

# Structure and function in a model coastal ecosystem: silicon, the benthos and eutrophication

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**ABSTRACT:** Lowering the N:Si ratio (14:1 to 1:1) in nutrient (N, P, Si) additions to large (13 m<sup>3</sup>) outdoor mesocosms with and without an intact benthic community generally resulted in higher standing stocks of diatoms. An enhanced diatom flora during the year-long experiment was not accompanied by a concomitant reduction in the extent of eutrophication caused by nutrient loading, as judged by oxygen concentration and metabolism or by chlorophyll *a* biomass. Enhanced growth of Atlantic menhaden *Brevoortia tyrannus* in the low N:Si ratio treatment suggested that diatoms promote transfer of energy to higher trophic levels. Removal of the benthic community and associated sediments had a dramatic effect on pelagic community structure. Zooplankton were holoplanktonic in character and higher trophic levels were dominated by ctenophores, medusae, chaetognaths and fish. In the presence of an intact benthos the zooplankton had a larger meroplanktonic component and higher trophic levels were dominated by larvae of benthic adults (anemones, shrimp) or temporary planktonic adults (mysids).

## INTRODUCTION

Eutrophication of marine waters owing to discharge of sewage and other nutrient additions represents an often severe and widespread problem (Gray 1982). Eutrophication has been associated with low oxygen, declining fish and shellfish stocks and other undesirable ecosystem level alterations (Officer & Ryther 1980). Such observations suggest that pollution exerts a strong influence on the structure of marine communities (Greve & Parsons 1977, Gray 1982). This hypothesis is interesting because it raises the possibility that modification of a pollutant rather than reduction of the magnitude of discharge can be used to preserve an acceptable level of environmental quality. For the manager, it might provide an alternative strategy. Scientifically, it challenges the ecologist to suggest modifications and predict their impact at the ecosystem level.

One such manipulation is alteration of the N:Si ratio of nutrients discharged in sewage effluent (Officer & Ryther 1980, Ryther & Officer 1981). These authors distinguish 2 basic sorts of phytoplankton communities: those dominated by diatoms and those dominated by flagellates or non-diatomaceous forms. They

further observe that (1) the latter group is often associated with the undesirable effects of eutrophication while diatoms are not, (2) diatoms require silicon for growth while flagellates do not, (3) diatoms are the preferred food of most grazers and form the basis of food chains which are 'beneficial' to man, and (4) flagellates by contrast often remain ungrazed or fuel food chains which are economically undesirable.

The key then is to promote the growth of diatoms. Diatoms require nitrogen and silicon in a ratio of about 1:1 (Redfield et al. 1963). The ratio of these elements in sewage effluent is usually well above this (Officer & Ryther 1980). Thus, dissolved silicon can be depleted well before available nitrogen and phosphorus are in short supply. This situation favors the predominance of 'flagellate' over diatom communities. Lowering the N:Si ratio of nutrients in sewage effluent by adding extra silicon should reverse this trend. Diatoms should flourish and problems associated with eutrophication should be alleviated.

As water depth decreases, the benthos plays an increasingly important role in both the production (Nixon et al. 1976, Nixon et al. 1980b) and consumption (Hargrave 1973) of pelagic primary production. In shallow marine systems, the biogeochemical function of the

benthos as a supplier of nutrients for phytoplankton has been well established (Zeitzschel 1980). Recently, however, attention has focused on trophic interactions between benthic macrofauna and water column communities (Cloern 1982, Carlson et al. 1984). It has been suggested that benthic communities can limit phytoplankton biomass, thereby exerting a local control over eutrophication (Officer et al. 1982). Zooplankton communities may be affected as well. Direct removal by benthic filter feeders may occur (Carlson et al. 1984). Potential depletion of phytoplankton by the benthos (Peterson & Black 1987) suggests competition between zooplankton and benthos for food resources. The trophic structure of a system may govern its response to eutrophication (e.g. lakes, Carpenter et al. 1985). The presence or absence of a trophic link between the water column and benthos is thus likely to be important in relatively shallow coastal waters.

We tested these hypotheses through a series of nutrient additions to the large outdoor mesocosm systems at the Marine Ecosystems Research Laboratory (MERL) in Rhode Island, USA. Nutrient-treated tanks received daily additions of nitrogen and phosphorus in equal magnitude and proportion. One series of tanks, however, received a nutrient mix with an N:Si ratio of 14:1 while for another group this ratio was 1:1. To test for benthic effects we added these nutrient mixes to mesocosms with and without an intact benthic community.

## METHODS

**Mesocosms.** The mesocosms (Table 1), located outdoors at the University of Rhode Island, Graduate School of Oceanography, are simplified models of shal-

Table 1. Summary of MERL mesocosm design. Tank construction is fiberglass reinforced resin with a white interior to maximize sunlight reflection. A 50 cm diameter plunger with 60 cm vertical excursion mixes a tank at a rate of 5 cycles  $\text{min}^{-1}$  for 2 h every 6 h. Sediments were collected from mid-Narragansett Bay

Tank diameter	1.83 m
Tank height	5.49 m
Water surface area	2.63 $\text{m}^2$
Water depth	5.00 m
Water volume	13.1 $\text{m}^3$
Sediment area	2.53 $\text{m}^2$
Sediment depth	0.37 m
Water column turnover	27 d

low, plankton-based coastal marine ecosystems. Temperature, light, mixing, water turnover and sediments (when present) are similar to the parent system, Narragansett Bay (Pilson et al. 1979, Nixon et al. 1980a,

Oviatt et al. 1986). Sea water, drawn from Narragansett Bay with a diaphragm pump, is distributed to the tanks via gravity flow from a head tank. Water is delivered to the tanks in four 120 l pulses per day during each mixing cycle. Water depth is maintained by a constant level siphon. Equal volumes of water flow in and out of the tanks during each pulsed 'feed'. There are no screens to impede the passage of animals in or out of the tanks, and feed and drain pipes are 2.5 cm in diameter.

**Experimental design.** The experimental design included 2 completely crossed factors: nutrients, with 3 levels, and sediment, with 2 levels. This resulted in 6 treatment combinations and 2 mesocosms were assigned to each combination.

