

# Response of benthic meiofauna to nutrient enrichment of experimental marine ecosystems

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**ABSTRACT:** The long-term (2.4 yr) response of benthic meiofauna to eutrophication of experimental marine ecosystems was studied at the Marine Ecosystems Research Laboratory, Graduate School of Oceanography, University of Rhode Island (USA). Ammonium, phosphate and silicate were added daily to the mesocosms in a logarithmic progression (0×, 1×, 2×, 4×, 8×, 16× and 32×), with the 1× addition being  $N = 2.88$ ,  $P = 0.225$ ,  $Si = 0.205 \text{ mmol m}^{-2} \text{ d}^{-1}$ . Phytoplankton production and biomass in the tanks increased with increasing nutrient enrichment. The benthic community gave a quantitatively less marked response to the gradient of nutrient input. The meiofauna showed remarkably little response in terms of total biomass and abundance, but significant effects were found on major taxa, leading to a changed meiofauna community structure. Nematode and juvenile polychaete abundance increased with increasing nutrient input, especially in early summer, whereas kinorhynchs, ostracods, harpacticoids and juvenile bivalves decreased. The lack of a positive biomass response of the total meiofauna in the enriched tanks suggests that the meiofauna was limited not only by the availability of food, but also by biotic interactions.

## INTRODUCTION

Eutrophication of coastal marine areas has received increasing attention in recent years, both in Europe (Rosenberg 1985) and North America (Goldberg 1982). Enhanced concentrations of inorganic nutrients and heavy plankton blooms have been recorded, as has oxygen deficiency in the bottom water below the pycnocline, e.g. in the southeastern Kattegat (Rosenberg 1985), and the Baltic Sea (Lassig 1987), and in Chesapeake Bay (Officer et al. 1984). Another common effect of eutrophication and organic enrichment is an increase in benthic macrofaunal biomass (Pearson & Rosenberg 1978). The mechanisms by which different compartments of a coastal marine ecosystem react to an increased input of inorganic nutrients are still, however, incompletely understood (Nixon et al. 1986). This is particularly true for the benthic meiofauna.

Studies of the effects of environmental perturbations on marine ecosystems have in recent years been stimulated by the use of mesocosms – large enclosures containing captive experimental ecosystems (Steele 1979, Donaghay 1984). At the Marine Ecosystems Research Laboratory (MERL), of the Graduate School of Oceanography, University of Rhode Island, USA, a

long-term ecosystem level eutrophication experiment was carried out from 1981 to 1983 (Nixon et al. 1984, 1986, Grassle et al. 1985, Oviatt et al. 1986). We studied the benthic meiofauna communities in the MERL mesocosms during this experiment, and examine 3 basic questions: (1) How do major meiofaunal taxa respond to an increased input of nutrients and the resulting increase in sedimentation of seston? (2) Were the meiofauna populations in the MERL mesocosms mainly limited by food or by other factors, such as disturbance or predation from benthic macrofauna? (3) Can the gross taxonomic composition of benthic meiofauna communities be used as an indicator of eutrophication and organic enrichment?

## MATERIALS AND METHODS

**The mesocosms.** The MERL mesocosms are designed to simulate shallow, unstratified, temperate marine ecosystems, such as Narragansett Bay, on which they are situated (Pilson et al. 1980). Each mesocosm contains a water column underlain by a tray with sediment (Fig. 1). The benthos is predominantly heterotrophic most of the year, as in Narragansett Bay. Water temper-

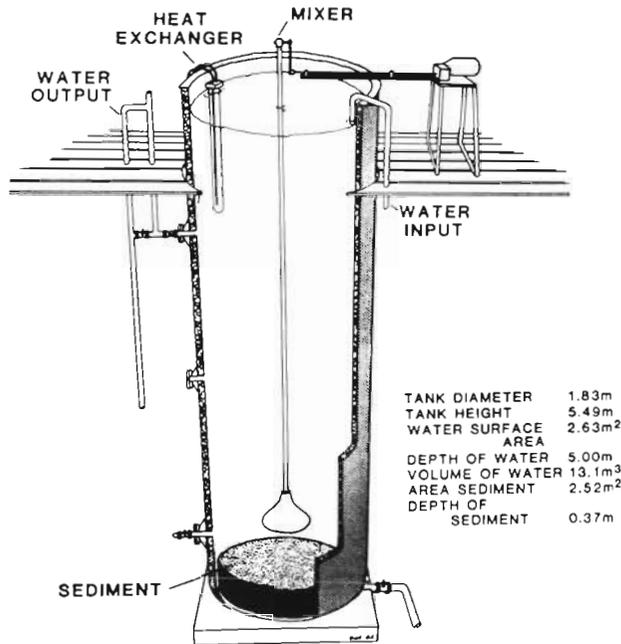


Fig. 1. Cross section of a MERL mesocosm showing input and output pipes, mixer, sediment container and heat exchanger. (Drawn by E. Klos)

ature in the tanks was maintained within 2 °C of that in the Bay, with maxima of ca 22 °C in July-August and minima of ca 1 °C in January-February (Frithsen et al. 1985b). A vertical plunger simulated the tidal mixing in the Bay (Nixon et al. 1980). The mean suspended loads in the mesocosms were similar to those in the Bay (ca 3 mg l<sup>-1</sup>; Oviatt et al. 1986). Seawater (27 to 31 ‰ S) was pumped in from 2 m above the bottom at a 4 m deep site, giving a turnover time of 27 d.

Sediment cores collected from a well-studied 7 m deep site in mid Narragansett Bay (Rudnick et al. 1985, Grassle et al. 1985), using a 0.25 m<sup>2</sup> USNEL spade box corer (Hunt & Smith 1983), were placed in the tanks in April 1981. The sediment was 18 % sand, 60 % silt and 23 % clay particles by weight (mean grain size 28 µm), with 47 % water content and 1.8 % total carbon content (0 to 4 cm sediment depth; Lambert & Oviatt 1986). The benthic macrofauna at this site is numerically dominated by 2 deposit feeders, the capitellid polychaete *Mediomastus ambiseta* (Hartman) and the bivalve *Nucula annulata* (Hampson) (Grassle et al. 1985).

