

Multiple Stressors in an Estuarine System: Effects of Nutrients, Trace Elements, and Trophic Complexity on Benthic Photosynthesis and Respiration

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ABSTRACT: The effects of nutrients, trace elements, and trophic complexity on benthic photosynthesis and respiration were studied in the Paxtuxent River estuary near St. Leonard, Maryland. Experiments were conducted over three years (1995–1997) in mesocosms containing riverine sediment and water. The experimental design was $2 \times 2 \times 3$ factorial with two levels of nutrients (ambient and + nutrients), two of trace elements (ambient and + trace elements), and three of trophic complexity (plankton, plankton + fish, and plankton + fish + benthos). Trace elements included arsenic (As), copper (Cu), and cadmium (Cd). The experiment was conducted three times in 1995 and 1997 and four times in 1996. In 1995 and 1996, sediments were muddy, while in the final year sediments were sandy. In mesocosms with sandy sediments, nutrient additions increased benthic photosynthesis overall, while trace element additions increased benthic photosynthesis in two of three experimental runs. Benthic photosynthesis in these mesocosms appeared to be related to nitrogen loading. Benthic respiration increased in nutrient and trace element amended mesocosms with sandy sediments, apparently in response to higher benthic photosynthesis. Increasing trophic complexity, particularly the presence of benthic organisms, also increased benthic respiration in mesocosms with sandy sediments. There were no effects of nutrient or trace element additions on benthic photosynthesis and respiration when the sediments were muddy. The lack of consistent responses to nutrient additions was surprising given that benthic respiration rates (and presumably nutrient regeneration) were similar in all three years, regardless of sediment type. Muddy sediments did not mask the effects of nutrient addition by supplying more nutrients to benthic microalgae than sandy sediments. In 1996, the presence of filter feeding bivalves increased the relative heterotrophy of sediments, measured as production:respiration. Consistent with increased heterotrophy, effluxes of ammonium and soluble reactive phosphorus from sediments were greater in mesocosms containing benthic organisms. Anthropogenically-induced changes in estuaries, such as loading of nutrients and trace elements or reduced trophic complexity, can have important effects on benthic processes and potentially pelagic processes through feedback mechanisms.

Introduction

Human activities in watersheds have caused major changes in water quality, resulting in increased loading of nutrients, organic matter, and sediment to rivers and estuaries (Frink 1991; Hopkinson and Vallino 1995; Paerl et al. 1998). Industrial activities and agriculture generate a mixture of chemicals, including nutrients and metals, some of which are inevitably discharged into aquatic ecosystems. Human population is frequently concentrated in coastal areas and many of our large cities are lo-

cated near bays and estuaries. As a result, coastal waters have received large inputs of nutrients, and in some cases metals, for many years.

In shallow portions of estuaries, benthic photosynthesis and respiration are important components of whole system metabolism. Benthic microalgal production can account for 5% to > 50% of whole system primary production in shallow estuarine and coastal waters (Gallagher and Daiber 1973; van Raalte et al. 1976; Sullivan and Moncrieff 1988; Sundbäck and Jönsson 1988), while benthic respiration accounts for ~ 25% of the organic matter respired in various estuaries (Nixon 1981). Nutrient and trace element (including metals) loading, resulting from human activities, can have significant impacts on benthic photosynthesis and respiration. Nutrient enrichment has been demonstrated to increase benthic algal production

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(van Raalte et al. 1976) and biomass (Granéli and Sundbäck 1985) in field experiments. In estuarine mesocosm experiments, addition of nutrients increased organic carbon deposition and sediment storage of nutrients (Oviatt et al. 1993). In this same experimental system, the addition of inorganic nitrogen increased flux of CO₂ and nitrogen from sediments, demonstrating increased benthic mineralization of organic matter, perhaps as a result of increased deposition (Oviatt et al. 1995). Metals can reduce productivity and biomass of benthic algae (Crossey and LaPointe 1988; Yu et al. 1995; Hill et al. 1997), and can inhibit respiration in epilithic biofilms and stream sediments (Hill and Gardner 1987; Hill et al. 1997). The effects of nutrients and trace elements on benthic production and respiration could have important implications for whole system metabolic response to these stressors in shallow portions of estuaries.

It is difficult to predict the response of benthic metabolism to a mixture of nutrients and trace elements given that these stressors can have opposing effects on benthic production and respiration. Our objectives were to determine the effects of nutrients and trace elements on benthic photosynthesis and respiration, and to determine how these stressors might interact to affect these processes. In previous research we demonstrated that nutrients and trace elements do significantly interact to affect phytoplankton production, water column chlorophyll *a*, and heterotrophic bacterial production (Breitburg et al. 1999). Germane to this study, the response of benthic metabolism to a complex mixture of nutrients and trace elements could be subject to interactions among these stressors. The effects of nutrients and trace elements on phytoplankton and bacterioplankton could have important feedbacks on benthic processes. Increased phytoplankton biomass could attenuate light reducing benthic production, or increased pelagic production could result in greater organic matter deposition, thereby increasing benthic respiration. The use of mesocosms allowed us to examine potential interactions between pelagic and benthic responses to stressors, which would not have been possible in laboratory or field studies.

Another objective of this research was to determine if trophic complexity had an effect on benthic metabolism. Nutrients and trace elements can alter the trophic structure of estuarine ecosystems (Breitburg et al. 1999). The resultant change in trophic structure could have direct effects on benthic metabolism, independent of the effects of added nutrients and trace elements. For example, the addition of the hard clam *Mercenaria mercenaria* to large estuarine mesocosms increased sedimentation of organic carbon (Doering et al. 1986), re-

sulting in greater carbon mineralization within, and dissolved inorganic nitrogen flux out of, sediments (Doering et al. 1986, 1987). Within these same experimental systems, higher rates of benthic nutrient regeneration in mesocosms containing intact benthos (primarily the polychaete, *Mediomastus ambiseta*, and the protobranch bivalve, *Nucula annulata*) contributed to increased whole system production (Doering 1989). The effects of an intact benthic community on benthic algal production in estuaries is unknown. Filter-feeding mollusks can increase water clarity and light penetration by removing phytoplankton (Lowe and Pillsbury 1995; Mittlebach et al. 1995; Nalepa et al. 1996; Strayer 1999), which could increase benthic microalgal production and biomass in shallow portions of estuaries. Bioturbation of sediments by benthic organisms could also affect benthic metabolism, resulting in higher sediment respiration rates by introducing oxygen into deeper sediment layers (Pelegri and Blackburn 1995; Riise and Roos 1997; Svensson 1997). If nutrients and trace elements were to alter the density or species composition of fish or benthic fauna, benthic photosynthesis and respiration could thereby be affected. The use of mesocosms allowed us to determine if trophic structure, in addition to nutrients and trace elements, affect benthic photosynthesis and respiration.

