00)	na	na	na	na
Sept 1997	0.85 (0.03)	12.03 (0.30)	0.69 (0.04)	4.15 (0.10)	0.02 (0.00)	0.08 (0.00)	na	na	na	na
May 1998	0.55 (0.01)	12.08 (0.21)	0.83 (0.04)	4.57 (0.15)	0.01 (0.00)	0.17 (0.01)	na	na	na	na

screen and preserving the screen contents in 5% buffered formaldehyde. We used mean copepod density (i.e., adults + copepodites l^{-1}) for each mesocosm run as a simple indicator of copepod abundance for analyses of treatment effects.

Hard-bodied microzooplankton larger than 20 μm (net microzooplankton), which include protists, small metazoans such as rotifers, and metazoan larvae and eggs, were sampled from mesocosms on the same dates as mesozooplankton by screening 8 l of hand-dipped water through a submerged 20-μm mesh screen, and then preserving the sample in 5% buffered formaldehyde. Net microzooplankton and copepod egg and nauplius abundances were not enumerated in the September 1996 mesocosm run, or in the highest two complexity treatments in some of the other mesocosm runs. Egg and nauplius and net microzooplankton data used in the following analyses are average abundance (organisms l^{-1}) in tanks in the second and third complexity levels, with the September 1996 mesocosm run not included. Zooplankton analyses in this paper will primarily focus on responses of mesozooplankton (i.e., calanoid copepod adults and copepodites) to nutrient and trace element additions.

Benthic Community and Molluscs

Mollusc and benthic treatments (fourth and fifth complexity levels) each received 50 juvenile oysters, *C. virginica* (1.8–3.0 mm^2 in shell cross-sectional area), and 80–100 juvenile clams *M. balthica* (0.4–1.4 mm^2 in shell cross-sectional area). Juvenile oysters were purchased from a local hatchery, and *Macoma* were collected from the Patuxent River. In Experiment 2 in 1997 and 1998, 2 adult oysters were also added to mollusc and benthic treatments to increase the potential effect of bivalve filtration on phytoplankton; these large oysters were not included in growth analyses. Benthic treatments also received 50–100 anemones, *D. leucolena* (0.17–0.97 mm^2 in area) that were collected from the Patuxent River. Anemones and juvenile oysters were placed on PVC panels suspended vertically in the mesocosms. Clams and mature oysters were added to the sediment.

The oyster is a suspension-feeder, feeding principally on phytoplankton, but also capable of ingesting other suspended food such as detritus and attached bacteria (Crosby et al. 1990; Langdon and Newell 1990; Baldwin and Newell 1991). *Macoma* is both a suspension feeder and surface deposit feeder (Ólafsson 1989; Lin and Hines 1994). *Diadumene* is a predator, feeding principally on zooplankton.

Clams, juvenile oysters, and anemones were videotaped and measured using an image analysis system prior to addition and at the end of the study.

Maximum diameter, minimum diameter, and cross-sectional area were measured for each individual. We used percent change in area as the primary statistic of growth for clams, juvenile oysters, and anemones because this statistic integrates growth in all dimensions. There were no significant differences in the sizes of bivalves or anemones added to stressor or complexity treatments. Because the sand used as a substrate in Experiment 2 in 1997–1998 was a suboptimal habitat for *Macoma* growth, clams grew little and sometimes suffered high mortality, so analyses for *Macoma* growth only include 1996 data, and seasonal analyses were not conducted.

Fish

Mummichogs are abundant shallow-water fishes in estuaries along the eastern coast of the U.S., are omnivores that feed on both plankton and benthos (including invertebrates, benthic algae, and detritus; e.g., Allen et al. 1994), and are tolerant of handling. Juveniles were collected with beach seines from mesohaline marshes along the Patuxent River. On the day prior to addition to the mesocosms, fish were measured to the nearest 0.5 mm in standard length (SL) and total length (TL) and wet weighed to the nearest 0.01 g (WW) after blotting with absorbent paper. There were no significant differences among stressor treatments in starting lengths or weights of fish (randomized block ANOVA on untransformed data: $p > 0.92$ for both comparisons). Fish were held overnight, and individuals injured during handling were replaced. Fish were added to the mesocosms immediately after the first zooplankton samples were taken. Seven to 9 individuals were added to each mesocosm, depending on the availability of similar-sized field-collected fish. At the end of the mesocosm run, fish were removed from the mesocosms, measured, and weighed live. Data used in analyses are mean starting and ending SL, TL, WW, and growth of fish. Some fish were either frozen or preserved in alcohol for later gut content analysis.

Statistical Analyses

Mixed model analyses (SAS Version 8: Proc Mixed) of log-transformed data were used to examine direct and interactive effects of nutrient additions (+N) and trace element additions (+T). Our a priori hypotheses were that nutrients would increase abundance and growth of organisms in +N treatments relative to Control treatments, and that trace metals would reduce abundance and growth in +T treatments relative to Controls and in +N+T treatments relative to +N treatments. The primary focus of the analyses presented here (except as noted) is an examination of stressor effects for each level of trophic complexity. Mixed models were used because they produce a better estimate of model error when random factors (mesocosm run) are included and because preliminary Levene's tests indicated that many response variables of interest were significantly heteroscedastic with respect to stressor and complexity treatments, even after log transformation. For analyses of individual experiments (i.e., 1996 or 1997–1998) the model included the main effects of stressor treatment and complexity treatment and their interaction. Mesocosm run was specified as random and as the subject in a repeated statement. Variance groupings were determined by testing potentially similar groups of treatments (based on visual inspection and preliminary Levene's tests) and examining fit statistics (Akaike's Information Criterion), followed by a Chi Square comparison of the model with grouped versus homogeneous variances. For tests including both years, we modified this model to include the independent and interactive effects of season. For phytoplankton, copepods, and fish, we included only those complexity treatments that were conducted in both years. This was not possible for oysters, but a preliminary analysis indicated that there were no significant effects of year, or effects of year-stressor interaction (effects potentially caused by nutrient release from muddy sediments), so we included all treatments in which oysters were present in the two-year combined analysis. ANOVA (Proc GLM: SAS Version 8) was used to test for differences among stressor treatments in the density or size of animals added to tanks. For clams, only Experiment 1 (1996) data were included, because clams did not grow or survive well in the sandy sediment that was substituted for muddy sediment in Experiment 2 (1997 and 1998). We did not test for the independent or interactive effects of season for clams.

Nonparametric Spearman's coefficient of rank correlation (SAS: Proc Corr) was used to explore relationships between abundance or growth of copepods, fish, and benthic invertebrates and individual variables related to environmental conditions or prey abundance. The number of correlation analyses conducted varied among consumer taxa depending on the resolution of our data on potential prey, because fewer data were available for fish prey than for prey of suspension feeders, on information from other studies on which environmental variables were likely to affect each consumers, and on the number of replicates for which data on each consumer were available. Because replication was lower for treatments that included clams ($n = 12$ using only 1996 data), we examined correlations only between growth and integrative measures of phytoplankton abundance and pro-

duction for clams, but examined relationships including a finer level of phytoplankton taxonomic resolution for copepods and oysters (n = 44 for oysters and n = 56 for copepods using data from complexity level 2).