**The experiment.** Six MERL mesocosm tanks received additions of nitrogen, phosphorus and silica as the inorganic salts NH<sub>4</sub>Cl, KH<sub>2</sub>PO<sub>4</sub> and NaSiO<sub>3</sub> · 9H<sub>2</sub>O, in molecular ratios characteristic of sewage entering upper Narragansett Bay (12.80 N:1.00 P:0.91 Si; Nixon 1981). The lowest level (1×) of nutrient addition (N = 7.57, P = 0.591, Si = 0.54 mmol tank<sup>-1</sup> d<sup>-1</sup>) corresponded to the estimated average daily per unit area input of dissolved inorganic nutrients into Narragansett

Bay from sewage and runoff. The other treatments were 2×, 4×, 8×, 16× and 32× multiples of this loading, approximately corresponding to the range of nutrient loadings found in natural systems (Nixon et al. 1986). Daily nutrient additions started on 1 June 1981 and continued until 26 September 1983. Three MERL mesocosms served as controls (= 0×). For detailed descriptions of the experimental setup, see Nixon et al. (1984) and Frithsen et al. (1985b, c, d). Water column characteristics (such as nutrients, oxygen, chlorophyll *a*, primary production and respiration) were measured during a mixing cycle, approximately weekly. Sediment porosity, Eh and benthic oxygen flux were measured seasonally throughout the experiment, as was sediment total carbon and nitrogen content during the last year (for methods see Lambert & Oviatt 1986).

**Meiofaunal methods.** Ten sediment cores were taken in each mesocosm approximately every 2 mo from May 1981 through September 1983, using a stick-mounted 5.07 cm<sup>2</sup> flow-through corer (Frithsen et al. 1983). The meiofauna was examined in the samples from May, June and September 1981, January, June and September 1982, and June and September 1983. The sampling locations were pre-selected randomly, but avoiding overlap. Cores were sectioned into 0 to 2 cm and 2 to 6 cm sediment depth horizons, and preserved in 10 % buffered seawater formalin with Rose Bengal (0.2 g l<sup>-1</sup>). Meiofauna was counted only in the 0 to 2 cm layer, which usually contains about 60 % of total meiofauna numbers in the Bay (75 to 100 % of taxa other than nematodes and foraminiferans), and follows the overall seasonal abundance and biomass trends in Narragansett Bay well (Frithsen et al. 1985a, Rudnick et al. 1985). Sediment cores were sieved individually through 500 and 300 µm sieves to extract the macrofauna. Animals retained on these sieves and belonging to taxa normally considered to be meiofaunal (i.e. Nematoda, Harpacticoida, Foraminifera, Halacarida, Ostracoda, Kinorhyncha and Turbellaria), as well as all animals passing the 300 µm sieve and retained on the 40 µm sieve, were counted as meiofauna. The sieved residue from all 10 cores from each tank on each occasion were pooled before the meiofauna was extracted by sieving through a series of sieves with mesh sizes 500, 300, 200, 100 and 40 µm. Before counting and sorting all meiofauna specimens into major taxa under a dissecting microscope at 25× magnification, the 300 µm sieve fraction was subsampled 1/2, the 200 µm fraction 1/4, nematodes in the 100 µm fraction 1/4, the rest of this fraction 1/8, and the 40 µm fraction 1/128, using an Elmgren (1973) sample splitter. Meiofauna ash-free dry weight was estimated from abundance by means of sieve-mesh specific conversion factors (Widbom 1984).

**Statistical analysis.** In all statistical tests, meiofaunal

Table 1. Selected environmental data. Macrofauna and sediment carbon data from Frithsen et al. (1985d); chlorophyll *a* values are averages for the preceding month, calculated from Frithsen et al. (1985b)

Load	Water column Chl <i>a</i> ( $\mu\text{g l}^{-1}$ )	Sediment carbon (% of dw)	Total macrof. biomass ( $\text{gC m}^{-2}$ )	Load	Water column Chl <i>a</i> ( $\mu\text{g l}^{-1}$ )	Sediment carbon (% of dw)	Total macrof. biomass ( $\text{gC m}^{-2}$ )
<b>May 1981</b>				<b>September 1982</b>			
0x	2	—	—	0x	2	2.1	5.8
0x	2	—	—	0x	3	—	6.7
0x	4	—	—	0x	3	1.9	3.7
1x	2	—	—	1x	2	—	12.5
2x	3	—	—	2x	3	—	7.1
4x	1	—	—	4x	6	1.9	1.9
8x	2	—	—	8x	2	2.2	52.8
16x	3	—	—	16x	7	2.0	21.8
32x	3	—	—	32x	75	—	2.4
<b>June 1981</b>				<b>April 1983</b>			
0x	5	—	4.5	0x	3	2.0	—
0x	7	—	4.3	0x	4	—	—
0x	7	—	5.0	0x	4	—	—
1x	6	—	5.6	1x	10	—	—
2x	16	—	4.3	2x	18	—	—
4x	14	—	5.1	4x	29	2.3	—
8x	29	—	5.4	8x	36	2.5	—
16x	21	—	7.0	16x	113	3.0	—
32x	46	—	—	32x	71	3.5	—
<b>September 1981</b>				<b>June 1983</b>			
0x	5	—	9.3	0x	2	2.3	11.5
0x	4	—	2.5	0x	6	—	3.6
0x	4	—	7.6	0x	3	—	6.1
1x	11	—	1.2	1x	2	—	15.5
2x	10	—	19.3	2x	24	—	0.3
4x	6	—	20.4	4x	17	2.3	0.7
8x	2	—	17.8	8x	3	2.4	32.4
16x	8	—	13.9	16x	43	2.7	2.0
32x	81	—	25.0	32x	82	5.0	60.5
<b>January 1982</b>				<b>September 1983</b>			
0x	8	—	6.2	0x	3	2.2	16.9
0x	11	—	2.9	0x	8	2.1	3.4
0x	13	—	3.1	0x	4	2.1	6.7
1x	21	—	15.3	1x	6	2.1	16.3
2x	6	—	10.4	2x	10	2.7	9.2
4x	61	—	15.2	4x	12	2.2	5.5
8x	8	—	24.2	8x	6	2.3	18.1
16x	61	—	29.2	16x	18	2.4	7.2
32x	74	—	8.4	32x	25	3.7	8.8
<b>June 1982</b>							
0x	2	2.2	6.4				
0x	2	—	11.6				
0x	3	—	9.6				
1x	6	—	24.4				
2x	3	—	8.5				
4x	6	2.1	16.4				
8x	2	2.3	36.0				
16x	91	—	10.2				
32x	69	3.1	11.6				