The levels of the nutrient factor were control (no nutrient addition),  $8\times$  (dissolved inorganic nutrients added to water column at a rate of 24.03 mmol nitrogen, 1.88 mmol phosphorus, and 1.71 mmol silicon  $\text{m}^{-2} \text{d}^{-1}$  – N:Si ratio = 14:1) and  $8\times + \text{Si}$  (24.03 mmol nitrogen, 1.88 mmol phosphorus and 24.03 mmol silicon  $\text{m}^{-2} \text{d}^{-1}$  – N:Si ratio = 1:1). Nitrogen was added in the form of  $\text{NH}_4\text{Cl}$ , phosphorus as  $\text{KH}_2\text{PO}_4$  and silicon as  $\text{Na}_2\text{SiO}_3 \cdot 9\text{H}_2\text{O}$ .

The sediment factor had 2 levels: with or without an intact benthic community. Sediment for the 6 tanks with a benthic community was collected from mid-Narragansett Bay using a 0.25  $\text{m}^2$  box corer as described by Hunt & Smith (1983). In the no-benthos treatment, sediments were omitted from the tanks, but material imported via feed water or produced in situ was allowed to accumulate on the bottom. Every 2 wk during summer, and less frequently during winter, tank bottoms were scrubbed with a plastic pad to prevent establishment of a macrofaunal community in the accumulated floc. The purpose of this no-benthos treatment was to exclude benthic macrofauna, while at the same time retaining the nutrient recycling function of bottom sediments.

The experiment commenced on 11 June 1985 and terminated 365 d later on 10 June 1986.

**Measurements.** System production, system respiration, benthic fluxes of nutrients and oxygen, chlorophyll *a*, total diatoms, zooplankton numbers and biomass, numbers of large pelagic fauna, benthic fauna and dissolved inorganic nutrient concentrations were measured at various intervals throughout the year-long experiment.

System production and respiration were estimated weekly by measuring oxygen concentrations at dawn, dusk and dawn in the tank water columns. Dissolved oxygen was measured by Winkler titration. Dawn minus dusk concentrations were corrected for diffusion to yield an estimate of system production (Oviatt et al. 1987). The difference between dusk concentration and

the following dawn concentration provided a measurement of system respiration (Oviatt et al. 1987).

Biomass of phytoplankton was determined weekly by analysis of chlorophyll *a* after Yentsch & Menzel (1963) and Lorenzen (1966) as modified by Lambert & Oviatt (1986) using Whatman GF/F glass fiber filters.

Concentrations of diatoms were determined according to Hasle (1978) on a weekly basis during bloom periods and less frequently during periods of low concentration ( $n = 28$  to 34 samples tank<sup>-1</sup>). Pooled samples from 3 depths were preserved in Lugol's iodine solution. The sample was allowed to settle overnight and counted (at least 500 cells) on an inverted microscope; most counts had a precision of 10 % (coefficient of variation).

Dissolved inorganic nutrients (NH<sub>3</sub>, NO<sub>2</sub>, NO<sub>3</sub>, PO<sub>4</sub> and SiO<sub>4</sub>) were determined weekly. A pooled sample from 3 depths was filtered (0.6 µm membrane filter) and frozen until analysis using a Technicon Autoanalyzer (Lambert & Oviatt 1986).

Zooplankton numbers and biomass were analyzed weekly in summer and fortnightly during winter. These were sampled by vertical net tow in the tank (64 µm mesh) filtering about 0.20 m<sup>3</sup> water. Actual volume filtered was determined with a flow meter. For biomass (>150 µm fraction) samples were rinsed with deionized water to remove salt, frozen, freeze-dried and weighed to the nearest 0.1 mg. When samples were heavily contaminated with phytoplankton, biomass was estimated from a relation between zooplankton numbers and biomass for uncontaminated samples (Lambert & Oviatt 1986).

Benthic macrofaunal samples were collected quarterly. On each sampling date, 10 random sediment cores (5.06 cm<sup>2</sup>) were collected with a flow-through core (Frithsen et al. 1983) to a depth of about 10 cm. Cores were sliced to yield a 0 to 2 cm and 2 to 6 cm depth fraction and each fraction was preserved in 10 % buffered formalin containing rose bengal.

After 2 mo, allowing uptake of stain and stabilization of formaldehyde dry weight, samples were washed through a nest of sieves (0.5 and 0.3 mm). Animals were identified and enumerated with the aid of a stereomicroscope. Bivalve biomass was determined by measuring shell length and converting this to organic carbon using the equations of Frithsen et al. (1986). Biomass of soft-bodied organisms was determined by conversion of dry weight to carbon (Frithsen et al. 1986).

Benthic fluxes of dissolved inorganic nutrients and oxygen were measured in a clear plexiglass chamber (vol. = 300 l) which encapsulated the entire 2.5 m<sup>2</sup> benthos (Doering et al. 1987). Fluxes were determined by following changes in concentration over time within the chamber. Initial and final samples were withdrawn by siphon after mixing with a hand operated stirring

bar. Control bottles were incubated on top of the chamber to correct fluxes for changes occurring in the water itself. Incubation time (3 to 10 h) varied inversely with temperature and oxygen was not allowed to drop below 80 % saturation. Fluxes were measured in all tanks with a benthos and in 3 of the 6 tanks without a benthos. A total of 9 measurements were taken throughout the year, being more frequent when water temperatures exceeded 5 °C.

About 4 wk into the experiment it became apparent that fish and other large pelagic fauna (>1 mm) had recruited into many of the tanks. These were sampled by towing a circular net (diameter just smaller than tank diameter) vertically through the water column. All tanks were sampled fortnightly from July 1985 to January 1986 and monthly thereafter. Numbers of fish, ctenophores, medusae and chaetognaths were determined non-destructively by concentrating these at the surface with the net. Two to three fish (Atlantic menhaden *Brevoortia tyrannus*) were removed from the tank for a short time to allow measurement of total length. Numbers of fish larvae present at the start of the experiment were determined from zooplankton net tow samples. During the course of the experiment, several menhaden ( $n = 5$ ) leaped onto the pier surrounding the tanks. Length and dry weight were determined to yield the following relation:

$$\text{Dry weight (g)} = 0.011 \text{ Length (cm)}^{2.382} \\ n = 5, r^2 = 0.991$$

**Statistical analysis.** For most parameters, data were integrated over time (trapezoidal technique) and an annual time-weighted mean calculated. This yielded 2 observations for each treatment combination. Statistically, data were evaluated using a 3-factor analysis of variance. The factors were nutrient addition (Control, 8×, 8× + Si), sediment (benthos, no-benthos) and replicate (the 2 tanks in each treatment combination). The replicates were considered to be random and nested within the nutrient by sediment interaction. The error term for *F*-tests in this design is the replicate (nutrient by sediment) mean square. Differences between main effect and interaction means were evaluated by the Student-Newman-Keuls test. Such a design and procedures for comparing means are summarized in Winer (1971).