For zooplankton and oysters, which are suspension feeders, we examined the relationships between zooplankton abundance and oyster growth and the following: salinity and temperature; total phytoplankton biomass (IVF), abundance, and carbon; phytoplankton size classes (i.e., 3–6, 6–20, > 20 μm); abundance of the dominant phytoplankton taxa (i.e., diatoms, flagellates, dinoflagellates, chlorophytes, cyanobacteria, chrysophytes, and cryptophytes); size classes of the dominant phytoplankton taxa; and total abundance of net microzooplankton. For fish, we examined the relationships of fish growth with salinity and temperature, copepod prey, and measures of benthic primary production and respiration. The latter two measurements were used as proxies for benthic prey availability because mummichogs can consume benthic algae and detritus, and because benthic prey were not sampled directly. A sequential Bonferroni-type procedure was used to control the false discovery rate for independent statistics, as described in Benjamini and Hochberg (1995).

Stepwise regressions and similar procedures were not performed because of strong correlations among some physical and biological variables. Additional statistical tests are described in the results. Unless otherwise noted, all growth analyses for fish and benthic invertebrates were conducted on tank averages in order to avoid problems of non-independence of samples. Zooplankton treatment effects were tested on mean densities from all relevant sample dates. Because the four-week experimental period (from the day of zooplankton addition to the day of the last sample) is less than the development time required for two complete generations of the dominant taxa, *A. tonsa* (Berggreen et al. 1988), as expected, there was only one peak in abundance of adult copepods after the initial additions. See Fig. 2 for an example of typical times series of zooplankton abundances compared to time series of IVF. Note that some phytoplankton results presented here differ from those in the companion paper by Riedel et al. (2003) because we have excluded data from the April 1996 mesocosm run from our analyses.

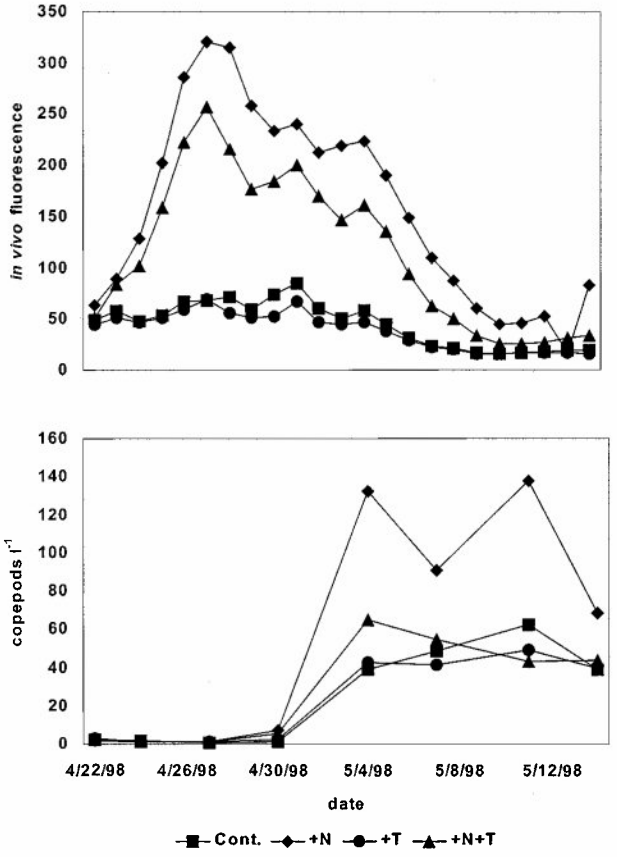

Fig. 2. Changes in (a) biomass of phytoplankton (fluorescence) and (b) abundance of copepods in May 1998 mesocosm run.

Results

General Responses to Stressor Additions

Primary producers and consumers in mesocosms were potentially influenced by direct and indirect effects of stressors, as well as by trophic complexity (i.e., predation and competition), stressor-independent variability in food quantity and quality, and natural environmental variation (e.g., temperature and salinity). To examine the effects of stressors across all complexity treatments, we examined the responses of major taxa in all relevant organism treatments in each experiment. Data are shown in Table 5.

There was a strong positive response to nutrients throughout most of the food web, while responses to trace elements tended to be weaker and more variable. Nutrient additions had a significant positive effect on phytoplankton biomass (IVF), copepod eggs and nauplii, copepods (copepodites + adults), and growth of clams, fish, and oysters (Fig. 3a, Tables 6 and 7). The responses of bivalves and fish to nutrient additions were dampened in magnitude compared to the responses of the lower food web, even though, where statistically significant, the direction of the response was the same (Fig. 3a). There was a decrease in absolute size of anemones in many of the mesocosm runs (Table 6), suggest-

TABLE 5. Organism responses to treatments, organized by season. Data for each mesocosm run are mean (± SE) using tank means as data points. Treatment means (± SE) represent data from all tanks in that treatment for which data are available. Level indicates complexity level where organism is present and included in analyses (see Methods). Net microzoo is >20 μm microzooplankton. na = data not available. * Not included in statistical analyses. SE shown for measures where n > 2. Statistical analyses for seasonal responses of fish (see Fig. 3b) use only complexity level 3 data (not shown).

Season	Mesocosm Date	Treatment	Phytoplankton Biomass (IVF) (Levels 1–5)	Net Microzoo (ind. l^{-1}) (Levels 2–3)	Copepod Eggs + Nauplii (ind. l^{-1}) (Levels 2–3)	Copepod Abundance (ind. l^{-1}) (Levels 2–5)	Clam Growth (% Change) (Levels 4–5)	Oyster Growth (% Change) (Levels 4–5)	Anemone Growth (% Change) (Level 5)	Fish Growth (Change in wt; mg) (Levels 3–5)
Spring	June 1996	Control	68.3 (13.6)	14	180	9 (6)	81	168	17*	351 (51)
Spring	June 1997	Control	37.2 (5.3)	201	144	8 (6)	3*	56	−22*	127 (15)
Spring	May 1998	Control	51.7 (4.8)	389	110	9 (6)	14*	104	11*	82 (32)
Summer	July 1996	Control	78.0 (30.4)	26	64	4 (1)	37	121	10*	233 (70)
Summer	Sept 1996	Control	34.7 (2.9)	na	na	2 (1)	19	110	5*	93 (31)
Summer	July 1997	Control	30.0 (2.2)	2,332	320	2 (0.5)	6*	19	−30*	249 (22)
Summer	Sept 1997	Control	37.3 (2.6)	820	94	3 (2)	−7*	11	29*	77 (18)
Spring	June 1996	+N	219.7 (32.3)	82	279	16 (7)	121	118	−23*	426 (27)
Spring	June 1997	+N	303.1 (48.3)	492	272	14 (11)	11*	102	−76*	110 (6)
Spring	May 1998	+N	153.5 (10.0)	607	171	26 (12)	27*	128	−12*	144 (31)
Summer	July 1996	+N	171.1 (30.3)	12	211	11 (5)	58	128	36*	327 (56)
Summer	Sept 1996	+N	135.5 (34.8)	na	na	5 (4)	68	130	−8*	90 (11)
Summer	July 1997	+N	77.6 (16.0)	3,546	435	12 (5)	2*	27	−1*	357 (17)
Summer	Sept 1997	+N	148.3 (13.9)	977	142	6 (2)	2*	20	3*	141 (19)
Spring	June 1996	+T	61.1 (11.6)	435	114	7 (4)	69	130	−1.4*	360 (86)
Spring	June 1997	+T	23.3 (3.3)	36	114	6 (5)	−3*	49	−41*	128 (9)
Spring	May 1998	+T	42.5 (3.7)	277	77	8 (6)	12*	112	5*	88 (19)
Summer	July 1996	+T	104.4 (38.3)	7	60	8 (1)	43	67	36*	240 (13)
Summer	Sept 1996	+T	40.1 (6.5)	na	na	2 (1)	27	110	24*	98 (43)
Summer	July 1997	+T	31.6 (3.7)	2,506	348	5 (3)	1*	17	−20*	223 (35)
Summer	Sept 1997	+T	37.6 (2.6)	48	71	3 (2)	−5*	13	−17*	88 (11)
Spring	June 1996	+N+T	168.8 (23.4)	25	178	17 (9)	93	142	27*	413 (25)
Spring	June 1997	+N+T	72.2 (20.5)	135	311	18 (13)	0*	68	−38*	168 (18)
Spring	May 1998	+N+T	119.0 (17.3)	295	124	10 (7)	16*	131	−25*	100 (21)
Summer	July 1996	+N+T	265.3 (75.1)	38	217	10 (3)	39	141	41*	252 (39)
Summer	Sept 1996	+N+T	123.3 (22.7)	na	na	2 (1)	48	109	24*	95 (10)
Summer	July 1997	+N+T	67.0 (11.6)	4,670	315	10 (7)	−2*	38	−15*	406 (63)
Summer	Sept 1997	+N+T	125.7 (15.0)	44	234	11 (6)	−3*	19	−16*	166 (36)