data from 19 June 1981 have been considered as pre-experimental, since the meiofauna populations could hardly respond to the nutrient enrichment in 18 d. The abundance and biomass of total meiofauna and abundance of individual taxa were tested against the gradient of nutrient loading and against experimental time

(year), using Spearman's coefficient of rank correlation (Sokal & Rohlf 1981). For experimental data the tests against nutrient loading were performed on mean ranks (first ranking the tanks at each date, then averaging over dates) for the first (Sep 1981 to Jun 1982) and second experimental year (Sep 1982 to Sep 1983) sepa-

rately, as well as for the whole experimental period. Pre-experimental data were ranked only for June 1981, since not all tanks were sampled in May 1981. The tests against time were performed on data from June and September each year, ranked for each tank separately. For 2 taxa showing an appreciable response only in the most highly enriched tanks, pairwise comparisons were made with 2-tailed Mann-Whitney U-test (Sokal & Rohlf 1981) on mean ranks, comparing the most highly loaded tanks (8x, 16x and 32x) with controls and lower loadings combined. Meiofauna community structure was studied by ordinating all samples (non-normalized data) with a principal components analysis (SAS Institute 1982).

## RESULTS

### Environmental data

The phytoplankton communities in the tanks responded with increasing chlorophyll *a* content and primary production up the nutrient addition gradient (Table 1; Nixon et al. 1986, Oviatt et al. 1986), with the exception of the 8x tank, where comparatively low such values were obtained from September 1981 on. This was probably due to the rapid development in this tank of a very dense population of the suspension-feeding bivalve *Mulinia lateralis* (Say) (up to  $10^5$  ind.  $m^{-2}$  in July 1981; Frithsen et al. 1985d). Water column oxygen concentrations alternated between super-saturation (most often during winter-spring blooms) and under-saturation (mostly from mid-summer to autumn). The amplitude of these oscillations increased with increasing nutrient input (Frithsen et al. 1985b, Oviatt et al. 1986).

Total sediment carbon (0 to 2 cm) showed gradually increasing values up the nutrient enrichment gradient in April–June. During other periods only the 32x tank consistently showed values appreciably higher than the control tanks (Table 1). The other sediment variables measured at the end of the experiment also indicated greatest enrichment in the 32x tank from June 1982 onwards (Frithsen et al. 1985d).

The total macrofaunal biomass and benthic nighttime respiration initially showed slowly increasing values up the nutrient addition gradient, but from winter 1981/82 on the biomass response disappeared (Table 1; Frithsen et al. 1985d, Nixon et al. 1986). The total macrofauna abundance, however, peaked in the 32x tank, with very high numbers of small polychaetes. During the first year this peak consisted of the capitellid *Mediomastus ambiseta* (Nixon et al. 1984, Grassle et al. 1985), and later of the spionids *Streblospio benedicti* (Webster) and *Polydora ligni* (Webster) (Frithsen et al. 1985d).

### Meiofaunal taxa

Abundance and biomass of total meiofauna, and the numerically dominating nematodes, showed a general decline with time, which was statistically significant in the control tanks, and for biomass also in loaded tanks (Fig. 2; Table 2). This trend was broken by high total abundances of 13 to  $14 \times 10^6$  ind.  $m^{-2}$  and biomasses in some highly productive tanks in June 1982 and 1983,

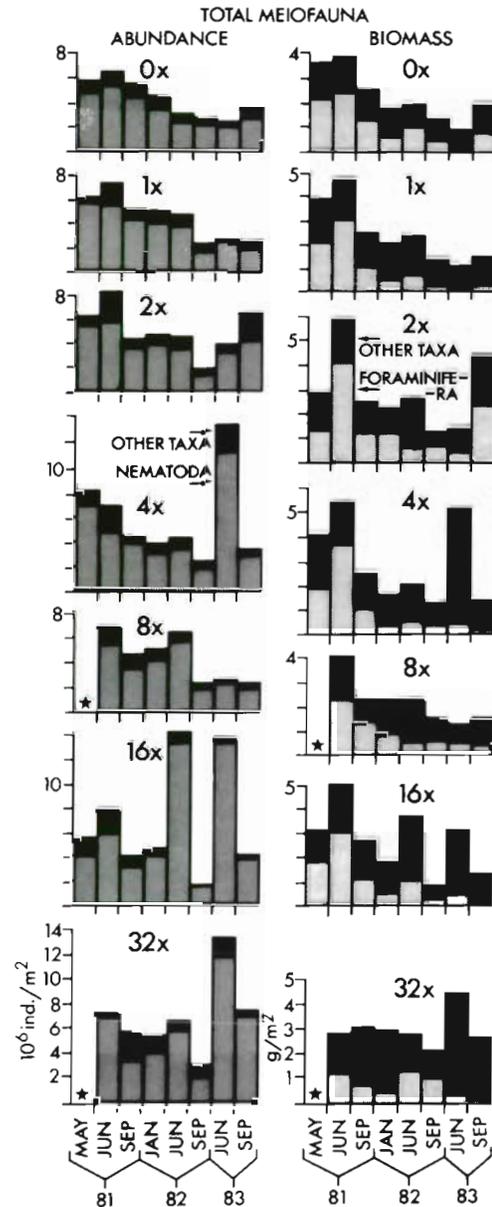


Fig. 2. Total meiofauna abundance ( $10^6$  ind.  $m^{-2}$ ) and ash-free dry weight ( $g m^{-2}$ ) from the different nutrient addition treatments. (★) No data

resulting in a significant positive treatment effect for nematodes (Table 2), and a biomass peak in the 2x tank in September 1983. Low values were noted in the