The research presented was conducted as part of the COASTES project (Complexity and Stressors in Estuarine Systems), the objective of which is to examine effects of multiple stressors on estuarine ecosystem variables (Breitburg et al. 1999). In this paper we report on the effects of nutrients, trace elements, and trophic complexity on benthic primary production and respiration over 3 years. During one year we also studied the effects of these stressors on nutrient flux from sediments. The experimental results are relevant to shallow portions of estuaries receiving increased loads of nutrients and trace elements as a result of human activities.

Materials and Methods

EXPERIMENTAL DESIGN

The effects of nutrients, trace elements, and trophic complexity on benthic photosynthesis and respiration were tested using sediments from the Patuxent River estuary, near St. Leonard, Maryland. The experimental set up is described by Breitburg et al. (1999) for 1996 mesocosm experiments, with minor variations for 1995 and 1997. The experiment was conducted in 1-m³ cylindrical fiberglass mesocosms (1.07 m diameter × 1.22 m height) and was carried out during spring-early fall over three years, 1995–1997, in a factorial, random-

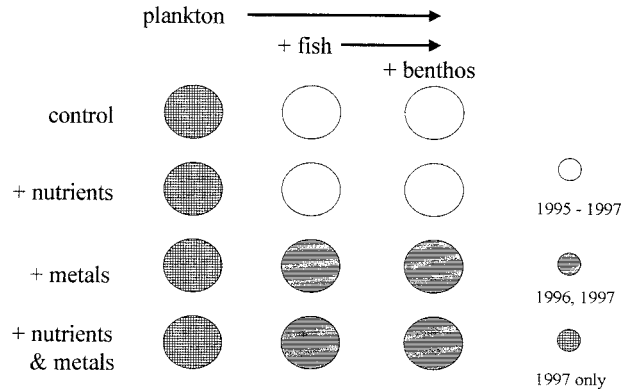


Fig. 1. Summary of experimental treatments for all three years of the experiment.

ized block design. There were three experimental runs during 1995 and 1997 and four runs during 1996 with each experimental run constituting a block. The mesocosms were set up in a completely crossed design. A total of 20 mesocosms were set up for each run. The experiment reported here was conducted in a subset of these mesocosms containing sediments. In 1995, there were two levels of nutrients \times two levels of trophic complexity (four mesocosms total per experimental run). In 1996, there were two levels of nutrients \times two levels of trace elements \times two levels of trophic complexity (eight mesocosms total per experimental run). In 1997, there were two levels of nutrients \times two levels of trace elements \times three levels of trophic complexity (twelve mesocosms total per experimental run; Fig. 1). The experimental design allowed data analysis within individual years using month (= experimental run) as a blocking factor.

Mesocosms were located in outdoor raceways containing flowing estuarine water. This continuous flow maintained mesocosm water temperature close to that of the Patuxent estuary. Mesocosms were filled with water from the estuary that had been filtered through 35- μm mesh plankton nets to remove larger planktonic organisms (salinity 6–17‰). Ten percent of the water in each mesocosm was exchanged daily for estuary water nominally filtered to 1 μm . Water was stirred in mesocosms with PVC paddlewheels. Opaque PVC liners were attached to the inside of each mesocosm to block light penetration. Liners were removed and cleaned weekly to limit effects of periphyton on pelagic processes.

Sediment cores (10–15 cm depth) were collected using a non-metallic box corer. Cores were heat-treated to kill macrofauna, and transferred intact to sediment trays (50 cm diameter) in each of the mesocosms (Breitburg et al. 1999). During 1995 and 1996 sediments were collected from the St.

TABLE 1. Nutrient and trace element additions to mesocosms.

Year		Nutrients (mmol Mesocosm ⁻¹ d ⁻¹)		Trace Elements (nmol Mesocosm ⁻¹ d ⁻¹)		
		NO ₃ ⁻	PO ₄ ³⁻	As	Cu	Cd
1995–1996	days 7–8	8.05	0.50	83.5	39.5	4.4
	days 9–28	1.61	0.10	16.7	7.9	0.9
1997	days 7–8	8.05	0.50	83.5	59.0	2.2
	days 9–28	1.61	0.10	16.7	11.8	0.4

Leonard's Creek estuary, a tributary of the Patuxent River estuary. These sediments were muddy sand. During 1997 sandy sediments were collected from the Patuxent River estuary.

Experimental runs each consisted of a 7-d acclimation period (after addition of sediments) followed by a 28-d experimental period. Tanks received 100 l d⁻¹ filtered Patuxent River estuary water as exchange water containing ambient dissolved nitrogen, phosphorus, and trace element concentrations. On days 7 and 8, mesocosms were spiked with nutrients and trace elements as appropriate to rapidly elevate concentrations at the beginning of the experimental period (Table 1). After day 8, lower concentrations of nutrients and trace elements were continuously added to appropriate mesocosms using a peristaltic pump. The level of trace element addition was expected to have some effects on lower trophic levels without directly impairing higher organisms (Sanders and Riedel 1998). Total dissolved inorganic nitrogen additions were chosen to approximate 1.5 times the ambient loading to the surface layer of the Patuxent River estuary calculated from 1984–1996 averages (Hagy 1996). These nitrogen additions were approximately 1.3–2.4 times the ambient loading to mesocosms, and dissolved inorganic phosphorus additions were approximately 1.8–6 times the ambient loading to mesocosms (Table 2).

Two levels of trophic complexity were included in 1995 and 1996 experimental runs. These were an assemblage containing fish and one containing fish and benthos. Both treatments included phytoplankton, bacterioplankton, and zooplankton. In 1997 an additional level of trophic complexity was added in which mesocosms contained plankton with no fish or benthos. On days 9 and 10 of each experimental run, fish and benthic organisms were added to appropriate mesocosms. Fish added to mesocosms were juvenile mummichogs (*Fundulus heteroclitus*). The benthic invertebrates added to + benthos mesocosms were the eastern oyster (*Crassostrea virginica*), a clam (*Macoma balthica*), and a sea anemone (*Diadumene leucolena*). A total of 8 fish were added to each + fish mesocosm. Mean starting mass was 0.04–0.22 g fish⁻¹ over the duration of the experiment. Fifty oysters, averaging 1.0–2.0

TABLE 2. Mean values of selected chemical, biological, and physical characteristics of mesocosms. nm = not measured.