## RESULTS

### Experimental manipulations

In general, the desired experimental manipulations were realized. N:Si ratios in tanks dosed with nutrients approximated 1.0 when the addition ratio was 1:1 and



were substantially greater ( $p < 0.001$ ) than this when the addition ratio was 14:1 (range 4.5 to 10.5, Table 2).

In nutrient-treated tanks the floc, which accumulated on the bottom of tanks without sediment, retained the biogeochemical function of an intact benthos by recycling nutrients to the water column (Table 3). Since benthic fluxes of nutrients were measured in only 1 of 2 replicates in tanks without sediment only a qualitative estimate of the benthos treatment effect is possible. Annually, fluxes of nitrogen and phosphorus were perhaps slightly larger in tanks without sediment than in tanks with the intact community, while the return of silica to the water column was somewhat less than expected, especially in the  $8\times$  treatment. By contrast, removal of sediments in controls severely reduced the nutrient recycling capacity of the benthos, often by an order of magnitude (Table 3).

Benthic macrofauna were successfully excluded from tanks without sediment. Occasional brushing of the bottom seemed to prevent recruitment of most forms, although towards the end of the experiment, some annelid scale worms were observed crawling in the floc of nutrient-treated tanks.

**Nutrient concentrations.** Time-weighted (annual) daily concentrations (Table 2) of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) were similar in both nutrient treatments ( $8\times$ ,  $8\times + \text{Si}$ ). Concentrations were significantly higher than in controls ( $p < 0.0001$ ). The presence or absence of a

benthos had no statistically discernible effect. DIN was about equally partitioned between ammonia and nitrate + nitrite in all treatments.

Dissolved silicate was significantly higher in the  $8\times + \text{Si}$  tanks than in controls or  $8\times$  treatments ( $p < 0.0005$ ). Concentrations in controls and  $8\times$  treatments were similar. Within each of the nutrient treatments, sedimented tanks maintained higher dissolved silicate concentrations than tanks without a benthos ( $p < 0.05$ ).

N:P ratios ranged from 1.8 in controls to between 10 and 11 in nutrient treatments, suggesting nitrogen limitation. Both nutrient treatments ( $8\times$  and  $8\times + \text{Si}$ ) exhibited higher N:P ratios than controls ( $p < 0.0001$ ).

### Oxygen concentration

Annual mean oxygen concentration (Table 4) at dawn was lower in controls than in nutrient treatments ( $8\times$  and  $8\times + \text{Si}$ ) ( $p < 0.0001$ ). Within controls, sedimented tanks had a somewhat lower oxygen concentration than tanks without sediment; about  $0.6 \text{ mg l}^{-1}$ . Within the nutrient treatments, tanks with sediment maintained oxygen concentrations about  $1.6 \text{ mg l}^{-1}$  lower than those without sediment. The only potential effect of additional silica was observed in nutrient-treated tanks without sediment. Here, the  $8\times + \text{Si}$  treatment exhibited a higher oxygen concentration than its  $8\times$  counterpart ( $12.78 \text{ mg l}^{-1}$ ). But again, the difference

Table 2. Time-weighted mean daily concentrations and molar ratios of dissolved inorganic nutrients in  $\mu\text{mol l}^{-1}$  (DIN =  $\text{NH}_3 + \text{NO}_2 + \text{NO}_3$ ). Values are averages of 2 replicate tanks

Treatments		DIN	$\text{PO}_4$	$\text{SiO}_4$	N:Si	N:P
Nutrient	Sediment					
Control	With	1.20	0.65	16.82	0.08	1.8
	Without	0.92	0.50	7.00	0.13	1.8
$8\times$	With	65.03	6.01	15.54	4.5	10.8
	Without	59.28	6.44	5.71	10.5	9.2
$8\times + \text{Si}$	With	62.70	6.41	74.90	0.90	9.8
	Without	53.50	5.79	49.81	1.07	9.2

Table 3. Time-weighted mean daily fluxes ( $\text{mmol m}^{-2} \text{ d}^{-1}$ ) of nutrients and oxygen across the sediment-water interface. For sediment tanks values for both replicates are given. Positive values indicate efflux, negative values uptake by sediments

Flux	Control		Treatment $8\times$		$8\times + \text{Si}$	
	Sed.	No sed.	Sed.	No sed.	Sed.	No sed.
DIN	1.63, 1.71	0.18	3.03, 3.40	4.99	3.69, 3.86	4.43
SRP	0.09, 0.12	-0.004	0.26, 0.33	0.71	0.23, 0.55	0.66
$\text{SiO}_4$	2.24, 2.71	0.07	3.03, 4.28	1.66	4.79, 6.12	4.45
N:Si	0.60, 0.70	2.6	0.8, 1.0	3.0	0.6, 0.8	1.0
N:P	14.2, 18.1	-	10.3, 11.6	7.0	7.0, 16.0	6.7
$\text{O}_2$	-0.74, -0.71	-0.17	-1.47, -1.10	-0.62	-1.89, -0.94	-0.79

Table 4. System production, respiration, net production, mean and minimum concentrations of oxygen during the experiment. Values are averages of 2 replicate tanks

Treatments		Production	Respiration	Net	Average	Minimum
Nutrient	Sediment	(g O <sub>2</sub> m <sup>-2</sup> yr <sup>-1</sup> )	(g O <sub>2</sub> m <sup>-2</sup> yr <sup>-1</sup> )	production (g O <sub>2</sub> m <sup>-2</sup> yr <sup>-1</sup> )	oxygen (mg O <sub>2</sub> l <sup>-1</sup> )	oxygen (mg O <sub>2</sub> l <sup>-1</sup> )
Control	With	554	453	104	8.97	6.30
	Without	450	306	144	9.49	7.00
8 ×	With	1438	1166	271	10.95	4.39
	Without	1587	1170	417	12.13	6.55
8 × + Si	With	1306	1119	170	10.80	4.10
	Without	1599	1231	369	12.78	7.43

was slight. In summary, the addition of nutrients resulted in higher oxygen concentrations. The presence of sediments modified this effect, causing tanks with sediments to exhibit lower concentrations than their unsedimented partners.