Table 2. Values of Spearman's coefficient of rank correlation ( $r_s$ ) from tests of meiofauna abundance and biomass against the gradient of nutrient enrichment and against experimental time (year), together with corresponding  $p$ -values (in brackets). Asterisks indicate level of statistical significance: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$

	Nutrient load				Time	
	Pre-expt	Expt Year 1	Expt Year 2	Expt total	Control tanks	Loaded tanks
Foraminifera (monothalamous)	0.186 (0.598)	-0.043 (0.904)	-0.579 (0.102)	-0.492 (0.164)	-0.795 (0.001)**	-0.562 (<0.001)***
Foraminifera (polyth. calc.)	-0.407 (0.250)	-0.170 (0.630)	-0.502 (0.156)	-0.407 (0.250)	-0.598 (0.014)*	-0.786 (<0.001)***
Foraminifera (polyth. aren.)	0.390 (0.270)	-0.744 (0.035)*	-0.658 (0.063)	-0.915 (0.010)*	-0.086 (0.723)	-0.353 (0.037)*
Kinorhyncha	0.068 (0.848)	-0.434 (0.220)	-0.746 (0.035)*	-0.661 (0.062)	0.020 (0.935)	-0.316 (0.062)
Nematoda	0.373 (0.292)	0.402 (0.256)	0.536 (0.129)	0.931 (0.009)**	-0.677 (0.005)**	-0.097 (0.565)
Polychaeta	-0.547 (0.122)	0.698 (0.048)*	0.186 (0.598)	0.664 (0.060)	-0.279 (0.250)	0.209 (0.216)
Harpacticoida	0.220 (0.533)	-0.552 (0.119)	-0.111 (0.753)	-0.111 (0.753)	0.086 (0.723)	-0.031 (0.856)
Ostracoda	0.649 (0.066)	-0.746 (0.035)*	-0.574 (0.104)	-0.644 (0.068)	0.595 (0.014)*	-0.476 (0.005)**
Bivalvia	-0.443 (0.211)	-0.863 (0.015)*	-0.868 (0.014)*	-0.864 (0.014)*	-0.846 (<0.001)***	-0.777 (<0.001)***
Total meiofauna abundance	0.203 (0.565)	0.395 (0.264)	0.364 (0.304)	0.556 (0.116)	-0.757 (0.002)**	-0.199 (0.240)
Total meiofauna biomass	-0.008 (0.981)	0.593 (0.093)	0.255 (0.470)	0.661 (0.062)	-0.717 (0.003)**	-0.395 (0.020)*
Permanent meiofauna biomass	0.000 (1.000)	0.434 (0.220)	0.068 (0.847)	0.373 (0.292)	-0.677 (0.005)**	-0.483 (0.004)**
Temporary meiofauna biomass	-0.323 (0.360)	0.462 (0.192)	0.136 (0.701)	0.373 (0.270)	-0.561 (0.021)*	-0.302 (0.074)
Nem./cop.-ratio	-0.220 (0.533)	0.698 (0.048)*	0.528 (0.136)	0.698 (0.048)*	-0.518 (0.033)*	-0.240 (0.156)

8× tank, especially during the last year, coinciding with its low chlorophyll *a* content and primary production. Neither total abundance nor biomass showed a significant response to the nutrient addition gradient (Table 2).

Foraminiferans (Fig. 3) and juvenile bivalves (Fig. 5) also showed a significant decreasing trend throughout the experiment (Table 2). For both these taxa the decline was broken by a sudden peak in September 1983, for juvenile bivalves (normally dominated by *Nucula annulata*), caused by a heavy spatfall of *Mulinia lateralis*. Like in mid Narragansett Bay (Said 1951) the foraminiferans in the tanks were highly dominated by polythalamous calcareous forms, especially *Elphidium* spp. and *Ammonia beccarii* (L.). Comparatively low numbers in highly loaded tanks resulted in a significant negativ treatment effect for juvenile bivalves and polythalamous arenaceous foraminiferans (Table 2).

Ostracods and kinorhynchs (Fig. 4) showed the highest numbers in controls and low to moderate loadings

and very low values in the 3 most highly loaded tanks from January 1982 on. During the last year not a single ostracod was found in these tanks. The Spearman's rank correlation indicated a significant treatment effect for kinorhynchs during the last year, but for ostracods only during the first year (Table 2). However, a significant difference between the highest loadings (8×, 16×, 32×) and the other tanks (Mann-Whitney U-test,  $p < 0.05$ ) indicated a treatment effect during the last year as well. Harpacticoid copepods (Fig. 3) also showed peak values in low to moderately loaded tanks. On most occasions lower numbers of adults and copepodites were noted in tanks with higher nutrient loadings (8×, 16× and 32×), which thereby differed significantly from controls and low to moderate loadings combined (Mann-Whitney U-test,  $p < 0.05$ ).