Year	Ambient Loading† (mmol Mesocosm ⁻¹ d ⁻¹)			Physical Variables		Indices of Algal Abundance				Sediment chl <i>a</i> ‡ (µg cm ⁻²)		
	DIN	DIP	Sal. (‰)	Temp. (°C)	Water column POC (mmol C m ⁻³)		In Vivo Fluorescence					
					Control	+N	+T	+NT	Control		+N	+T
1995												
June–July	2.98	0.05	13.0	28.0	nm	nm	nm	nm	nm	nm	nm	nm
July–Aug	3.06	0.07	14.5	29.0	nm	nm	nm	nm	nm	nm	nm	nm
Sept–Oct	2.77	0.06	16.3	23.8	nm	nm	nm	nm	nm	nm	nm	nm
1996												
April	5.30	0.06	9.4	12.9	Control	+N	+T	+NT	Control	+N	+T	+NT
June	2.03	0.08	7.5	22.7	530	544	323	593	89	132	71	108
July–Aug	1.68	0.06	8.5	26.1	495	442	263	633	55	170	56	233
Sept	1.76	0.12	10.2	24.2	1,009	452	1,178	1,950	165	378	314	599
1997												
May–June	1.96	0.02	9.6	18.2	89	1,215	323	715	35	327	73	306
July	1.67	0.05	11.8	28.1	Control	+N	+T	+NT	Control	+N	+T	+NT
Aug–Sept	1.16	0.08	13.9	24.3	259	2,039	170	453	27	343	26	74
					233	715	191	247	30	60	29	45
					203	753	228	844	42	99	30	88

† Mean ambient loading due to daily exchange of mesocosm water with river water.

‡ Mean value from 4 randomly sampled mesocosms.

cm² in shell area, were glued to PVC panels suspended vertically in the + benthos mesocosms. Approximately 100 clams, averaging 0.4–0.8 cm² in shell area, were added to the sediment tray in each of the + benthos mesocosms. Plastic plates (PVC) with attached anemones were also suspended vertically in the + benthos mesocosms. Each + benthos mesocosm had the same number of anemones within a given experimental run (approximately 40).

BENTHIC OXYGEN AND NUTRIENT FLUX

Benthic oxygen flux was measured during the second or third week of each experimental run. An acrylic lid (diameter = 55 cm) was lowered onto the lip of the sediment tray in each mesocosm to form a chamber, isolating sediments from the water column. The chamber lid was weighted and had foam backing on the outer edge holding the lid in place and providing a seal. The water inside the chamber was continuously stirred by an acrylic paddlewheel driven by a small AC motor connected via an acrylic axle. Stirring was relatively slow (5 rpm) to prevent sediment resuspension. The axle was inserted through a bulk head connector in the center of the chamber lid.

Each lid had a sampling port, a plastic fitting with attached tygon tubing, as well as a water inlet port. Water samples were drawn from the sample port with a 60 ml syringe. As water was drawn out of the chamber, its volume was replaced by water flowing into the inlet port. A latex glove attached to the inside of the water inlet port prevented exchange of nutrients and oxygen between chamber water and mesocosm water. At the time chamber lids were installed, eight 60 ml BOD bottles filled with mesocosm water were placed in each mesocosm. These bottles were used as controls to correct for water column processes occurring within the sealed chambers.

One hour after lid installation, initial samples were drawn from each chamber and from control bottles to measure dissolved oxygen (YSI oxygen meter) and nutrient concentrations. Samples for nutrient analyses were immediately filtered through a Whatman GF/F syringe filter and stored frozen prior to analysis for ammonium, nitrate (+ nitrite), and soluble reactive phosphorus (Lachat QuikChem Analyzer—Lachat QuikChem Methods 31-107-06-1-A, 31-107-04-1-A, and 31-115-01-3-A, respectively). Subsequent samples were drawn approximately every hour for 3 h to determine change in oxygen and nutrient concentrations over time. At the end of the 4 h sampling period, lids were removed from the sediment trays for at least 2 h. Oxygen and nutrient fluxes were then measured in the dark either by covering lids with

black plastic, or by conducting experiments at night. Sampling was conducted as above.

Benthic respiration was measured as oxygen consumption in the dark, and benthic gross primary production (GPP) was determined from the net increase in oxygen in the light plus oxygen consumption due to respiration. Respiration includes all processes which result in sediment oxygen consumption (i.e., aerobic respiration, nitrification, and oxidation of reduced sulfur, iron, and manganese). Values of GPP and respiration were corrected for changes in water column controls. Benthic photosynthesis:benthic respiration (P:R) was estimated for a 24-h period. Respiration was assumed constant over the 24-h period and photosynthesis was assumed constant over the duration of a photoperiod. Duration of the photoperiod was taken as sunrise to sunset on the day of oxygen flux measurements. The assumption of constant photosynthetic rate over the entire photoperiod and the fact that oxygen flux measurements were purposely conducted on clear, sunny days may result in overestimation of P:R. However, oxygen concentrations in chambers increased linearly with time, regardless of the time of day measurements were conducted, suggesting that photosynthetic rates were relatively constant during the day. Photosynthetic rates were probably lower very near dawn and dusk. While P:R may be overestimated, the effects of stressors on the relative heterotrophy of sediments can be validly assessed.

WATER COLUMN MEASUREMENTS

Samples were collected weekly for dissolved and particulate organic carbon analysis (DOC and POC, respectively). Filtered samples for DOC were analyzed with a Shimadzu 5000 TOC analyzer using high temperature oxidation. Particulates retained by the filter (POC) were analyzed with CE-440 elemental analyzer (Exeter Analytical, Inc.). Filtered samples (Whatman GF/F glass fiber filters) were analyzed for ammonium, nitrate, and orthophosphate with a Lachat QuikChem Analyzer as above.

STATISTICAL ANALYSIS

Analysis of variance (Systat version 6.0.1) was used to examine direct and interactive effects of nutrients (N), trace elements (T), and trophic complexity (C) on benthic photosynthesis and respiration. In analysis of all experimental runs within a year, month (= experimental run) was used as a blocking term. The general model was: response variable = constant + month + N + C for 1995, and response variable = constant + month + N + T + C + N × T + N × C + T × C for 1996 and 1997. In analysis of individual experimental runs,

TABLE 3. Effects of stressors on benthic primary production, respiration, primary production, photosynthesis:respiration, water column particulate carbon, and nutrient flux – summary of responses. Significant effects ($p < 0.05$) are indicated by + (increased rate or increased nutrient efflux), – (decreased rate or decreased efflux), and ± (mixed response depending on month).