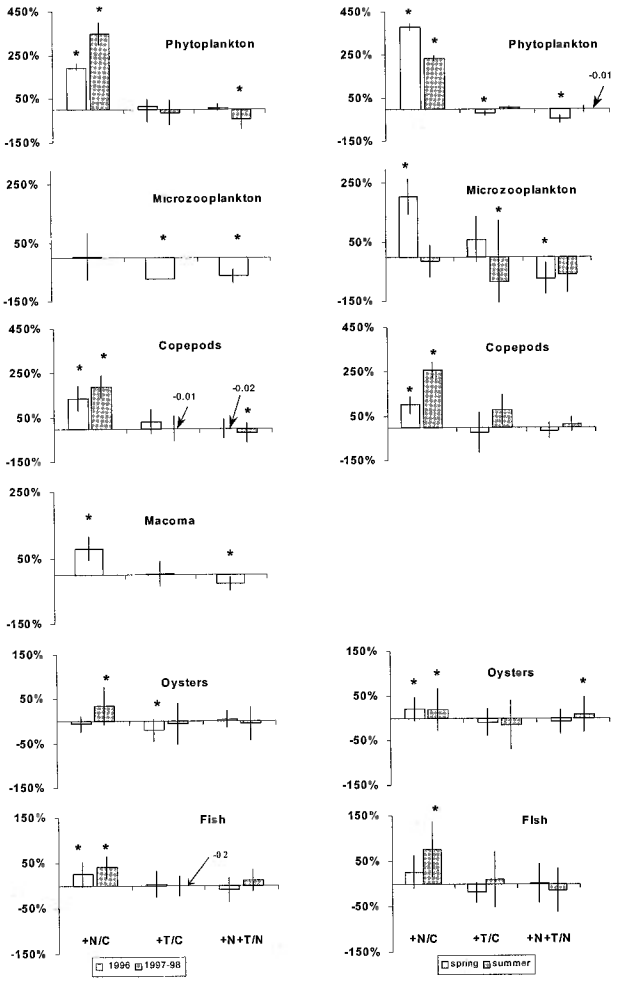

Fig. 3. Percentage change in organism measures relative to control treatments (mean ± SE). Data reflect mean of all pertinent stressor treatments compared to mean of respective controls (data from Table 5) for (a) all mesocosm runs in each experiment and (b) spring mesocosm runs compared to summer mesocosm runs. Spring and summer are defined as in Table 2. See Table 6 for statistical significance of treatment effects (ANOVA, SNK a posteriori test). Analyses were not conducted for seasonal effects of stressors on clam growth, for main effects of stressors on clam growth in 1997, or for seasonal effects on microzooplankton. Data for fish in 3b (seasonal effects of stressors) include complexity level 3 only and do not correspond to data in Table 5 (see text).

ing that these animals were not growing well in these experiments.

The effects of trace elements could potentially be seen in comparisons between organism responses in +T treatments and controls, or between +T+N treatments and +N treatments. Trace element additions (+T) resulted in a significant reduction in phytoplankton biomass and oyster growth was seen in the first experiment, and microzooplankton and copepod egg and nauplius abundance were reduced in both experiments (Tables 6 and 7, Fig.3a). Trace elements (+T treatments) had no significant effect on copepod abundance, or fish and clam growth. When the responses to +N+T treatments were compared to responses in +N treatments, microzooplankton abundances and clam growth were reduced as were the responses of phytoplankton assemblages and copepods in the second experiment.

Seasonal Patterns of Stressor Effects

Because seasonal patterns in trace element effects and trace element plus nutrient interactions were seen in measures of phytoplankton abundance and production (Breitburg et al. 1999; Riedel et al. 2003), we examined the effects of nutrients and trace element additions separately for the late spring (May and June) and summer (July, August, and September) mesocosm runs using data from both experiments, but only where complexity treatments were the same (see results and statistical methods described above and Table 7). During the spring, nutrient additions had a significant positive effect on phytoplankton biomass, microzooplankton and copepod abundance, and oyster growth. The response of suspension-feeding microzooplankton, copepods, and oysters to nutrient additions was dampened in magnitude relative to the response of phytoplankton, and the response of fish, although not statistically significant, averaged less than that of copepods (Fig. 3b).

During spring, trace element additions resulted in a significant decrease in phytoplankton biomass in +T treatments compared to controls and in +N+T treatments compared to +N treatments.

TABLE 6. Treatment means (± SE) of organism responses. Means represent data from all relevant tanks and across all relevant mesocosm runs in that treatment. n = replicates for each stressor treatment. See Table 6 and text for data included in means. Net microzoo is > 20 μm microzooplankton. * Anemones not included in statistical analyses or discussion.

Treatment	Phytoplankton Biomass (IVF) n = 35	Net Microzoo (ind. l^{-1}) n = 12	Copepod Eggs + Nauplii (ind. l^{-1}) n = 12	Copepod Abundance (ind. l^{-1}) n = 28	Clam Growth (% Change) n = 3	Oyster Growth (% Change) n = 11	Anemone Growth* (% Change) n = 7	Fish Growth (Change in wt; mg) n = 21
Control	48.1 (5.3)	630.6 (275)	152 (27)	5 (2)	46 (18)	70 (16)	3 (8)	173 (25)
+N	172.7 (15.2)	953 (419)	252 (39)	13 (3)	82 (20)	85 (15)	−11 (13)	228 (30)
+T	48.7 (6.8)	552 (350)	131 (35)	6 (1)	46 (12)	63 (14)	−2 (10)	175 (25)
+N+T	134.5 (15.6)	868 (516)	230 (27)	11 (3)	60 (17)	82 (5)	0 (12)	229 (30)

TABLE 7. Seasonal responses of organisms to treatments using data shown in Table 5 (p values of estimate are shown, numbers in bold are $p < 0.05$). Experiment indicates whether data used in analyses are from Experiment 1 (1996) or Experiment 2 (1997–1998) or both experiments. Numbers in parentheses indicate which complexity levels were included in statistical analyses. Treatments N≠C, T≠C, NT≠N indicate the comparison of responses of +N to Control, +T to Control, and +N+T to +N, respectively. ALL indicates all relevant mesocosm runs. * September 1996 data not available. See text for details of statistical methods.