In control tanks (with and without sediment) and nutrient-treated tanks without sediment, oxygen concentrations never fell below 6 mg l<sup>-1</sup> during the year-long experiment (Table 4). Statistically these treatments were indistinguishable with respect to the lowest observed oxygen concentration. By contrast, the combined effects of nutrient addition and the presence of sediments appeared to drive oxygen concentrations lower than in other treatments. Thus, nutrient-treated tanks with sediment achieved the lowest oxygen concentrations, approaching 4 mg l<sup>-1</sup> ( $p < 0.05$ ).

#### System production and respiration of oxygen

Production of oxygen over the course of the experiment was similar in all nutrient-treated tanks. These were on average about 3 times more productive than controls ( $p < 0.0001$ ). In general, sediment had no statistically apparent effect on production ( $p = 0.17$ ).

Annual respiration of oxygen showed the same pattern as production. Nutrient-treated tanks consumed about 3 times as much oxygen as controls ( $p < 0.0005$ ).

Net system production was higher in nutrient-treated tanks (8 × and 8 × + Si) than in controls ( $p < 0.05$ ). Within a given nutrient addition treatment (Control, 8 × or 8 × + Si) tanks without sediment had a higher net production of oxygen than tanks with sediment ( $p < 0.05$ ).

#### Benthic flux of oxygen

On an annual basis the bottoms of all tanks, whether sedimented or unsedimented, consumed oxygen (Table 3). In sedimented tanks, no statistical differences

between treatments were found but on average controls exhibited the smallest fluxes and 8 × + Si tanks the largest with the 8 × treatment being intermediate. Qualitative comparison of tanks with and without sediment suggests that flux of oxygen into the bottom of tanks with sediment was greater than in tanks without a benthos.

#### Chlorophyll a

Mean phytoplankton biomass, as measured by chlorophyll a (Fig. 1), showed differing responses to nutrient addition, which were dependent on the presence or absence of a benthos. In tanks with sediment no statistical difference between the 8 × and 8 × + Si treatments was observed, although both of these treatments maintained a chlorophyll biomass which averaged about 4 times that observed in controls ( $p < 0.002$ ).

In tanks without sediment, the 3 nutrient treatments were statistically different from each other ( $p < 0.002$ ) and were ordered as follows: Control < 8 × < 8 × + Si. The 8 × treatment maintained about 6 times the chlorophyll biomass of controls while biomass in the 8 × + Si treatment averaged 8 times that in controls.

Collectively, the tanks fell into 3 statistically discernible groups ( $p < 0.005$ ): all control tanks (lowest biomass), all 8 × tanks and 8 × + Si tanks with sediment (intermediate biomass), and 8 × + Si tanks without sediment (highest biomass). Thus, chlorophyll biomass was clearly enhanced by additional silica in tanks without sediment.

#### Total diatoms

Annual mean daily concentrations of diatoms are shown in Fig. 1. Within a given treatment, replicate tanks agreed reasonably well except for the 8 × + Si tanks with sediment. Here, diatom abundance spanned an order of magnitude (10<sup>3</sup> to 10<sup>4</sup> ml<sup>-1</sup>). This poor replication, not observed for chlorophyll, reduced the

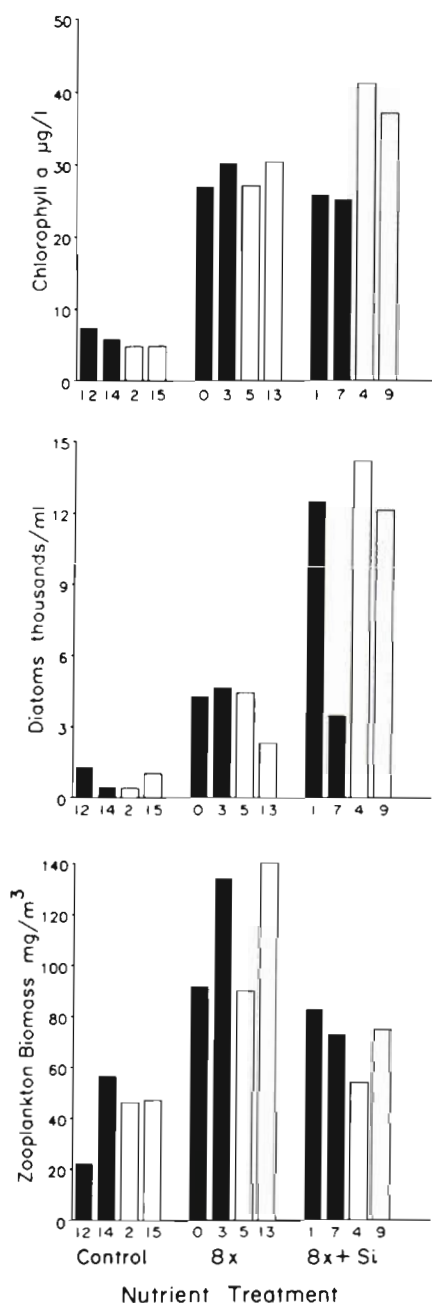


Fig. 1 Annual mean concentration of chlorophyll a (top), diatoms (middle) and dry weight biomass of zooplankton (bottom) in 3 nutrient treatments. Numbers on horizontal axis are tank numbers of individual mesocosms. Solid bars: mesocosms with an intact benthos; open bars: mesocosms without a benthos

power of statistical tests. Therefore, tanks with and without sediments were analyzed separately.

In tanks without sediment, controls had the lowest abundances, 8x tanks intermediate abundances and 8x + Si tanks the highest abundances. On average 8x tanks had about 4.7 times the diatom abundances observed in controls. In tanks with additional silica

abundances were 18 times those in controls and about 4 times those of the 8x treatments. Statistically, the 8x + Si tanks were different from the 8x and control tanks ( $p < 0.05$ ). The latter treatments were statistically indistinguishable.