Benthic Process	Nutrient Addition	Trace Element Addition	Nutrient × Trace Element Interaction	Trophic Complexity
GPP				
1995	no effect			no effect
1996	no effect	no effect	no effect	no effect
1997	+	±	no effect	no effect
Respiration				
1995	no effect			no effect
1996	no effect	no effect	no effect	no effect
1997	+	+	no effect	+
P:R				
1995	no effect			no effect
1996	no effect	no effect	no effect	–
1997	no effect	no effect	no effect	no effect
Water column				
POC				
1996	+	no effect	no effect	no effect
1997	+	–	no effect	no effect
Ammonium Flux				
1996	no effect	no effect	no effect	+
Phosphorus Flux				
1996	–	no effect	no effect	+

the general model was: response variable = constant + N + C for 1995 and response variable = constant + N + T + C + N × T for 1996 and 1997 (in exploratory analyses we found no interactions between C and other stressors, and these interactions were excluded from the final ANOVA models to improve the power of the analyses). Particulate carbon data were log transformed to improve normality of distribution. Other data did not require transformations to control variance or to improve normality of distributions.

Results

BENTHIC GROSS PRIMARY PRODUCTION

Average oxygen production in mesocosms was $6,434 \pm 292 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ($\bar{x} \pm \text{SE}$, $n = 91$). Primary production was similar among years with oxygen production rates of $6,455 \pm 698$, $6,183 \pm 514$, and $6,645 \pm 381 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ in 1995, 1996, and 1997, respectively ($n = 23$, $n = 32$, and $n = 36$).

Benthic primary production was most affected by stressors in 1997, when mesocosms had sandy sediments (Table 3). In 1997, nutrient addition significantly increased benthic GPP (Fig. 2a; $p = 0.003$). This nutrient effect was strongest in September 1997 when primary production in + nutrient mesocosms was nearly twice that in control

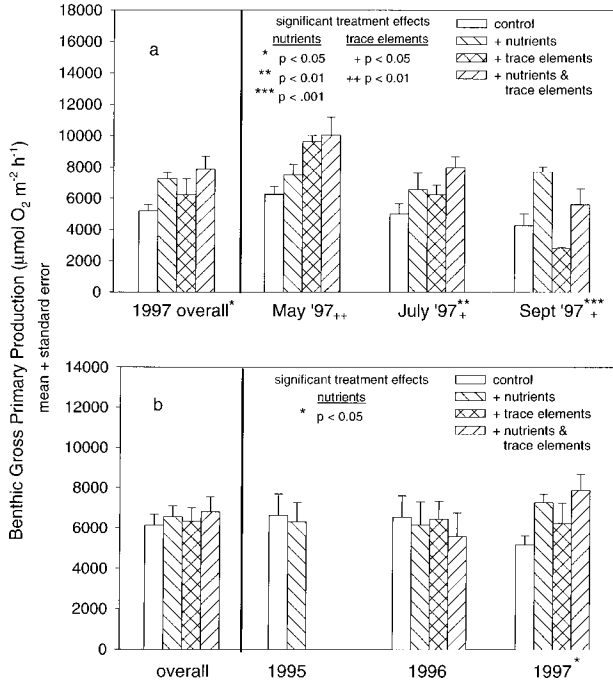


Fig. 2. Benthic gross primary production in mesocosms exposed to different stressor treatments in a) 1997 and b) all 3 years of the experiment. Values are mean \pm standard error. Significant treatment effects of nutrients and trace elements detected using ANOVA model specified in text.

mesocosms. Trace elements also affected primary production in 1997, significantly increasing production in May and July. Trace element additions significantly reduced benthic production in September and the effect of trace elements was not significant for 1997 overall ($p = 0.15$). Trophic complexity had no significant effect on benthic production in 1997 ($p = 0.18$) and there were no significant interactions among stressors. In 1995 and 1996 when mesocosms had muddy sediments, benthic primary production was not affected by nutrients, trace elements, or trophic complexity (Fig. 2b).

Primary production did vary significantly with month ($p < 0.001$) during each year of the experiment. Benthic production was consistently highest in early summer, decreasing throughout the late summer and early autumn.

RESPIRATION

Benthic respiration rates were more variable from year to year than were benthic production rates. Sediments consumed $2,232 \pm 132 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ($\bar{x} \pm \text{SE}$, $n = 91$). Consumption rates by year were $1,697 \pm 289$, $2,811 \pm 207$, and $2,059 \pm 176 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ in 1995, 1996, and 1997, respectively ($n = 23$, $n = 32$, and $n = 36$).

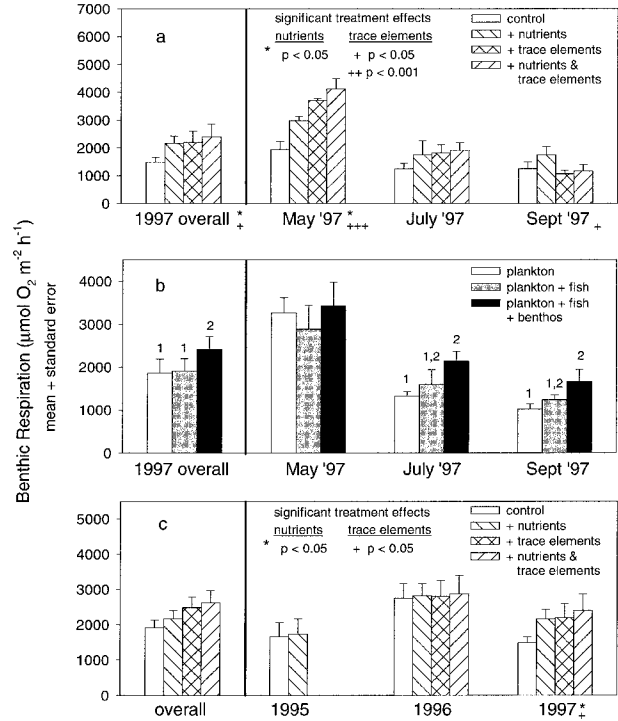


Fig. 3. Benthic respiration in mesocosms a) receiving nutrient and trace element additions in 1997, b) with different levels of trophic complexity, and c) receiving nutrient and trace element additions for all 3 years of the experiment. Values are mean \pm standard error. Significant treatment effects of nutrients, trace elements, and trophic complexity detected using ANOVA model specified in text. Significant differences among levels of trophic complexity denoted by differences in number over bar.