	Experiment (Complexity Level)	All			Spring			Summer		
		N≠C	T≠C	NT≠N	N≠C	T≠C	NT≠N	N≠C	T≠C	NT≠N
Phytoplankton (IVF)	both (1–3)				**<0.0001**	**0.0021**	**0.0004**	**<0.0001**	0.420	0.986
	1 (1–5)	**<0.0001**	0.300	0.262						
	2 (1–5)	**<0.0001**	0.060	**0.0002**						
Microzooplankton*	both (2, 3)	0.092	**0.044**	**0.005**	**0.010**	0.951	**0.005**	0.810	**0.006**	0.225
Eggs and nauplii	both (2, 3)	**0.0006**	**0.030**	0.440	0.140	0.230	0.330	**0.0006**	0.080	0.980
Copepods	both (2, 3)				**0.009**	0.151	0.314	**0.0003**	0.551	0.891
	1 (2–5)	**0.0003**	0.151	0.329						
	2 (2–5)	**0.0001**	0.720	**0.002**						
Clam growth	1 (4, 5)	**0.0002**	0.611	**0.022**						
Oyster growth	both (4, 5)				**0.021**	0.289	0.191	**0.017**	0.217	**0.043**
	1 (4, 5)	0.468	**0.029**	0.591						
	2 (4, 5)	**0.004**	0.585	0.929						
Fish growth	both (3)				0.458	0.349	0.843	**0.0003**	0.761	0.498
	1 (3–5)	**0.013**	0.937	0.329						
	2 (3–5)	**0.004**	0.633	0.548						

With the exception of microzooplankton, abundance and growth of consumers in +T treatments were no different from controls. Microzooplankton abundance was reduced in spring +N+T treatments relative to spring +N treatments. Copepod abundances and fish growth were no different in +N+T treatments compared to +N treatments.

During the summer mesocosm runs, nutrient additions (+N) had a positive impact on phytoplankton biomass, copepod abundance, and oyster and fish growth. In the summer, trace element additions (+T) did not alter phytoplankton biomass or oyster and fish growth. Microzooplankton abundance was reduced in +T treatments relative to controls. Unlike in the spring mesocosm runs, the responses of phytoplankton biomass, and abundance and growth of all consumers with the exception of oysters were unaffected in +N+T treatments when compared to responses in +N treatments. Oyster growth was higher in +N+T treatments than in +N treatments in summer.

Specific Responses in Stressor Treatments

Phytoplankton

Averaged across all seasons and treatments, the dominant phytoplankton taxa (i.e., those taxa that composed 1% or more of the total abundance) were diatoms, flagellates, dinoflagellates, chlorophytes, cyanobacteria, chrysophytes, and cryptophytes. Centric diatoms represented 60% of the total cell count and 91% of the total phytoplankton carbon. Riedel et al. (2003) describe the responses of major phytoplankton taxa. Briefly, trace element and nutrient additions had different seasonal patterns of effects, and sometimes had interactive effects on phytoplankton biomass and cell density. The abundance of most major taxa increased in response to nutrient additions (controls versus +N and +N+T treatments) across all seasons, and in both spring and summer. No phytoplankton taxa showed a significant response to trace metal additions across all seasons or during summer. During spring, centric diatoms were significantly less abundant in +T tanks than in controls, and in +N+T tanks than in +N tanks ($p < 0.001$ for both comparisons). Much of the change in centric diatom abundance and carbon in spring trace metal addition tanks reflected the response of a large centric diatom, *Dactyliosolen fragilissimus* (*nomen novum,* formerly *Rhizosolenia fragilissima*).

Microzooplankton

Net microzooplankton abundances were significantly higher in +N treatments than in controls in spring, and lower in +T treatments in summer, while abundances were significantly lower in +N+T treatments compared to +N treatments in spring (Table 7). There was strong variability in microzooplankton abundances, which made it difficult to detect trends in responses to stressor treatments (Tables 5 and 6). For example, in the June 1996 mesocosm run, high abundances of the rotifer *Synchaeta* occurred in +T treatments, but not in the control, +N, or +N+T treatments.

Copepods

When both spring and summer were considered, copepod (adult + copepodite) responses to nutrient additions generally followed the same pattern as that of phytoplankton biomass, but the response

TABLE 8. Results of non-parametric Spearman's coefficient of rank correlation analyses (Spearman's rho, ρ). Numbers in bold are statistically significant (see statistical methods section). Analyses include physical factors and potential prey, and pooled data from all stressor treatments. Phytoplankton taxa and size categories are in terms of abundance. na = not applicable. Correlation tests with benthic primary production and respiration had smaller sample sizes, as noted.

Variables	Copepods (n = 28)	Oysters (n = 44)	Clams (n = 12)	Fish (n = 84)
Physical variables				
Salinity	**−0.49, 0.01**	**−0.85, 0.0001**	−0.59, 0.04	
Temperature	−0.36, 0.03	**−0.75, 0.0001**	−0.47, 0.12	**0.38, 0.001**
Potential prey				
Copepod abundance	na	na	na	**0.56, 0.001**
Benthic respiration (inverse)	na	na	−0.09, 0.78	**0.49, 0.001 (n = 48)**
Benthic primary production	na	na	0.35, 0.27	**0.32, 0.05 (n = 48)**
Net microzooplankton abundance	0.05, 0.82	na	na	na
Phytoplankton biomass indicators				
IVF	**0.68, 0.001**	**0.44, 0.01**	0.58, 0.05	na
Total carbon	0.41, 0.05	0.10, 0.25	0.38, 0.23	na
Total abundance	**0.63, 0.001**	**0.53, 0.001**	0.56, 0.05	na
Total chlorophyll *a*	**0.63, 0.001**	**0.46, 0.01**	**0.77, 0.01**	na
Primary production	**0.428, 0.023**	0.07, 0.63	0.67, 0.05	na
Phytoplankton size categories				
3–6 μm	**0.57, 0.01**	**0.70, 0.0001**	na	na
6–20 μm	**0.55, 0.01**	**0.68, 0.0001**	na	na
>20 μm	0.290, 0.13	0.63, 0.07	na	na
Dominant phytoplankton taxa diatoms				
Total diatoms	0.43, 0.05	0.06, 0.29	na	na
3–6 μm	**0.51, 0.01**	**0.47, 0.01**	na	na
6–20 μm	0.05, 0.81	0.47, 0.002	na	na
>20 μm	0.26, 0.19	0.03, 0.83	na	na
Flagellates				
Total flagellates	**0.50, 0.01**	**0.75, 0.0001**	na	na
3–6 μm	**0.50, 0.01**	**0.68, 0.0001**	na	na
6–20 μm	0.05, 0.79	0.09, 0.56	na	na
Dinoflagellates				
Total dinoflagellates	**0.75, 0.0001**	**0.62, 0.0001**	na	na
3–6 μm		0.016, 0.30	na	na
6–20 μm	**0.60, 0.001**	**0.66, 0.0001**	na	na
>20 μm	0.11, 0.59	0.06, 0.29	na	na
Chlorophytes				
Total chlorophytes	0.47, 0.05	**0.68, 0.0001**	na	na
3–6 μm	−0.11, 0.57	0.04, 0.80	na	na
6–20 μm	**0.63, 0.001**	**0.67, 0.0001**	na	na
>20 μm	−0.03, 0.88	0.17, 0.26	na	na
Cyanobacteria				
Total cyanobacteria	**−0.63, 0.001**	−0.14, 0.37	na	na
3–6 μm	0.03, 0.86			na
6–20 μm	**−0.67, 0.001**	−0.14, 0.37	na	na
Cryptophytes	**0.52, 0.01**	**0.43, 0.01**	na	na
Chrysophytes	−0.46, 0.05	**−0.49, 0.001**	na	na