Although mean abundances for the nutrient treatments in tanks with sediment showed the same pattern as in tanks without sediment (Control < 8x < 8x + Si) no statistical differences were found.

### Zooplankton

Zooplankton biomass was highest ( $p < 0.05$ ) in the 8x tanks (Fig. 1). Although the 8x + Si tanks tended to be greater than controls, no statistical difference between these treatments was found. The presence or absence of a benthos had no statistically significant effect. Total numbers of zooplankton (not shown) exhibited a pattern identical to that for biomass.

The composition of the zooplankton community appeared related to both nutrient addition and presence or absence of sediment. In all control tanks, the relative abundances (%) of holoplanktonic forms and the meroplankton of benthic macrofaunal adults were similar with holoplankton predominant (>90 % of the total). Upon nutrient addition, the proportion of meroplankton was greater (arcsin-transformed data,  $t$ -test,  $p < 0.05$ ,  $df = 6$ ) while that of holoplankton smaller (arcsin-transformed data,  $t$ -test,  $p < 0.05$ ,  $df = 6$ ) in tanks with sediment than in those without. Thus, when sediments were present the response of the zooplankton community to nutrient addition was to shift towards a larger temporary component (Fig. 2).

Perhaps the most striking effect on zooplankton community structure was manifested at higher trophic levels and occurred in tanks without sediment. Predatory (carnivorous) holoplankton were significantly more prevalent in the water columns of tanks without sediment ( $p < 0.0001$ , Fig. 2). These forms included copepods as well as ctenophores (*Mnemiopsis leidyi*, *Pleurobrachia* sp.), medusae (*Aurelia* sp.), and chaetognaths (*Sagitta* sp.). The latter 3 types did not successfully recruit in tanks with sediment. Control tanks without sediment had higher standing stocks of such predators than their nutrient-treated counterparts (8x and 8x + Si,  $p < 0.05$ ). The addition of nutrients (regardless of ratio) resulted in a decreased abundance of carnivorous holoplankton.

By contrast, densities of carnivorous meroplankton (mysids, larvae of anemones and shrimp) did not show such an obvious distributional pattern (Fig. 2). In some treatments (e.g. 8x + Si), tanks with sediment had demonstrably higher densities than those without. In others, (control and 8x) the presence of sediment did

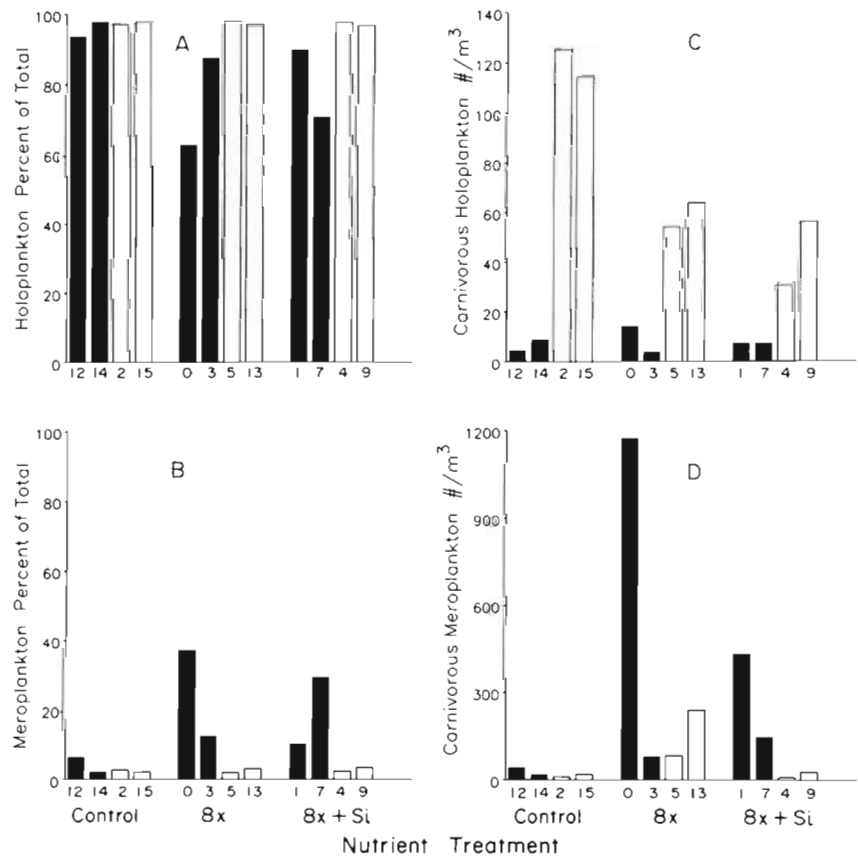


Fig. 2. Holozooplankton and merozooplankton in 3 nutrient treatments. (A) Annual mean percent holozooplankton. (B) Annual mean percent merozooplankton. (C) Annual mean number of carnivorous holozooplankton. (D) Annual mean number of carnivorous merozooplankton. Numbers on horizontal axis are tank numbers of individual mesocosms. Solid bars: mesocosms with a benthos; open bars: mesocosms without a benthos

not have so clear an effect. Analysis of transformed data ( $\log + 1$ ) revealed a tendency of tanks with sediment to have higher densities of carnivorous merozooplankton than those without ( $p < 0.10$ ).

### Fish

Atlantic menhaden *Brevoortia tyrannus* recruited successfully in all tanks lacking a benthos. These pelagic fish were never observed or captured in tanks with sediment. Abundance declined in all tanks from 11 June 1985 to 31 January 1986 when no fish were seen or captured (Fig. 3). Abundance was similar in all treatments on all sampling dates ( $p = 0.92$ ).

Menhaden increased in length during their residence in the tanks (Fig. 3). Measurement of menhaden larvae recovered from zooplankton tows indicated that on 11 June 1985 (the beginning of the experiment) fish in all no-sediment tanks were of similar size (ca 0.3 cm,  $p > 0.05$ ). Routine measurement of total length (cm) commenced on 6 September 1985 when lengths averaged 5.15 cm in controls, 8.95 cm in 8x tanks and 9.93 cm in 8x + Si tanks. These means were statistically different from each other ( $p < 0.05$ ). This statistically significant difference in size across treatments was

maintained on all subsequent sampling dates until the fish disappeared.