As with benthic production, respiration was generally most responsive to stressors in 1997. The addition of nutrients to mesocosms significantly increased benthic respiration in 1997 ($p = 0.03$) as did addition of trace elements ($p = 0.02$). The response of respiration to nutrients and trace elements was strongest in May 1997 (Fig. 3a). In September 1997, trace elements significantly reduced benthic respiration ($p = 0.04$). Trophic complexity had a significant effect on benthic respiration in 1997 ($p = 0.05$). Increasing trophic complexity tended to increase benthic respiration rates, and mesocosms with clams, oysters, and anemones had the highest benthic respiration rates (Fig. 3b). There were no significant interactions among stressors in 1997. In 1995 and 1996 when mesocosm sediments were sandy mud, respiration was not affected by nutrients, trace elements, or trophic complexity (Fig. 3c).

Respiration varied significantly with month ($p < 0.001$) during all 3 years of the experiment. As with primary production, respiration tended to be high-

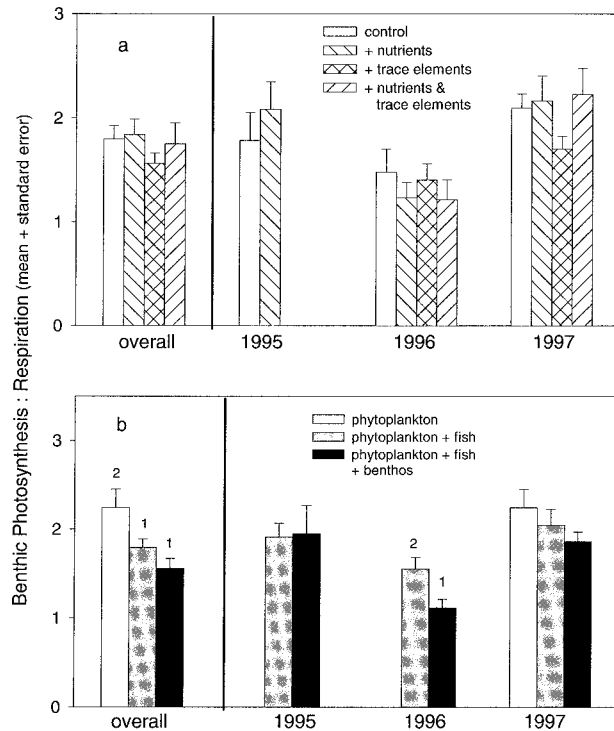


Fig. 4. Benthic photosynthesis:respiration in mesocosms exposed to a) different chemical stressors and b) different levels of trophic complexity in all 3 years of the experiment. Values are mean \pm standard error. Significant treatment effects of trophic complexity detected using the ANOVA model specified in the text. Significant differences among levels of trophic complexity denoted by difference in number over bars.

est in early summer and decreased throughout late summer and early autumn.

BENTHIC PHOTOSYNTHESIS:RESPIRATION

Sediments were net autotrophic throughout the experiment. Overall, P:R was 1.76 ± 0.07 ($\bar{x} \pm SE$, $n = 84$). Photosynthesis:respiration was similar in 1995 and 1997 (1.94 ± 0.18 and 2.05 ± 0.10 , respectively). Sediments were relatively more autotrophic in those years than in 1996 ($P:R = 1.33 \pm 0.09$).

The addition of nutrients to mesocosms marginally increased net autotrophy on sandy sediments in 1997 (Fig. 4a; $p = 0.06$). Nutrients additions had no effect on net autotrophy during 1995 or 1996 and trace element additions had no effect on P:R in any year. Trophic complexity significantly affected P:R during 1996 ($p = 0.01$), as the addition of higher trophic levels tended to increase sediment respiration (Fig. 4b). This effect of benthic organisms was apparent in 1997 as well, although not significant ($p = 0.14$). There were no significant interactions among stressors during any year of the experiment.

WATER COLUMN PARTICULATE ORGANIC CARBON

Water column POC concentration, measured as an index of planktonic biomass, averaged 672 ± 110 mmol C m^{-3} in 1996 and 528 ± 105 mmol C m^{-3} in 1997 ($n = 32$ and 36 , respectively; Table 2). Particulate carbon was not measured in 1995. Water column POC was correlated with in vivo fluorescence ($r = 0.73$, $p < 0.001$), a separate metric of phytoplankton biomass. Particulate carbon was more sensitive to stressors than in vivo fluorescence. Water column POC increased with nutrient amendment in both 1996 ($p = 0.036$) and 1997 ($p < 0.001$). Trace elements significantly reduced water column POC in 1997 ($p = 0.008$). However, there was no effect of trace elements on POC in 1996 ($p = 0.614$). Benthic organisms reduced water column POC in mesocosms in 1997 ($p = 0.013$). In 1996 there was no effect of benthic organisms on water column particulate carbon ($p = 0.214$).

NUTRIENT FLUXES

In 1996, sediments were a net source of ammonium. The flux was generally greater in the dark than in the light. In the light, ammonium flux was 36.3 ± 18.4 $\mu\text{mol N m}^{-2} \text{h}^{-1}$ ($\bar{x} \pm SE$, $n = 32$). In the dark, the flux was 101.0 ± 31.3 $\mu\text{mol N m}^{-2} \text{h}^{-1}$. Trophic complexity significantly affected ammonium flux at night ($p = 0.05$) and had a marginally significant effect on flux during the day ($p = 0.06$). The presence of benthic organisms apparently increased ammonium flux from sediments (Fig. 5a), consistent with increased sediment heterotrophy (decreased P:R; Fig. 4b). Nutrient and trace element additions had no effect on ammonium flux and there were no significant interactions among stressors.

Sediments were also a net source of dissolved inorganic phosphorus in 1996. During the day inorganic phosphorus flux was 1.0 ± 0.6 $\mu\text{mol P m}^{-2} \text{h}^{-1}$ ($\bar{x} \pm SE$, $n = 32$). At night, flux was 0.8 ± 1.1 $\mu\text{mol P m}^{-2} \text{h}^{-1}$. Trophic complexity had a significant effect on phosphate flux in the dark ($p = 0.04$) resulting in net efflux (Fig. 5b). The addition of nutrients had a significant effect on phosphate flux during the day ($p = 0.01$) resulting in a net flux of phosphate into sediments (Fig. 5c). Trace element additions had no effect on phosphorus flux and there were no significant interactions among stressors.