The juvenile polychaetes in the meiofauna were the same species that dominated the macrofauna. The abundance of juvenile polychaetes was initially low in all tanks, and remained so in the control and 1× tanks throughout the experiment (Fig. 5). In the 32× tank

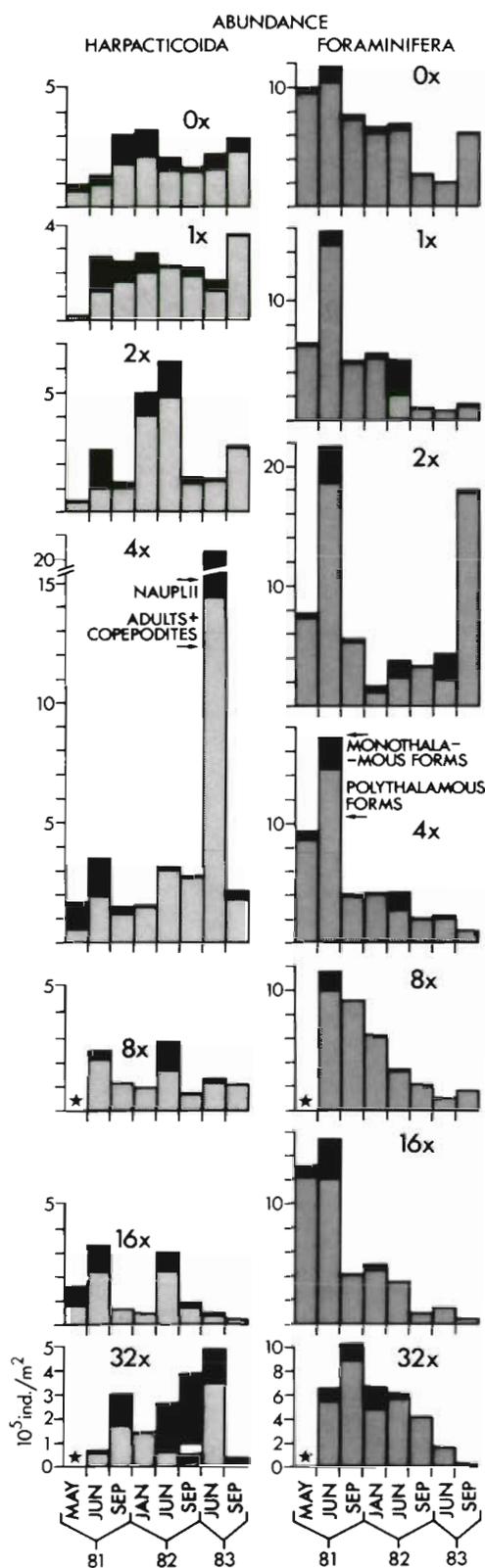


Fig. 3. Harpacticoid copepod and foraminiferan abundance ( $10^5$  ind.  $m^{-2}$ ) from the different nutrient addition treatments. (★) No data

juvenile polychaete abundance increased more than 700-fold to September 1981, and remained high for most of the experiment. There was a significant positive correlation with nutrient loading during the first experimental year (Table 2).

#### Meiofaunal community structure

The first 2 components from the principal components analysis are represented in Fig. 6. Each sample is represented by the value of the nutrient loading of its tank. The larger the distance between the sample points, the lower the similarity in community structure of the samples. The eigenvectors in Table 3 show that Principal Component 1 is most heavily influenced (positively) by foraminiferans and bivalves. These declined in numbers with time (Table 2). The Principal Component 1 axis is thus to be considered mainly as a time axis, with a scale running from the right to the left. Principal Component 2 is influenced mostly by kinorhynchs and ostracods (positively), and by polychaetes and nematodes (negatively). As kinorhynchs and ostracods showed a negative, and nematodes and polychaetes a positive, response to the nutrient addition gradient (Table 2), this axis is primarily a negative nutrient load axis.

Table 3. Eigenvectors for the first 2 axes from principal components analysis of all 70 meiofauna samples from the MERL eutrophication experiment

	PRIN 1	PRIN 2
<i>Foraminifera</i>		
monothalamous	0.444	-0.173
polyth. calcareous	0.558	-0.145
polyth. arenaceous	0.467	0.056
<i>Turbellaria</i>	0.014	0.252
<i>Kinorhyncha</i>	0.039	0.549
<i>Nematoda</i>	0.062	-0.449
<i>Polychaeta</i>	-0.174	-0.481
<i>Harpacticoida</i>	-0.038	0.014
<i>Ostracoda</i>	0.125	0.386
<i>Bivalvia</i>	0.471	0.008

Before the start of nutrient additions on 1 June 1981, the meiofauna communities were quite similar in all the experimental tanks, as all points from May 1981 are comparatively close together. In June 1981, after 18 d of nutrient addition, there is still no load-related pattern, but the swarm of points is more spread out, presumably due to a variable timing in the different tanks of the normal early summer increase of the meiofauna populations (Rudnick et al. 1985). A gradual change in meiofaunal community structure with time was found in all tanks, but by September 1982 com-

community structure seems to have stabilized. From September 1981 on, a structuring of the sample points within each date in response to the gradient of nutrient addition can be noticed. The most highly productive tanks, 16 $\times$  and 32 $\times$ , fall out down the Principal Component 2 axis, and the control tanks are clustered well together in September 1982 and June 1983.

## DISCUSSION

### Response of taxonomic groups and total meiofauna

While experimental ecosystems, such as the MERL mesocosms, allow controlled studies of the ecosystem

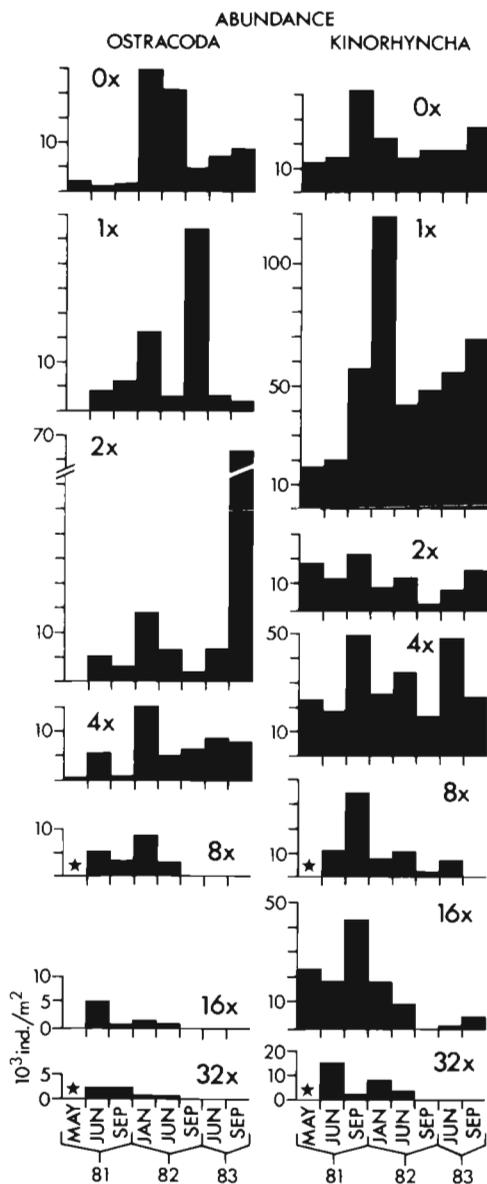


Fig. 4. Ostracod and kinorhynch abundance ( $10^3$  ind.  $m^{-2}$ ) from the different nutrient addition treatments. (★) No data