The effects of the experimental manipulations on Atlantic menhaden were clear. The presence of sediments prevented successful recruitment. Addition of nutrients (independent of N:Si ratio) had no effect on abundance but produced larger fish. The N:Si ratio of nutrient additions was also important. In tanks with additional silica (8x + Si, N:Si = 1.0) fish were larger than in those with a high N:Si ratio (8x, N:Si = 14). Although actual growth rates were not calculated, the size data indicate that growth was enhanced by addition of nutrients (8x and 8x + Si > controls) and that lowering the N:Si ratio caused growth to increase further (8x + Si > 8x).

### Benthic biomass

The biomass of benthic macrofaunal organisms in tanks with sediment sampled by the 5 cm<sup>2</sup> cores is given in Table 5. Because of the great discrepancy in biomass between replicates of the 8x + Si nutrient treatment no statistical differences between treatments was detected either for total biomass or biomass of small filter feeding organisms. The latter group com-

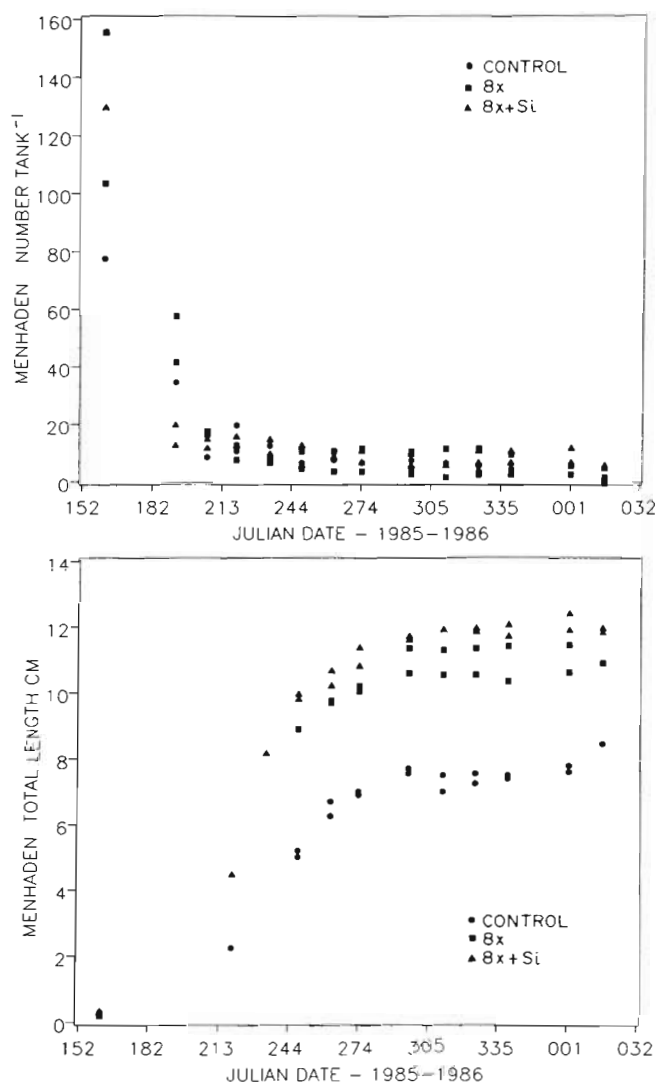


Fig. 3. *Brevoortia tyrannus*. Mean abundance of Atlantic menhaden sampled (top) and mean total length (bottom) in each mesocosm without sediment during June 1985 to January 1986

prised both obligate forms (e.g. bivalves) and facultative forms (spionid polychaetes, amphipods).

## DISCUSSION

### The nitrogen:silicon ratio

This experiment tested the general hypothesis that reduction of the N:Si ratio in sewage-derived nutrients would lead to an enhanced diatom flora and a concomitant amelioration of the undesirable aspects of nutrient discharge to the environment (Officer & Ryther 1980, Ryther & Officer 1981).

Evidence in support of this scenario has been

Table 5. Time-weighted mean benthic macrofaunal biomass and biomass of benthic filter feeders in tanks with sediment

Treatment	Tank	Benthic biomass (g C m <sup>-2</sup> )	Benthic filter feeder biomass (g C m <sup>-2</sup> )
Control	12	3.48	0.70
	14	2.39	0.51
8 ×	0	5.04	1.73
	3	6.85	1.48
8 × + Si	1	0.75	0.16
	7	8.84	2.74

reviewed previously (Officer & Ryther 1980, Ryther & Officer 1981). It suffices to mention that lack of silicon has been associated with decreased diatom abundance or dominance in lakes (Kilham 1971, Schelske & Stoermer 1972, Schelske et al. 1984), estuaries (Prati 1965, McLaughlin et al. 1982), coastal waters (van Bennekom et al. 1975) and experimental enclosures (Parsons et al. 1978). Addition of silicon to natural waters can cause an increase in diatom abundance both in the sea (Menzel et al. 1963) and in lakes (Stoermer et al. 1971). Observations of shifts in phytoplankton community structure from diatoms to flagellates (Taslakian & Hardy 1976) or from net plankton to nanoplankton (McCormick & Quinn 1975, Revelante & Gilmartin 1978) in response to nutrient enrichment (N and P) are consistent with this scenario but there are exceptions (see Paasche 1980). Lastly, the N:Si ratio of dissolved inorganic nutrients can be an important determinant of which nutrient becomes limiting to phytoplankton first (Levasseur & Theriault 1987).

Alteration of the N:Si ratio of nutrient additions to mesocosms, with or without sediments, did not dramatically alter the metabolic response of these systems to eutrophication. Production, respiration, net production and mean concentration of oxygen were all higher in nutrient treated tanks than in controls. The lowest observed oxygen concentrations occurred in nutrient-treated tanks with sediments (about 4 mg O<sub>2</sub> l<sup>-1</sup>). No effect of N:Si ratio was apparent on any of these variables. Our results suggest that lowering the N:Si ratio (14:1 to 1:1) of a nutrient discharge will do little to ameliorate 'oxygen problems' stemming from nutrient loading. Our experiment was conducted at only one nitrogen loading level (8×). Available data suggest that estuaries receiving a lower nutrient loading do not experience low oxygen problems (Oviatt et al. 1986).