Nitrate flux was a minor component of inorganic nitrogen flux. There was a net efflux of nitrate from sediments during both day and night. Nitrate flux during the day was 2.9 ± 1.3 $\mu\text{mol N m}^{-2} \text{h}^{-1}$ ($\bar{x} \pm SE$, $n = 32$). At night, flux was 0.8 ± 0.8 $\mu\text{mol N m}^{-2} \text{h}^{-1}$. There were no effects of nutrients,

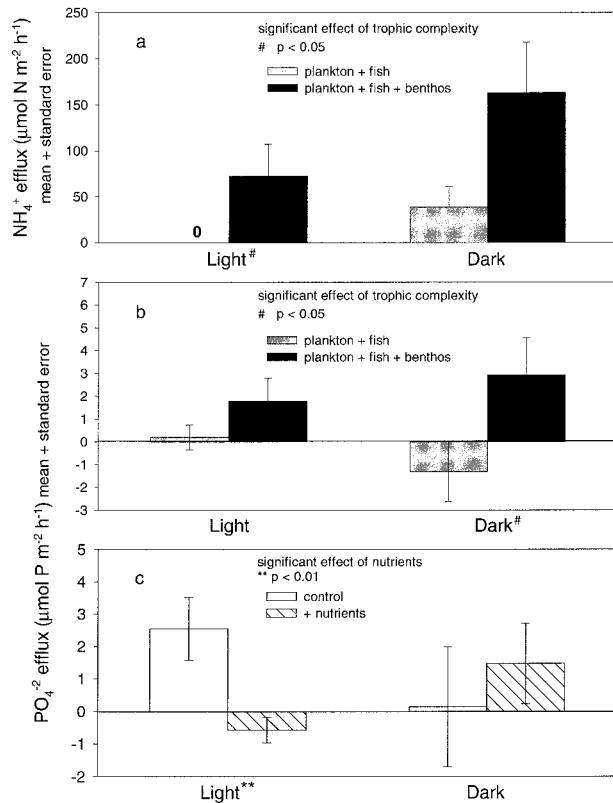


Fig. 5. Nutrient flux from mesocosm sediments in 1996 in the light and dark. Effects of a) trophic complexity on ammonium flux, b) trophic complexity on phosphate flux, and c) nutrient addition on phosphate flux. Values are mean \pm standard error. Significant treatment effects of trophic complexity and nutrient additions detected using ANOVA model specified in text.

trace elements, or trophic complexity on nitrate flux and there were no significant interactions among stressors.

Discussion

The rates of benthic respiration measured in these mesocosm experiments were similar to other measured rates in mesohaline regions of Chesapeake Bay (salinity 8–20‰) during the spring and summer (Boynton and Kemp 1985; Officer et al. 1985; Roden et al. 1995). Patuxent River estuary sediments are generally heterotrophic in the deeper main channel (> 10 m), as demonstrated by net sediment oxygen consumption and net inorganic nitrogen and phosphorus flux from sediments (Boynton and Kemp 1985; Boynton et al. 1995). Net oxygen and nutrient fluxes from sediments have not been measured in the shallow portion of the Patuxent River estuary. Sediments in shallow estuaries, or shallow portions of deeper estuaries, can be net autotrophic during spring and summer (Sundbäck et al. 1996) and can be an important

sink for nutrients (Granéli and Sundbäck 1985; Sundbäck and Granéli 1988; Nilsson et al. 1991). In the current mesocosm experiments, sediments were collected from shallow areas in the Patuxent River estuary and were net autotrophic. The experimental results have greatest relevance to shallow estuarine areas with high photosynthetic activity in sediments.

EFFECTS OF NUTRIENTS AND TRACE ELEMENTS ON BENTHIC PROCESSES

Both nutrient and trace element additions stimulated benthic production and respiration in 1997. The effects of nutrient and trace element additions on benthic processes may have been direct or the result of benthic-pelagic interactions and feedback. Previous laboratory experiments using sediment cores have demonstrated increased benthic algal biomass (Granéli and Sundbäck 1985; Sundbäck and Granéli 1988) and production (Sundbäck and Granéli 1988; Nilsson et al. 1991) as a result of nutrient additions. The use of 1-m³ mesocosms allowed us to explore these primary effects of nutrient and trace element additions, as well as possible benthic-pelagic interactions which could moderate responses.

Conceptually, benthic microalgae could respond directly to nutrient inputs, increasing nutrient uptake and primary production relative to microalgae in control mesocosms (Fig. 6a,b). Benthic respiration, in turn, could increase in response to the increased organic carbon produced by benthic microalgae. Alternately, increased nutrients could increase phytoplankton production (Fig. 6c). Benthic respiration is commonly related to particulate carbon deposition associated with phytoplankton production (Osinga et al. 1996; Cerco and Seitzinger 1997; Nixon 1981; Witek et al. 1997). Therefore, an increase in phytoplankton production could result in higher benthic respiration. Nutrients regenerated by respiration would then be available to benthic microalgae, stimulating benthic production.

In the first scenario for nutrient amendment, we expect benthic microalgae to directly exploit the added nutrients (Fig. 6b). We should observe a relationship between nutrient loading and benthic primary production. Benthic respiration is exploiting benthic GPP as a carbon source and we should observe a relationship between benthic GPP and benthic respiration. In the second scenario for nutrient amendment (Fig. 6c), we expect that deposition of particulate carbon increases in response to higher nutrient loading, and that deposition of this carbon stimulates benthic respiration. We should observe a relationship between POC and benthic respiration. We expect that benthic GPP is

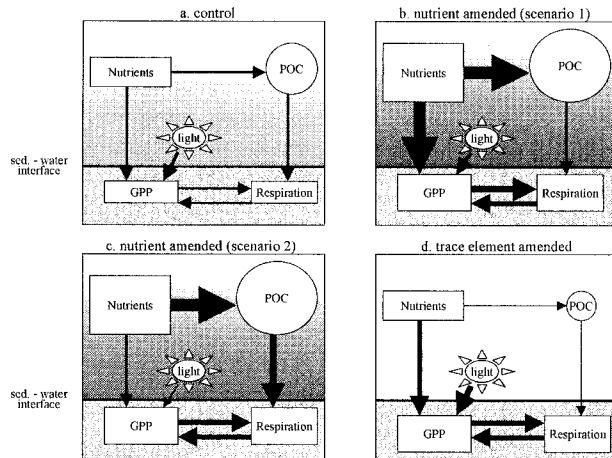


Fig. 6. Model of carbon and nutrient flow in 1997 mesocosms. a) Control mesocosms. Nutrients go into phytoplankton biomass (POC) and support benthic algal primary production (GPP). GPP and POC provide carbon to support benthic respiration. Respiration regenerates nutrients used by benthic microalgae (mesocosms were net autotrophic so there is no net flux of nutrients from sediments). b) Nutrient amended mesocosms—scenario 1. Increased nutrient loading results in increased nutrient uptake by phytoplankton and benthic algae. Carbon flow from GPP to respiration increases (indicated by thickness of arrow). Light attenuation by POC increases, potentially affecting GPP (indicated by water column shading). c) Nutrient amended mesocosms—scenario 2. Increased nutrient loading results in increased POC and deposition of POC to sediments. Increased deposition stimulates respiration providing more nutrients to GPP. Light attenuation by POC increases, potentially affecting GPP (indicated by water column shading). d) Trace element amended mesocosms. Trace element toxicity decreases POC resulting in less competition for nutrients between phytoplankton and benthic algae. Nutrient uptake by benthic algae increases resulting in higher GPP and respiration.