to trace elements was not significant. In Experiment 2, copepod abundance followed the response of phytoplankton and microzooplankton when +N+T treatments were compared to +N treatments.

To investigate the roles of physical and biotic factors (listed above and in Table 8) in controlling copepod responses to stressor treatments, we conducted correlation analyses where we restricted our comparisons to complexity treatments with no fish predators (complexity level 2) to avoid high variability in copepod and phytoplankton abundance associated with comparisons between mesocosms with and without fish predators and bivalve competitors. There was no significant relationship between copepod abundance and temperature, but there was a negative relationship with salinity. There were significant positive correlations be-

tween copepod abundance and total phytoplankton abundance and biomass (IVF), chl *a* concentration, and abundance of 3–6 μm phytoplankton size classes, as well as total abundance of dinoflagellates, cryptophytes, and flagellates. There was a significant negative correlation between copepod abundance and cyanobacteria abundance. When size classes of individual phytoplankton taxa were considered, 3–6 μm diatoms, and 6–20 μm dinoflagellates and chlorophytes were positively correlated with copepod abundance. There was a significant negative correlation with 6–20 μm cyanobacteria. Copepod abundance was not correlated with large (> 20 μm) diatoms, which frequently dominated phytoplankton assemblages in these experiments (Riedel et al. 2003).

To examine the effects of predation by fish on copepod responses to stressors, we compared the responses of copepods in complexity level 2 treatments (without fish predators) to responses in complexity level 3 treatments (with fish predators). As with the seasonal analyses, we restricted our analyses to complexity treatments 2 and 3. Across all mesocosm runs, copepod abundances were lower in mesocosms with fish predators compared to those without fish ($p < 0.0001$, Fig. 4a). We then compared the effects of nutrient and trace element additions on copepod abundances in complexity level 2 to abundances in complexity level 3 (Fig. 4b). Although fish predation severely reduced copepod abundance, nutrient enrichment resulted in significant increases in copepod abundance in treatments both with and without fish predation, when +N treatments were compared to controls (Fig. 4b). There were no significant effects of trace element additions in either case, nor was there a significant difference in the magnitude of the nutrient effect between the two organism treatments ($p = 0.31$).

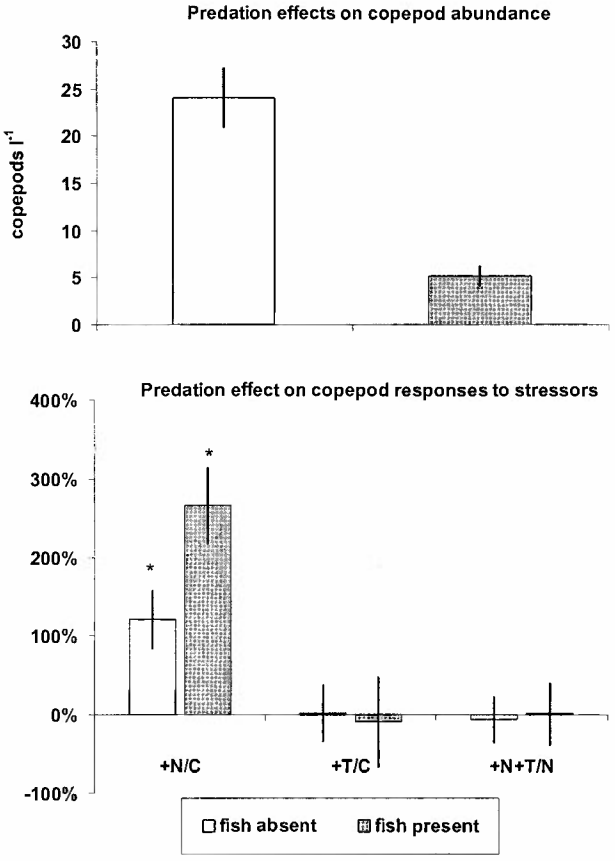

Fig. 4. (a) Abundance of copepods (mean ± SE) in mesocosms without predation (complexity level 2) and with predation (complexity level 3). (b) Stressor effects in tanks without fish predation and in tanks with fish predation.

Benthic Invertebrates

Clam and oyster growth increased in response to nutrient additions, and in the case of oysters in Experiment 1, decreased in response to trace element additions (Fig. 3a, Table 7). When seasonal effects were examined, positive responses to nutrients, but not to the direct effects of trace elements, were seen for oysters in summer and spring. The effect of trace elements was seen in summer as increased growth in +N+T treatments compared to +N treatments (Fig. 3b). Overall, there was substantial variability in bivalve growth among mesocosm runs and among treatments (Tables 5 and 6).

The same suite of physical and biotic variables was used to examine factors potentially influencing oyster growth as were compared with zooplankton abundance (Table 8). Because of the reduced sample size, we only examined correlations between growth and integrative measures of phytoplankton abundance and production for clams. Because *Macoma* is a deposit feeder as well as a suspension feeder, we used data on benthic respiration and primary production that were available from a subset of mesocosms as measures of benthic prey ($n = 12$; Seitzinger and Laursen unpublished data). The inverse of benthic respiration was used as a measure of available benthic carbon. Because these data do not provide information on species composition of benthic organisms, we could not distinguish effects of stressors on prey abundance from effects on taxonomic composition of potential prey. In addition, benthic respiration and photosynthesis were only measured in the tanks once per mesocosm run.

Oyster growth was negatively correlated with temperature and salinity (Table 8). Oyster growth was positively correlated with abundance and carbon of most major phytoplankton taxa (flagellates,

dinoflagellates, chlorophytes, and cryptophytes) and with phytoplankton biomass (IVF) and abundance, and chl *a*. The abundance of the 3–6 μm and the 6–20 μm size fractions were positively related to oyster growth. There was a negative relationship with chrysophyte abundance, and as was the case with copepods, no significant relationship with > 20 μm diatoms. For *Macoma,* there was a positive relationship between growth and total chl *a*.

Anemones showed little relationship to any of the variables. Mean copepod densities were very low in the tanks with anemones (mean = 2.4 ± 2.0). Anemone growth was highly variable and in many treatments, the mean growth rate was negative, suggesting that there was insufficient food available for them.