effects of environmental stresses, such as an increased nutrient input, they must nevertheless be simplifications of nature. Thus, nutrients were added as inorganic salts, whereas real sewage contains further nutrients in particulate and organic forms (e.g. Nixon 1981). Away from the zone of primary organic enrichment such nutrients will, however, mainly affect ecosystem processes only after remineralization to the inorganic form, making this a justifiable simplification. Furthermore, the dose-response experimental design did not allow for replication of the individual load levels. The absence in the tanks of large natural predators seems to have allowed individual tanks to develop aberrant macrobenthic assemblages, such as the *Mulinia* pavement and a dense population of the mud anemone *Cerianthopsis americanus* (Verrill) in the 8 $\times$  tank, or the dense populations of the epibenthic shrimp *Crangon septemspinosa* (Say) present at times in some tanks (Nixon et al. 1986). Such deviations may be due to initial stochastic differences between tanks in their benthic community composition, and are likely to increase in importance with time. Thus, the results from the first experimental year are likely to be a better indicator of meiofauna response to eutrophication in nature than those of the second year.

While the water column biology of the MERL tanks showed clear dose-response relationships of the expected type throughout the experiment (Nixon et al. 1986), the benthic response was less clear. The absence of a significant dose-effect response of the total benthic meiofauna, in terms of abundance or biomass (Table 2), is a remarkable result in view of the massive nutrient enrichment of the most heavily loaded tanks. In fact, the meiofauna showed a gradually decreasing abundance and biomass with time in most tanks, and especially in the control tanks (Table 2). Since the length of the experiment far exceeded the generation time of most meiofaunal organisms, this decrease cannot be explained as a simple gradual die-off.

Nevertheless, most meiofauna taxa showed some response to the nutrient enrichment gradient. Nematode abundance, and thus also total meiofauna abundance, tended to peak in highly productive tanks (4 $\times$ , 16 $\times$  and 32 $\times$ ) in June (Fig. 2), in good agreement with the seasonal dynamics of the natural meiofauna community at the sediment-collection site (Rudnick et al. 1985). In June 1983 increased total abundances were found in the 4 $\times$ , 16 $\times$  and 32 $\times$  tanks, whereas in June 1982 a very high abundance was noted only in the 16 $\times$  tank. This pattern may be connected to the high numbers of the epibenthic sand shrimp *Crangon septemspinosa* present at times in the 4 $\times$  and 16 $\times$  tanks (Nixon et al. 1986). *Crangon crangon* is a heavy predator on macrofaunal polychaetes, but does not notice-

ably affect the abundance of benthic meiofauna (Reise 1979). It seems therefore likely that predation by the dense populations of *Crangon* had a strong negative influence on the populations of the dominating polychaete species in the tanks, the capitellid *Mediomastus ambiseta*, and the spionids *Streblospio benedicti* and *Polydora ligni*. *M. ambiseta* is a non-selective, sub-surface deposit feeder (Fauchald & Jumars 1979), which has been reported to cause a dramatic decline in meiofauna (mainly nematode) numbers in microcosms (Federle et al. 1983). The 2 spionids *S. benedicti* and *P. ligni* may likewise influence the meiofauna negatively through their feeding behaviour (Watling 1975, Dauer et al. 1981). The dominant polychaetes in the tanks thus presumably competed with or preyed upon meiofauna, and the net effect of *Crangon* predation would be to facilitate an increase of meiofauna populations in response to the nutrient enrichment by reducing the polychaete populations, e.g. in the 16× tank in June 1982 and 1983 and in the 4× tank in June 1983 (Frithsen et al. 1985d). In the 32× tank, where high nematode numbers in June 1983 coexisted with a comparatively dense population of the facultatively suspension-feeding (Levin 1986) *S. benedicti*, the higher food availability (Table 1) may have alleviated competition.

Several crustacean groups increased in moderately enriched tanks, but showed very low numbers in the 3 highest nutrient loadings in 1982 and 1983, e.g. planktonic copepods (Sullivan & Ritacco 1985a, b), benthic amphipods (Frithsen et al. 1985d) and ostracods (Fig. 4). Sullivan & Ritacco (1985b) concluded that un-ionized ammonia concentrations of more than  $10 \mu\text{mol l}^{-1}$ , present at times in the 16× and 32× tanks, and once in spring 1982 in the 8× tank, were toxic to the copepods. This may have been the case also for the ostracods in the MERL tanks, but the abundance of benthic harpacticoids was not negatively affected at times of high un-ionized ammonia concentrations in the water column. Both ostracods and harpacticoids are sensitive to low oxygen concentrations (e.g. Elmgren 1975), which may well have occurred at times in the sediment of the highly productive 16× and 32× tanks, even though total water column anoxia was noted only once, in the 32× tank in August 1982. If the overlying water is well oxygenated, however, some species of harpacticoids can be favoured by even higher concentrations of sediment organic carbon than found in the 32× tank (Gee et al. 1985, Moore & Pearson 1985).