Aesthetically, the accumulation of phytoplankton biomass in the water column is considered an undesirable consequence of eutrophication (Ryther & Officer 1981). Chlorophyll *a* concentrations were higher in



nutrient-treated tanks than in controls, as might be predicted. Lowering the N:Si ratio either had no influence on this general nutrient effect (tanks with sediment) or on average allowed a higher level of biomass to persist (tanks without sediment). Therefore, we suggest that manipulation of the N:Si ratio of a nutrient discharge will have little effect on the visual quality of receiving waters.

Despite a negligible effect on the character of eutrophication, alteration of the N:Si ratio clearly affected the abundance of diatoms in the mesocosms especially in tanks without sediment. Although the difference was not statistically significant, standing stocks of diatoms in tanks receiving nutrients with an N:Si ratio of 14:1 tended to be higher than controls. Enhancement of diatom abundance by addition of nitrogen alone has been observed previously in 500 l microcosms (Sanders et al. 1987). Some enhancement may be expected in our case because silicon was added to these tanks, albeit in small amounts relative to nitrogen. Of the 4 tanks receiving nitrogen and silica in equal proportion, 3 developed relatively high ( $10^4 \text{ ml}^{-1}$ ) standing stocks of diatoms (1 sedimented tank and both tanks without sediment). Thus, in tanks without sediment, the response of the diatom community to silica enhancement was dramatic and statistically significant. In tanks with sediments the response was variable: abundance in one tank equivalent to tanks without sediment and abundance in the other being indistinguishable from high ratio (14:1) addition tanks.

At first inspection, diatom abundance in the tanks without sediment conforms to the hypothesis, advanced by Officer & Ryther (1980), that the availability of silicon, especially in relation to other nutrients, is an important determinant of diatom population abundance. In fact, nutrient loading (= nitrogen + silicon,  $\text{mmoles m}^{-2} \text{ d}^{-1}$ ) and annualized mean diatom abundance are highly correlated ( $r^2 = 0.853$ ,  $p < 0.01$ ,  $n = 6$ ) in these tanks. On the other hand, zooplankton biomass was highest in the  $8\times$  tanks and lower in both the controls and  $8\times + \text{Si}$  tanks. Grazing, either pelagic or benthic, can also be an important control of phytoplankton abundance (Martin 1965, Cloern 1982,

Deason & Smayda 1982, Officer et al. 1982) and may explain some of the differences in diatom abundance. In order to clarify the situation, a stepwise multiple regression model (Table 6) was constructed to explain variability in diatom abundance. Independent variables included in the model were nutrient loading (as previously described) and potential grazing biomasses of zooplankton and fish. The stepwise technique yielded a 2 variable model consisting of nutrient loading and zooplankton biomass, which explained respectively 85 and 14 % of the variation in diatom abundance (total = 99 %). The signs of regression coefficients are consistent with a positive effect of nutrients and a negative effect of grazing on abundance. The model suggests that both nutrient supply and zooplankton grazing regulated diatom abundance in tanks without sediment. Based on amount of variation explained it appears that nutrient supply was the dominant factor.

In tanks with sediment, nutrient loading (N + Si) explained only about half the variability in diatom abundance ( $r^2 = 0.552$ ,  $p < 0.09$ ). This was no doubt due to the poor replication in the  $8\times + \text{Si}$  treatment. Benthic biomass in these 2 tanks varied inversely with diatom abundance. The tank with high diatom abundance had a benthic biomass lower than control tanks while the other replicate had the highest benthic biomass of any tank. Just why the 2 tanks had such disparate infaunal biomasses remains unknown. At the end of the experiment, however, the low biomass tank had a significant number (ca 40) of epibenthic shrimp *Crangon septemspinosa*. Such shrimp are known to effect both infaunal biomass and species composition (Nelson 1981). Thus, we hypothesize that epibenthic predation was the cause. A stepwise regression model (Table 6) including nutrient loading and grazer biomasses as independent variables was again constructed to explain variability in diatom abundance. Nutrient loading (N + Si) accounted for 55 % of the variability while the biomass of benthic filter feeders accounted for about 40 % (total = 95 %). Again the signs of the regression coefficients are consistent with a positive effect of nutrient loading and a negative effect

Table 6. Stepwise Regression Models explaining variation in diatom abundance. Nutrient loading equalled the sum of nitrogen and silicon additions in  $\text{mmol tank}^{-1} \text{ d}^{-1}$   $n = 6$  in each case. ns: not significant

Treatment	Variables	Partial $R^2$	$p$	Reg. coefficient
No-sediment	Nutrient loading	0.863	0.009	+111.05
	Zooplankton biomass	0.140	0.005	-60.08
	Fish biomass	—	ns	—
Sediment	Nutrient loading	0.552	0.09	+79.87
	Benthic filter feeder biomass	0.405	0.01	-3141.54
	Zooplankton biomass	—	ns	—

of benthic grazing on diatom abundance. As in tanks without sediment, the model suggests that the amounts of nitrogen and silica added to the tanks played an important role in determining diatom abundance. Statistically, zooplankton biomass and by inference, zooplankton grazing, was unimportant. Rather the model suggests that benthic filter feeders exerted a significant control on diatom abundance in tanks with sediment. Again, judging by the proportion of variability explained, benthic grazers were nearly as important as nutrient loading in these tanks. This result is in accord with the calculations of Cloern (1982), Officer et al. (1982) and Nichols (1985) which suggest that benthic filter feeders are an important control of phytoplankton biomass in South San Francisco Bay, a shallow, eutrophied estuary.

An appropriate N:Si ratio (1.0) by enhancing diatoms is also hypothesized to promote a trophically more desirable and productive ecosystem (Officer & Ryther 1980). Results from the tanks without sediment are consistent with the idea that a diatom-based food chain allows more efficient transfer of energy to higher trophic levels either through fewer links (Ryther 1969) or higher food quality (Greve & Parsons 1977).