Fish

Fish averaged 17.2 ± 0.3 mm SL and 100 ± 10 mg in WW at the start of the mesocosm run, and grew to 25.0 ± 0.4 mm SL and 300 ± 10 mg in WW. Fish responses to nutrient additions were always lower in magnitude than the responses of their copepod prey (Fig. 3).

Fish grew significantly more in both length and weight in treatments with nutrient additions than in those without added nutrients in both mesocosm experiments, and during summer in complexity level 3 (fish tanks; Fig. 3, Table 5). In contrast to the relatively consistent effects of nutrients, trace elements had no significant effect on fish growth in either mesocosm experiment or in analyses of the spring runs in which trace elements had significant negative effects on phytoplankton. The nutrient-trace element interaction that was observed for phytoplankton was not reflected in fish growth.

Examination of fish gut contents confirmed that both zooplankton and benthic prey were consumed by fish in mesocosms. Of the potential prey consumed by fish, we only have direct counts of zooplankton abundances because periodic sampling for benthic prey would potentially have killed clams and disrupted other benthic processes that were being monitored. As with *Macoma,* we used data on benthic respiration and photosynthesis that were available from a subset of mesocosms (n = 48; Seitzinger and Laursen unpublished data) as a measure of benthic prey abundance, and used the inverse of benthic respiration as a measure of available benthic carbon.

Fish growth was positively correlated with temperature as well as with copepod abundance, benthic primary production, and the inverse of benthic respiration (Table 8). Analyses that included benthic respiration, copepod density, starting weight and temperature, as well as stressor treatment indicated that neither trace element nor nutrient additions per se explained a significant portion of the variance (ANOVA $p > 0.49$ for stressor treatments).

Discussion

In coastal systems, input of stressors from anthropogenic sources can influence the standing stock and growth of animals through both direct and indirect pathways. Contaminants can be lethal or cause disease or slow growth by directly interfering with physiological processes (e.g., Zarooglian and Morrison 1981; Sullivan et al. 1983; Cecchine and Snell 1999). High nutrient loadings potentially affect consumer populations by altering the abundance and taxonomic composition of prey, and by degrading habitat as a result of low dissolved oxygen, reduced water clarity, and altered benthic community diversity (Oviatt et al. 1993; Dauer 2000). Similarly, at levels that are not lethal to higher organisms, contaminants such as trace elements can alter productivity and species composition of primary producers (Thomas and Siebert 1977; Hall and Anderson 1995; Payne and Price 1999). The effects of multiple stressors such as nutrients and trace elements on upper trophic levels in coastal systems are modulated by physical and biological attributes of the system (Breitburg et al. 1999; Cloern 2001), and therefore ecosystem responses to these stressors may not be directly correlated with nutrient and trace element loading rates.

Our experiments were designed to test food web effects, and for upper trophic levels, asked a simple question: To what extent are the direct effects of nutrients and trace elements on primary producers mirrored in upper trophic levels? The potential for increased nutrients and trace element loadings to indirectly influence upper trophic levels through the food web will depend on the magnitude and direction of the direct effects on primary producers. When the effect of nutrients and contaminants is not uniformly expressed by all species within an assemblage of primary producers, the magnitude of the response of consumers may be a function of the structure of the food web, including the degree of omnivory and predation; the ability of consumers to switch between different types of prey; and the time scales over which consumers respond to changes in food availability.

Magnitude of Responses

While the magnitude of the responses varied among taxa, our results show that nutrient-induced increases in phytoplankton biomass were consistently reflected in increases in growth or abundance of higher trophic levels. All organisms tested

in these experiments, with the exception of anemones and microzooplankton, responded to increased nutrients with increased growth or abundance, regardless of whether or not the principal items in their diet were primary producers (Fig. 3). Although generally smaller in magnitude than the phytoplankton response, the magnitude of the zooplankton response was greater than that of bivalve and fish responses. Undoubtedly, part of the difference between the magnitude of phytoplankton and upper trophic level responses to nutrients resulted from the inefficiency of energy transfer through the food web (Fenchel 1988; Baird and Ulanowicz 1989). Our correlation analyses (Table 8) suggest that the magnitude of the indirect responses of suspension feeders to nutrient additions relative to the magnitude of the direct responses, of phytoplankton, may also be influenced by changes in prey taxonomic composition. Physical factors such as temperature and salinity may also play a role.

In contrast to the effects of nutrients, our results also suggest that the seasonally strong effect of trace elements (i.e., +T versus control and +N+T versus +N) on phytoplankton biomass and production and microzooplankton abundance is not consistently transmitted to upper trophic levels through food web interactions. The concentrations of trace elements we tested were purposely selected to be below those known to have lethal or chronic effects on animals in the mesohaline Patuxent River (Breitburg et al. 1999), because our goal was to test for more subtle effects that might be mediated through food web interactions. If there was a direct effect of trace elements on organisms in our experiments, responses would most likely originate from reduced survival of microzooplankton and copepod juveniles, which should be more sensitive to toxins than adult copepods (e.g., Kusk and Petersen 1997; Lores and Pennock 1999), or fish and bivalves. Trace element concentrations measured in mesocosms (Table 4) were below threshold levels measured for toxicity of calanoid adults and nauplii (Arnott and Ahsanullah 1979; Sullivan et al. 1983; Toudal and Riisgård 1987), and we did not detect a reduction in nauplius or egg abundances. The lack of evidence for mortality or externally obvious pathology of fish and bivalves when combinations of trace elements, rather than individual trace elements, were elevated by an order of magnitude above background in these experiments is also not surprising.

There was a potential direct effect of trace elements on protistan microzooplankton, as seen in the lower net microzooplankton abundances in +T treatments (Fig. 3, Table 6). Copper concentrations as low as 5 $\mu g\ l^{-1}$ can change the relative abundance of dominant ciliates species in large scale enclosures (Beers et al. 1977). Given that the concentration of copper measured in our +T and +N+T treatments was approximately 5 $\mu g\ l^{-1}$ (Table 4), it is possible that total copper and free cupric ion concentrations in our trace element treatments were close to those that inhibit ciliate growth.

Diet Breadth, Predation, and Consumer Responses

The lack of consistent responses of copepods, bivalves, and fish to trace element additions, even during those mesocosm runs in which phytoplankton biomass was reduced by trace elements (Table 7) may reflect either the typically smaller magnitude of the phytoplankton response to trace element additions compared to the response to nutrient additions, or the large variation in magnitude and direction of the response to trace elements among taxa that comprise the prey community (Breitburg et al. 1999). All animals we tested (except perhaps anemones), are omnivores and feed at multiple trophic levels. All responded positively to nutrient additions, but responses to trace elements varied among taxa. Copepods, oysters, and fish have the ability to modify feeding rates in response to changes in food quality, as well as to changes in food quantity. Their ability to switch to alternate prey, when abundance of dominant prey was reduced, may have stabilized consumer responses when confronted with shifts in prey assemblages (Polis and Strong 1996; Closs et al. 1999).