exploiting nutrients regenerated by benthic respiration. We should observe a relationship between benthic GPP and respiration.

We used a simple correlation approach to explore these scenarios for increased benthic primary production and respiration in 1997. Consistent with both nutrient amendment scenarios, we found that benthic respiration and benthic primary production were strongly correlated (Fig. 7a, $r = 0.83$, $p = 0.0001$). Benthic respiration was not correlated with water column POC (Fig. 7b, $r = 0.01$, $p = 0.96$). Although nutrient additions significantly increased water column POC (presumably due to increased phytoplankton production), this new carbon source was apparently not an important energy source for benthic respiration. This suggests that the second nutrient amendment scenario, namely that increased deposition of water column POC would increase benthic respiration and, in turn, benthic primary production, is incorrect.

Benthic primary production, in contrast to water column POC, could have been an important source of labile carbon for benthic heterotrophic bacteria. In support of the first nutrient amendment scenario, we would expect a relationship between nutrient loading and benthic primary production. Within nutrient treatments, benthic GPP was correlated with nitrogen loading ($r = 0.78$, $p < 0.001$ in mesocosms without added nutrients; $r = 0.48$, $p = 0.06$ in mesocosms with added nutrients), reflecting a seasonal pattern in which primary production and nitrogen loading were highest in May, intermediate in July, and lowest in September (Fig. 7c). This seasonal pattern of nitrogen loading to mesocosms is a result of temporal differences in combined nitrogen in the incoming water. Benthic GPP was also correlated with nitrogen loading across nutrient treatments ($r = 0.61$, $p < 0.001$), consistent with the finding that nutrient additions increased benthic GPP within experimental runs in July and September (Fig. 2a). Superimposed on this nitrogen loading effect was a treatment effect associated with added nitrogen plus phosphorus. The addition of nitrogen plus phosphorus resulted in higher water column POC coincident with a decrease in average mid-day light at the sediment surface (512 versus $129 \mu\text{E m}^{-2} \text{s}^{-1}$ in May, 358 versus $282 \mu\text{E m}^{-2} \text{s}^{-1}$ in July, and 836 versus $668 \mu\text{E m}^{-2} \text{s}^{-1}$ in September for control and nutrient amended mesocosms, respectively). Light attenuation by POC could have suppressed benthic GPP in mesocosms amended with nutrients, limiting the ability of microphytobenthos to exploit added nutrients. This shading effect may have been greatest in May, when bottom light attenuation was most apparent and benthic GPP did not increase in response to nutrient additions (Fig. 2a). Shading by water column POC may have moderated the response of benthic GPP to nitrogen loading across nutrient addition treatments.

Benthic GPP was negatively correlated with phosphorus loading within nutrient addition treatments ($r = -0.80$, $p < 0.001$ in mesocosms without added nutrients; $r = -0.48$, $p = 0.04$ in mesocosms with added nutrients; Fig. 7d). It is unlikely that phosphorus loading had any negative effect on benthic GPP, as nitrogen plus phosphorus additions increased benthic GPP within experimental runs during July and September (Fig. 2a). Benthic GPP followed a seasonal pattern (highest in May, intermediate in July, and lowest in September) which was counter to the seasonal pattern of phosphorus loading (lowest in May, intermediate in July, and highest in September). These results suggest that nitrogen loading, and not phosphorus loading, limited benthic GPP in these mesocosm experiments.

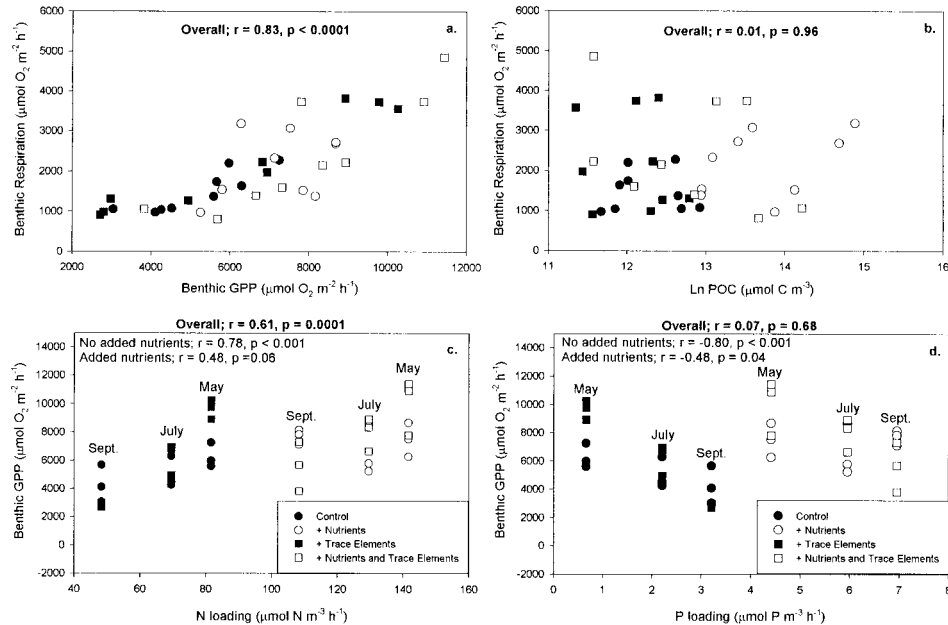


Fig. 7. Relationships between benthic processes and water column variables. a) Relationship between benthic gross primary production (GPP) and benthic respiration. b) Relationship between water column particulate organic carbon (POC) and benthic respiration. c) Relationship between inorganic nitrogen loading and benthic GPP. d) Relationship between inorganic phosphorus loading and benthic GPP. Included are Pearson correlation coefficients with Bonferroni probabilities.