Although quantitative measurements of food chain transfers are lacking, the available data suggest greater efficiency in the treatment with additional silica ( $8\times + \text{Si}$ , no-sediment). Differences in fish size, and hence growth, among the 3 treatments were probably not due to treatment-related differences in density, as density was statistically invariant across treatments without sediment. The observed differences were more likely a function of nutrient addition. The large differences in fish size between the controls and the 2 nutrient addition treatments (4.0 cm) may be attributable to the higher level of production, the generally greater number of diatoms, or both, which resulted from nutrient addition. The smaller difference in size (1.0 cm) resulting from manipulation of the N:Si ratio ( $8\times$  vs  $8\times + \text{Si}$ ), was probably not a function of production; this was statistically similar in both treatments. Qualitatively, this suggests a more efficient transfer of energy to higher trophic levels (fish) in the  $8\times + \text{Si}$  treatment where diatoms were more abundant. Unfortunately, data were insufficient to evaluate tanks with sediment in a similar fashion.

With respect to the ideas expressed in the 2 papers by Officer & Ryther (1980) and Ryther & Officer (1981) our results are equivocal. On the one hand, alteration of the N:Si ratio of nutrients in sewage effluent did nothing dramatic by way of 'ecosystem improvement'. Although enhanced fish growth resulted, this was not as dramatic as that caused by addition of nutrients in a ratio resembling sewage effluent. By contrast, however, our results do support many of the ideas concern-

ing diatoms, especially the importance of N:Si supply ratio and grazing by both zooplankton and benthos in regulating diatom abundance.

### The benthos

In addition, the experiment also examined the effect of the benthos on ecosystem structure and function. The importance of the biogeochemical link between the water column and benthos in shallow marine systems has been well established (Hargrave 1973, Nixon et al. 1980b, Zeitzschel 1980, Klump & Martens 1983, Kelly & Nixon 1984). Although there were differences in benthic fluxes related both to the presence and absence of intact sediment and to nutrient addition, we believe that these are not of primary importance to the discussion to follow. Rather we argue that the presence of benthic macrofauna and/or bottom sediment itself was the treatment effect most responsible for the differences we observed.

We have already seen that the primary grazing control on diatoms was probably different in tanks with and without a benthos. Zooplankton appeared important in tanks without a benthic macrofaunal community whereas benthic filter feeders were important in tanks with sediment. This result agrees with the findings of Cloern (1982) that, in shallow water, the primary herbivorous trophic link may be benthic rather than pelagic. A spatial shift, from water column to benthos, of the primary herbivore link may have important consequences for pelagic food webs (Nichols 1985). Such shifts, precipitated by increases in benthic biomass, can be caused by low river flow conditions (Nichols 1985), apparently random invasions (Cohen et al. 1984), or perhaps by eutrophication (Frithsen et al. unpubl.).

The structure of the pelagic consumer communities that developed in tanks with and without sediment was dramatically different. Chaetognaths, ctenophores, and planktivorous fish were present in tanks without sediment, while these forms were absent from tanks with sediment. Meroplankton, including predators and other forms, tended to be more abundant in tanks with sediment. Although the magnitude of these differences was probably affected by nutrient addition, the cause of them was undoubtedly the omission of an intact benthic community.

The causes of these differences are not known but speculation suggests several ways in which the benthos may have affected pelagic communities during the experiment.

(1) Direct herbivory. The two  $8\times + \text{Si}$  tanks with sediment maintained similar chl *a* biomasses yet very different diatom abundances. By inference, the phytoplankton community structure must have been quite

different in these 2 tanks. The high biomass of benthic filter feeders in the tank with fewer diatoms, contrasted with high diatom abundance and a depauperate benthos, suggests that benthic feeders preferentially removed diatoms, altering phytoplankton community structure.

(2) Meroplankton-holoplankton interactions. Total abundance and biomass of zooplankton did not vary as a function of sediment. Both sedimented and unsedimented control tanks had similar relative abundances of holo- and meroplankton. Nutrient addition to tanks without sediment caused no change in composition. In tanks with sediment, however, the proportion of meroplankton increased significantly. Carnivores tended to be holoplanktonic in tanks lacking a benthic community and meroplanktonic when the bottom community was left intact. These observations suggest competitive, predatory or otherwise inhibitory interactions between meroplankton and holoplankton with meroplankton being ascendent.

(3) Inhibition of recruitment. The presence of ctenophores, chaetognaths and fish in tanks without sediment coupled with their virtual absence in tanks with sediment could be due to recruitment failure in the presence of sediment. Failure could result from a number of factors including predation by or competition with benthic adults, or interactions with meroplankton in the water column.

(4) Physical factors. It is certainly possible that the presence of resuspended sediment particles was responsible for the observed differences. Our experiment did not isolate macrofauna and sediment in separate treatments.

There is no question that benthic filter feeders consume phytoplankton directly (Winter 1978). Our results agree with speculations by Cloern (1982), that filter feeding benthic organisms can maintain structural differences in phytoplankton communities. Meroplankton have been observed to outnumber holoplankton in eutrophic waters and to utilize available food sources at a higher rate than holoplankton (Turner & Anderson 1983). Competitive interactions in the water column are thus possible. The idea that benthic adults may inhibit recruitment of their own larvae was suggested by Thorson (1957) and is inherent in the concept of trophic group amensalism (Rhoads & Young 1970). This inhibition may be effected through substrate disturbance (Rhoads & Young 1970, Wilson 1981) and predation of juveniles (Wilson 1981) or pelagic larvae (Breese & Phibbs 1972). With respect to holoplankton, deposit feeders could consume resting eggs of holoplankton, which can be an important source of copepod recruits (Sullivan & McManus 1986). Suspension feeders may consume adults, larvae (Carlson et al. 1984) and perhaps eggs of pelagic organisms.

In our experiment, the presence of an intact benthic community shifted the obligate pelagic community towards truncated metazoan food chains. A suppression of higher trophic levels in the obligate pelagic community may allow the benthos to increase its share of available resources either as pelagic meroplankton or as adults in the sediments.

Our system is both shallow and well mixed. These factors may exaggerate coupling of the benthic and pelagic subsystems. Nevertheless, our results indicate that the benthos can have a profound effect on pelagic community structure. The magnitude of this interaction will no doubt depend on the strength of coupling between these subsystems.

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