While fish predation reduced copepod abundances across all treatments (Fig. 4a), the effects of nutrient enhancement were not affected (Fig. 4b). Although there was not a statistically significant difference between the nutrient response in the presence of fish and the response in the absence of fish, the latter was on average 150% higher than the former. The existence of a positive nutrient response of copepods in the presence of fish reveals that predation did not eliminate zooplankton responses to nutrient-induced increases in phytoplankton abundance, unlike in other mesocosm studies where nutrient enrichment did not increase zooplankton abundance in the presence of planktivorous fish (summarized in Micheli 1999).

For fish, the effects of nutrient additions on growth were similar in direction to those of other taxa, but were more similar in magnitude to bivalve responses than to responses of plankton. Nutrient additions resulted in a tripling in phytoplankton biomass and a doubling in copepod abundance, but only a 20–30% increase in fish growth. Fish in these experiments fed on both planktonic and

benthic prey, so responses to stressor effects on abundance of copepod prey may have been dampened because benthic food was also available. Experiments in the MERL and seagrass mesocosms drawing water from Narragansett Bay found 5–50% increases in fish growth with 5–8 fold increases in nitrogen loading for winter flounder (*Pseudopleuronectes americanus*), sticklebacks (*Apeltes quadracus*), Atlantic silversides (*Menidia menidia*), and Atlantic menhaden (*Brevoortia tyrannus*; Keller et al. 1990; Buckley and Nixon unpublished data). The high fish growth rates in the control mesocosms of 5% d^{-1} wet weight (0.34 mm d^{-1} SL) may also have left little scope for increases in growth with nutrient additions. Our results do suggest that the effects of increasing nutrient loading on the lower food web can cascade to higher trophic levels and increase fish biomass in coastal systems. This conclusion is in agreement with predictions based on fish harvests (Nixon et al. 1986; Caddy and Garibaldi 2000; de Leiva Moreno et al. 2000), but differs from Micheli's (1999) predictions.

While copepod abundance qualitatively followed the general pattern of phytoplankton responses to nutrients, it did not follow the pattern of the trace element responses of either phytoplankton or microzooplankton (Fig. 3a,b). In spring, the decrease in phytoplankton biomass and microzooplankton abundance in +N+T treatments to levels below that of +N treatments was not accompanied by a significant decrease in copepod abundance (Fig. 3b). During spring the only phytoplankton taxa that were affected by trace element additions were centric diatoms (Riedel et al. 2003). This suggests that variability in the responses to stressors among phytoplankton species may have dampened the negative impact of trace elements on total phytoplankton biomass, and that copepods were able to use species of phytoplankton that were not affected by trace elements. Copepods are selective feeders and field studies of *A. tonsa* egg production show that dinoflagellates are important determinants of fecundity (White and Roman 1992). Fecundity of *A. tonsa* feeding on *Prorocentrum minimum,* the dominant dinoflagellate in our mesocosms, is high relative to fecundity of females feeding on the diatom *Thalassiosira weissflogii,* while clearance rates and fecundity of *A. tonsa* feeding on the large (~10 μm × 50 μm) chain-forming centric *D. fragilissimus,* which dominated spring phytoplankton assemblages in our mesocosms, is similar to that of starved copepods (Bundy unpublished data). *P. minimum* was unaffected by trace element treatments, while *D. fragilissimus* abundance declined in trace element treatments (ANOVA on rank-transformed data, $p < 0.0001$, SNK a posteriori test at $p < 0.05$). Therefore, a reduction in the numerically dominant member of the phytoplankton community (large centric diatoms) in spring due to trace element additions (Breitburg et al. 1999; Riedel et al. 2003) may have had little effect on copepod populations, because the preferred phytoplankton prey (dinoflagellates) were unaffected.

We also failed to detect any significant effects, or strong but statistically nonsignificant trends of trace metals on fish growth. Fish growth averaged 7% higher in trace metal addition mesocosm runs than in controls, and 5% higher in multiple stressor treatments than in mesocosms with only nutrients added. Experiments testing the effects of copper on juvenile chum salmon (*Onchorhnychus keta*) suggested that growth responses of fish were more strongly related to changes in prey assemblages than to direct toxicity effects (Koeller and Parsons 1977). A lack of a significant indirect effect of elevated trace elements on fish growth may not be surprising given the small and variable effect of trace elements on fish prey (Fig. 3a,b). Our mesocosm results do not eliminate the potential for growth effects on fish exposed to the same concentrations and combinations we tested but exposed for longer durations, or effects on growth of other fish species. However, field enclosure experiments that were 2–3 mo in duration, and tested effects of nutrient and trace metal concentrations elevated to similar levels as those in the mesocosm experiments, revealed no negative effects of trace metals on naked gobies (*Gobiosoma bosc*), Atlantic silversides, striped bass, or mummichog growth or survival (Breitburg unpublished data).

Responses of bivalves to nutrient additions were positive in 1996 mesocosm runs for clams, and for 1997–1998 mesocosm runs for oysters; however, the responses were lower in magnitude and highly variable compared to those of copepods, which feed on the same prey. A negative response of oysters to trace element additions were seen in Experiment 1 (1996) +T treatments, and a negative response to trace elements was seen for clams in the +N+T versus +N treatments in 1996 (Fig. 3a). Oyster and clam growth was influenced by food availability and environmental conditions (e.g., salinity and temperature; Table 8). For bivalves, fluctuations in food availability and species composition of the prey community, the presence or absence of nutrient rich sediments, and environmental factors may have contributed to the high variability in responses to stressor-induced changes in phytoplankton.

As was the case with copepod abundance, the composition of the phytoplankton community appeared to have a significant effect on oyster growth: there was a positive relationship of oyster

growth rate to the abundance of phytoplankton in the 3–6 μm and the 6–20 μm size ranges, which oysters are most efficient at filtering (Newell and Langdon 1996). In contrast to oysters, *Macoma* can function as deposit feeders or as suspension feeders, depending on the availability of benthic prey (Ólafsson 1989; Lin and Hines 1994). The positive relationship between *Macoma* growth and total planktonic chlorophyll indicates that *Macoma* was responding to changes in the biomass of phytoplankton suspended in the overlying water column. In muddy sediments, *Macoma* actively siphons food organisms deposited or growing on the sediment surface while in sandy sediments it feeds more directly on plankton as a suspension feeder and can switch its feeding effort between planktonic and benthic food (Ólafsson 1989; Lin and Hines 1994). Therefore, *Macoma* may also have responded to changes in microbenthic algae and sedimented phytoplankton on the sediment surface.

A strong seasonal effect of the environment was reflected in the negative correlation with salinity on both bivalve species. Although spring to summer increases in temperatures were similar in both years, salinity remained much lower in 1996 while it increased substantially in 1997. For oysters the prevalence of the parasite *Perkinsus marinus,* which can lower growth rates (Paynter and Burreson 1991), increases with salinity. High water temperatures, as occurred in the late summer of 1997 (Table 2), approached the tolerance limit of *Macoma* (Kennedy and Mihursky 1971) and, coupled with the effects of the sandy substrate used in 1997–1998, most likely caused both the low growth rates and high mortalities of this species that were observed in those mesocosm runs. Summer growth rates of both clams and oysters were significantly higher in Experiment 1 than Experiment 2.