There is more evidence to support the first scenario for nutrient amendment (Fig. 6b), namely that added nutrients (specifically nitrogen) were exploited by microphytobenthos, increasing benthic GPP and respiration. The fact that these sediments were net autotrophic also supports this scenario, as benthic respiration could not have regenerated enough nutrients to support measured primary production. Support for this scenario is weakened by the complex relationship between nitrogen loading and benthic primary production. The use of mesocosms in preference of laboratory incubations complicates the interpretation of experimental results by incorporating feedbacks, such as the responses of water column organisms (particularly phytoplankton) to nutrient loading. Feedback mechanisms may be important determinants of how benthic primary production and respiration respond to added nutrients. Increased water column POC in nutrient-amended mesocosms could have resulted in shading of benthic microalgae, explaining the relationship between nitrogen loading and benthic primary production. The use of mesocosms provides a more realistic, although more complex, view of how benthic processes may respond to nutrient additions in shallow portions of estuaries.

Trace elements could inhibit photosynthetic activity of both phytoplankton and benthic microalgae. In May and July 1997 trace element additions

resulted in increased benthic primary production and respiration. A plausible scenario is that inhibition of phytoplankton (as measured by a decrease in water column POC) allowed benthic microalgae to better exploit water column nutrients, by reducing competition for these nutrients (Fig. 6d). The relationship between benthic GPP and nitrogen loading lends support to this scenario. The measured increase in benthic respiration likely was in response to increased benthic primary production as a carbon source.

EFFECTS OF TROPHIC COMPLEXITY ON BENTHIC RESPIRATION

In 1997 experiments, trophic complexity had a direct effect on benthic respiration that was not reflected in benthic GPP. This increased respiration could be attributable to filter feeding, which can facilitate the export of carbon from the water column to sediments through defecation (Haven and Morales-Alamo 1966, 1972; Grant et al. 1995; Roditi et al. 1997). The filter-feeding clam *M. mercenaria* increased both gross and net sedimentation of particulate carbon in estuarine mesocosms (Doering et al. 1986). Benthic remineralization, as measured by dissolved inorganic nitrogen flux (Doering et al. 1986, 1987) or as sediment oxygen consumption and CO_2 flux (Doering et al. 1987), was greater in mesocosms containing *M. mercenaria*. Newell (1965) suggested that organic particles

(feces and pseudofeces) egested by deposit feeding bivalves were rapidly recolonized by microbes. Similarly, filter feeding with concurrent fecal production could stimulate benthic microbial growth (and therefore, respiration) by maintaining a logarithmic growth phase of bacteria on newly deposited fecal pellets (Dame 1996). Higher respiration rates might also be attributed to the contribution of benthic organisms to total benthic respiration. *M. balthica* was the only macroorganism present in the sealed chambers. Oxygen consumption by *M. balthica* was estimated using the relationships between shell length, biomass, and respiration developed by Emerson et al. (1988) for the clam *Mya arenaria*. In 1997, estimated respiration by *M. balthica* averaged $130 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$, accounting for ~20% of the increased oxygen consumption relative to control (i.e., no benthic organisms). This suggests that carbon export to sediments through defecation could be another important source of carbon to benthic respiration. As respiration was not related to water column particulate carbon, fecal matter may have been a higher quality of organic carbon than photodetritus deposited from the water column.

The effect of trophic complexity on respiration has important implications for phytoplankton production in estuaries. Sediment-water column interactions are important in terms of nutrient dynamics in aquatic systems (Zeitzschel 1980; Boynton and Kemp 1985; Boynton et al. 1995; Reay et al. 1995; Nixon et al. 1996). Efflux of nutrients from sediments due to benthic respiration can account for 10–100% of the nutrient requirement for phytoplankton production in lakes, shallow estuaries, and coastal waters (Flint and Kamykowski 1984; Reay et al. 1995; Vanluijn et al. 1995), while benthic algal production can reduce the efflux of nutrients from sediments (Carlton and Wetzel 1988; Sundbäck and Granéli 1988; Nilsson et al. 1991; Seitzinger and Pilling 1992; Cerco and Seitzinger 1997) limiting nutrient availability for phytoplankton. The balance between benthic GPP and respiration can regulate internal nutrient loading, thereby affecting phytoplankton production. In 1996, benthic organisms increased sediment heterotrophy in mesocosms, resulting in greater efflux of ammonium and phosphorus as by-products of respiration. In these mesocosms, nutrient efflux from sediments could have supported phytoplankton production of $4.6 \text{ mmol C m}^{-2} \text{ d}^{-1}$ compared with $0.50 \text{ mmol C m}^{-2} \text{ d}^{-1}$ in mesocosms with only fish. Phytoplankton production in 1996 mesocosm experiments averaged over all treatments was $41.7 \text{ mmol C m}^{-2} \text{ d}^{-1}$ (Breitburg et al. 1999; correcting whole system production for benthic production measured in the current study). Therefore, nutri-

ent flux from sediments could have supported approximately 11% of the nutrient requirement for phytoplankton production in mesocosms with benthic organisms and approximately 1% of the phytoplankton nutrient requirement in mesocosms lacking benthic organisms.

Summary

Human activities are driving changes in coastal waters. Increased nutrient loading is causing eutrophication in many estuarine systems, increasing phytoplankton production, while trace elements are potentially reducing productivity and species diversity of phytoplankton in certain areas, particularly those receiving industrial effluents. Our results suggest that human activities, which result in nutrient and trace element loading to estuaries, can result in greater benthic primary production and respiration, as well. The response of benthic primary production and respiration was not subject to nutrient-trace element interactions in contrast to water column primary production and bacterial production (Breitburg et al. 1999). In part, this may have been due to opposing effects of trace elements on benthic microalgae (i.e., toxicity to benthic microalgae versus release of benthic microalgae from competition with and shading by phytoplankton). In other systems that are shallow and nutrient rich, nutrient-trace element interactions could be important. Nutrient and trace element additions only affected benthic photosynthesis and respiration on sediments that were sandy. While natural interannual variability may have contributed to this, it is possible that sediment characteristics (i.e., sandy versus muddy) affected how benthic processes responded to increased nutrient and trace element loading. The results of this experiment have greatest relevance for shallow portions of estuaries with sandy sediments colonized by benthic microalgae. Perturbations that increase nutrient and trace element loading to estuaries may result in more extensive changes to these systems than previously realized when benthic, as well as pelagic, processes are considered.

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