Foraminiferans and juvenile bivalves showed decreasing trends in abundance throughout the experiment (Table 2). This was probably caused by a combination of low rates of reproduction in the tanks and of recruitment from outside. Foraminiferans, especially polythalamous forms, have been shown to be compara-

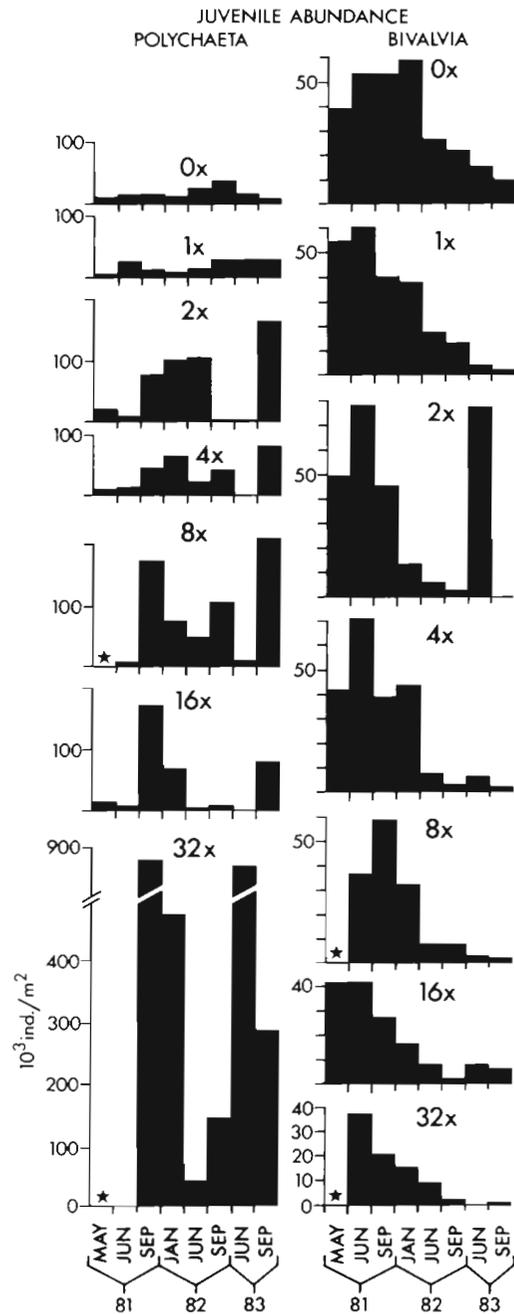


Fig. 5. Juvenile polychaete and bivalve abundance ( $10^3 \text{ ind. m}^{-2}$ ) from the different nutrient addition treatments. (\*) No data

tively slow colonizers of azoic sediments (Wefer & Richter 1976, Sherman & Coull 1980, Widbom 1983), with a low tendency for becoming resuspended from the sediment and transported through the water column. The meiofaunal bivalves were dominated by *Nucula annulata*. *Nucula* spp. have a direct release of benthic juveniles or just a short lecithotrophic larval stage (Sastry 1979), making recruitment particularly dependent on within-tank reproduction. The abundance and bio-

mass of adult *N. annulata* did not decline as much as for juveniles in the meiofauna fraction (Frithsen et al. 1985d), thus indicating populations of large, old specimens, not reproducing in the tanks.

### What limited the meiofauna populations?

Recently, changes under eutrophication in freshwater pelagic ecosystems have been discussed in terms of bottom-up control, from increased production, alleviating resource limitation of trophic levels, or top-down control, from changes in top-predator abundance, giving rise to trophic interactions cascading down the trophic chain. McQueen et al. (1986) suggest that bottom-up (producer) controls are most influential at lower trophic levels, top-down (consumer) controls at higher trophic levels. The same types of control may be expected to operate on the benthic fauna.

In nature, a positive correlation between biomass of benthic meiofauna and productivity has been demonstrated in areas of low benthic food availability, such as the deep sea (Thiel 1983) and the Baltic Sea (Elmgren 1978). In the MERL tanks, where even the control tanks are quite productive, no such general relationship could be detected. In fact, Rudnick et al. (1985) found the meiofauna community at the sediment collection site in mid Narragansett Bay the densest ever recorded in subtidal waters. They found clear peaks in abundance and biomass of practically all meiofauna taxa in June, which they suggested was due to increasing temperature in combination with excess food resources accumulated in the sediment during the winter-spring period. In the MERL eutrophication experiment, gradually increasing values of sediment carbon up the gradient of nutrient enrichment were obtained only in spring and early summer (Table 1), indicating an enhanced accumulation of organic matter derived from the spring bloom, especially in highly loaded tanks. This is supported by a radio-tracer experiment in one MERL mesocosm, where Rudnick & Oviatt (1986) found a time lag of several months between the deposition and mineralization of phytoplankton detritus, derived from the winter-spring bloom. In accordance with this pattern, meiofauna biomass peaked in some loaded tanks in June (Fig. 2). Rudnick et al. (1985) proposed food limitation as a possible explanation for the rapid seasonal decline of meiofauna and macrofauna numbers in late summer, a decline found also in the MERL tanks (Frithsen et al. 1985a, this paper).

Altogether, this suggests that the lack of an overall response of total meiofauna to the gradient of nutrient enrichment was due primarily to the absence during most of the year of a gradient in enrichment of the sediment corresponding to the enrichment of the water