Time Scale of Responses

These mesocosm experiments suggest that the degree to which the magnitude and variability of stressor-induced responses in phytoplankton biomass is transmitted to higher trophic levels varies, in part because these responses can depend on taxon-specific differences in life-history patterns. When consumers differ in the temporal scale of their responses to changes in prey availability or prey species composition, the magnitude of responses is also expected to differ (Polis and Strong 1996). The magnitude of the responses of copepods and oysters, which feed on similar prey, differed considerably (Fig. 3), and in general, the magnitude of the response to stressors in our experiments was less for fish and bivalves than for phytoplankton or copepods. An important difference in population dynamics between fish, bivalves, and copepods is the time scale over which they can potentially respond to stressor-induced changes in phytoplankton communities.

During our experiments, copepod populations had the potential to respond rapidly (i.e., within hours or days) to changes in prey abundance through changes in fecundity and development rates of individuals. *A. tonsa* time to maturity at 18°C is approximately 12 d when food is not limiting (Berggreen et al. 1988) and adult females continue to produce eggs for more than 3 wk after reaching maturity (Parrish and Wilson 1978). Our experiments, which were generally warmer than 18°C, likely included 2 or more cohorts (Fig. 2b). Copepods also respond within days to changes in food availability or changes in food quality by altering fecundity rates. Fecundity of the dominant copepod in our study, *A. tonsa,* responds within 24 h to changes in food quality and food quantity (Kiørboe et al. 1985; Berggreen et al. 1988). *A. tonsa* fecundity rates drop to nearly zero within 24 h of starvation and can rebound to food-satiated levels within 48 h of when nutritious food becomes available (Parrish and Wilson 1978; Durbin et al. 1983). This rapid-response capability should have allowed copepod populations to track changes in abundance and production of prey, unless predation pressure was high.

In contrast to calanoid copepods, most bivalves and fish tend to integrate short-term variability in food abundance and production through somatic growth rather than through reproduction. Due to longer generation times and their capacity to withstand fluctuations in food supply and food quality, the ability of bivalves and fish to either fully benefit from a short-term bloom, or to suffer mortality and reduced fecundity from a short-term decrease in prey, is reduced compared to that of copepods. This suggests that as the time scale of the potential population responses of consumers increases, the magnitude and temporal sensitivity of the responses become less correlated with the responses of the trophic levels on which they feed.

Relevance to the Patuxent River

Although strong correlations between primary productivity and consumer biomass have been seen in temperate estuaries (e.g., Mallin and Paerl 1994), the paradigm of a direct relationship between nutrient loadings and whole ecosystem productivity is currently under revision (reviewed by Cloern 2001). Cloern (2001) makes a convincing case that rather than a linear response of the estuarine food web to nutrient enrichment, we should expect a more complex response that depends in part on taxon-specific responses of primary producers, on the local characteristics of bio-

geochemical cycling (which can affect nutrient and trace element concentrations and bioavailability and which are influenced by the extent and longevity of hypoxia and land use practice), and on seasonal variations in nutrient limitation and nutrient ratios. In estuaries like the Patuxent River, responses of phytoplankton populations to multiple stressors may depend on seasonal variability in nutrient loadings, trace element biogeochemistry, and the intensity of other stressors (Sanders and Riedel 1993; Breitburg et al. 1999; Riedel et al. 2000; Wang and Dei 2001). The responses of grazers to the effects of stressors on phytoplankton may depend on changes in species composition of primary producers. Seasonal differences in loadings to the mesocosms, due to seasonal variability in trace element toxicity and nutrient availability in the dilution water drawn from the Patuxent River, may have influenced the effects of our nutrient and trace element manipulations. Although nutrient and trace element additions were kept relatively constant among the various mesocosm runs, variability in their effects on primary producers may have depended on seasonal and annual changes in the system. In this study, background levels of nitrogen in input water to control and +T mesocosms were 50% of the supplemented loadings to +N and +N+T treatments, while dissolved trace element concentrations in the Patuxent River are generally 20% of the concentrations measured in +T and +N+T treatments (Tables 3 and 4; Riedel et al. 2000). In the Patuxent River, seasonal inputs of trace elements can vary two- to five-fold, depending on seasonal differences in stream flow (Riedel et al. 2000).

Our experiments tested additional nutrient enrichment of an already eutrophic system, which is a situation of concern in many estuaries worldwide as human populations increase. The potential for an increase in upper trophic level biomass may depend on background levels against which additional nutrient enrichment is tested. Similar increases in nutrient loadings, and consequent algal responses might be more strongly transmitted to upper trophic levels in systems characterized by low nutrient loadings and by growth rates of consumers that are more severely constrained by prey abundance. For example, other enclosure studies conducted in coastal systems found that added nutrients resulted in increased secondary production of consumers (i.e., zooplankton and bivalves) and increased grazer biomass that was controlled by predation (Fulton 1984; Sullivan and Banzon 2000). In contrast to our study, where increases in abundance in +N treatments indicated that zooplankton were food-limited in control treatments, zooplankton abundances in the eutrophic estuary Roskilde Fjord, and the Eastern Mediterranean were not increased by nutrient enhancement of phytoplankton biomass, indicating that zooplankton were not food limited (Horsted et al. 1988; Pitta et al. 1998), or that the phytoplankton taxa that increased in biomass were not utilized by consumers.

For relatively long-lived species such as clams, oysters, and fish, our mesocosm experiments measured only the immediate effects of the stressors on growth, but there are potential cumulative effects of exposure to these stressors over several seasons or years. Simple reductions or increases in growth rates, similar to those we observed, can have dramatic effects on population growth and structure, and ultimately on interactions with other species. Harvests of demersal fishes tend to be highest in eutrophic systems, and harvests of planktivorous fishes peak in severely eutrophic or dystrophic semi-enclosed seas (Caddy and Garibaldi 2000; de Lieva Moreno et al. 2000).

Anthropogenic and natural disturbances to estuarine food webs can compound the influences of nutrient and trace element stressors. In Chesapeake Bay, nutrient reduction criteria proposed by federal and state agencies (Chesapeake 2000 Bay Agreement unpublished data) aim at reducing chl *a* concentrations in shallow and open water habitats. The average chl *a* concentrations in our nutrient enriched and control mesocosms (28 and 6 $\mu g\ l^{-1}$, respectively) closely bracket the chl *a* criteria proposed for the mesohaline Chesapeake Bay (maximum: 26.8 $\mu g\ l^{-1}$, median: 5.7 $\mu g\ l^{-1}$). If, as in our experiments, zooplankton abundances and fish and bivalve growth are lower in low nutrient regimes, one might expect that nutrient reduction strategies will result in lower zooplankton abundance, as well as lower fish and bivalve growth rates. The results of our trace element treatments suggest that consumers do not necessarily respond to decreases in total prey abundance with decreases in growth or a reduction in absolute abundance. The positive responses we observed to increased nutrient additions, coupled with the lack of a response to trace element additions, likely depended on changes in species composition of phytoplankton assemblages, as well as on changes in phytoplankton biomass and abundance. Elevated concentrations of trace elements may serve to confound the effects of nutrients. The results of these experiments suggest that to fully understand how stressors affect higher trophic levels in estuaries like the Patuxent River, the influence of multiple stressors on changes in species composition of primary producers, and the mechanisms that affect spatial and temporal variability in nutrient and trace element loadings must be investigated simultaneously.

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