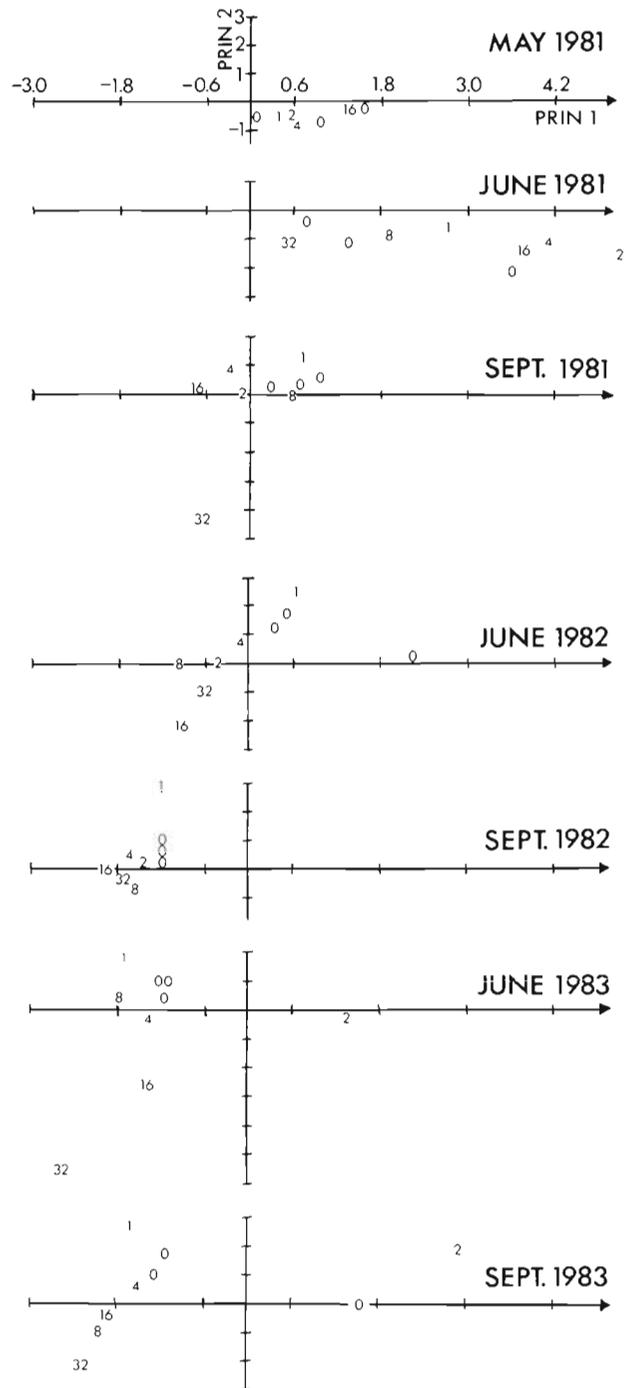


Fig. 6. Output from principal components analysis, showing differences between overall structure of the meiofauna communities in the different experimental tanks (see text for explanation). Each tank is represented by a figure indicating the nutrient loading in one coordinate system each for all June and September sampling occasions, together with the initial sampling in May 1981. PRIN: principal component

column. The meiofauna peaks in some loaded tanks in June, when enrichment of the sediment was evident, indicate the importance of food availability as one factor controlling the meiofauna populations. But as not

all loaded tanks showed an increased meiofauna biomass in June, and as the 32× tank, where the sediment carbon content was enhanced also during other periods, did not always show an increased biomass, other factors must also have been of importance. Presumably, the meiofauna populations were controlled by a combination of food availability, of particular importance in most tanks in autumn and winter, and biological interactions, such as predation and interference competition from the macrobenthos, which often counteracted the positive effect of an organic enrichment.

The pattern of meiofauna community response to nutrient enrichment thus seems to call for explanations in terms of both bottom-up (producer) and top-down (consumer) controls. The topdown control seems to have become increasingly important with time in the MERL tanks, where larger predators, such as fish and large decapods, were excluded, allowing dense populations of intermediate-sized predators, such as *Cranogon*, to develop in some tanks (Nixon et al. 1986).

#### Benthic meiofauna as indicator of organic enrichment

Several papers have evaluated benthic meiofauna as an indicator of pollution. Often the importance of species determinations have been stressed, e.g. concerning nematodes (Shaw et al. 1983, Platt et al. 1984) and harpacticoids (Heip 1980). But because of the time and expertise needed for species determination of meiofauna, the analysis will normally have to stop at major taxa in practical environmental quality assessment (cf. Raffaelli 1982). In the MERL eutrophication experiment clear differences in response were detected between major meiofaunal taxa, resulting in a changed community structure.

The ratio of nematode to copepod numbers has been proposed as a useful index for the monitoring of organic pollution on beaches (Raffaelli & Mason 1981, Raffaelli 1982), a proposal which has been questioned in several later papers (e.g. Coull et al. 1981, Lambshead 1984). Amjad & Gray (1983) calculated this ratio along a known gradient of organic enrichment in sublittoral soft sediment in Oslofjord, Norway, and found good agreement with the original proposal. However, contradictory results have been reported from sublittoral soft sediments, with increasing copepod densities, causing decreasing nematode/copepod ratios, associated with increasing organic enrichment (Vidakovic 1983, Gee et al. 1985, Moore & Pearson 1985). In the MERL eutrophication experiment, nematode/copepod ratios showed a significant positive correlation with nutrient loading (Table 3) and sediment carbon content (Spearman's rank correlation,  $r_s =$

0.882,  $p = 0.013$ ), which lends some support to the use of this ratio as an indicator of organic enrichment. But opportunistic harpacticoids are often the first colonizers of new habitats (Scheibel 1974, Chandler & Fleeger 1983, Widbom 1983) and the first meiofaunal group to recover from toxic pollution (e.g. oil spills; Elmgren et al. 1983). In such cases a low nematode/copepod ratio indicates a habitat in the early stages of recovery from severe perturbation, not an undisturbed habitat. If the nematode/copepod ratio is used, it should therefore be interpreted in the light of the full meiofauna community composition.

We conclude that the gross taxonomic composition of benthic meiofauna communities can be used as an indicator of organic enrichment, caused by eutrophication. The intricate relations between bottom-up control, by food availability, and top-down control from the macrofauna, that can be surmised for the meiofauna in the MERL tanks, suggest, however, that meiofaunal data are best evaluated together with macrofaunal data, when assessing the eutrophication status of an area. Since the macrofauna is comparatively well understood as an indicator of organic enrichment (e.g. Pearson & Rosenberg 1978), adding meiofaunal data in routine assessment may often be worth the added effort only in areas where the macrobenthos is reduced in species richness, such as the Baltic Sea or areas affected by hypoxia (e.g. Elmgren 1975).

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