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## Effects of predators and food resources on the macrobenthos of salt marsh creeks

by Wendy I. Wiltse,<sup>1,2</sup> Kenneth H. Foreman,<sup>3</sup> John M. Teal<sup>1</sup> and Ivan Valiela<sup>3</sup>

### ABSTRACT

We tested whether predation, disturbance and food resources controlled the density and taxonomic composition of benthic macrofauna in salt marsh tidal creeks by manipulating predator and food abundance. Cages that excluded fish, crabs, and shrimp were placed in two urea fertilized and two control creeks at Great Sippewissett Marsh, MA, in late May 1979 and were sampled over a 15-week period.

Densities of macrofauna peaked in early summer, then decreased markedly in natural sediments and inside partial cages that provided access to predator/disturbers. Inside predator exclusion cages, macrofaunal densities increased and remained high throughout the experiment. Comparisons of densities in natural and caged sediments indicated that predation and/or disturbance by fish, crabs, and shrimp depleted populations of *Paranais litoralis*, *Streblospio benedicti*, *Hydrobia* sp., *Nematostella vectensis*, and *Capitella* spp. during summer. In late summer few individuals remained in the natural community and no species was common. Bulk sediment properties were not significantly changed by cages.

The urea fertilizer treatment increased chlorophyll *a* concentration and percent nitrogen and carbon in sediments. Despite improved food value of fertilized sediments to deposit feeders, no increases in density or biomass of macrofauna were detected in fertilized creeks relative to controls. This indicates that food does not limit macrofaunal abundance in this habitat, even in the absence of predator/disturbers. Fertilization did prompt changes in the species composition of the macrofauna indicative of a stressed community. The oligochaete *P. litoralis* was the numerical dominant in fertilized creeks, which averaged fewer species per sample than control creeks. A polychaete, *S. benedicti*, predominated in control creeks.

### 1. Introduction

The study of physical and biological controls of species composition and abundance is central to ecology. Descriptive studies in marine soft-sediments have emphasized the roles of sedimentary features (e.g., Sanders, 1958; Gray, 1974; Whitlatch, 1981) and physical disturbance (Rhoads *et al.*, 1978; Santos and Simon, 1980). Recent experi-

1. Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, 02543, U.S.A.

2. Present address: Marine Sciences Institute, University of Connecticut, Avery Point, Groton, Connecticut, 06340, U.S.A.

3. Boston University Marine Program, Marine Biological Laboratory, Woods Hole, Massachusetts, 02543, U.S.A.

mental studies have demonstrated that predation and disturbance by consumers (reviewed in Peterson, 1979), resource competition (Woodin, 1974; Peterson, 1977, 1980; Peterson and Andre, 1980), interference competition (Rhoads and Young, 1970; Brenchley, 1981), and inhibition of larval settlement by adults and meiofauna (Woodin, 1976; Williams, 1980; Wilson, 1980; Watzin, 1983) influence community organization.

Studies of the interactions among these controlling factors are rare (e.g., Young and Young, 1978; Dauer *et al.*, 1982). Peterson (1979) reviewed studies from unvegetated estuarine and lagoon sediments in which predators appeared to keep densities of infauna low by either direct predation or disturbance and speculated on the importance of other mechanisms controlling benthic populations. Competitive exclusion did not occur at high infaunal densities within predator exclusion cages in any of the experiments conducted in soft-sediments. Although competition occurs among deposit feeders in soft sediments (Whitlatch, 1980; Wilson, 1981, 1983; Levin, 1982), it is not evident that competition regulates their abundance. For example, competition for food influences the growth rate and size distribution of the deposit feeding snails, *Hydrobia* spp. (Fenchel and Kofoed, 1976; Levinton and Bianchi, 1981), but has not been demonstrated to control population density in the field. Peterson (1979) suggests that predation, disturbance, and inhibition of larval settlement by adults may prevent resource limitation by maintaining densities below the carrying capacity of the environment. Furthermore, he contends that benthic invertebrates in soft-sediments survive competitive stress caused by high densities by suppressing growth and reproductive rates, and that interference between established adults does not generally cause rapid mortality.

To examine the relationship between predation and competition in a soft-sediment community, we experimentally altered predator abundance and food resources in salt marsh tidal creeks. Predator abundance was manipulated by the use of exclusion cages. If predation were important, we would expect higher densities of benthic macrofauna inside cages than in control areas outside cages. Food resources were manipulated by adding fertilizer to the creek bottoms and the surrounding marsh. If macrofaunal populations were food limited, we would expect higher densities in fertilized than control creeks, especially inside cages.

## 2. Materials and methods

*a. Study site.* Experiments were conducted in four small intertidal creeks at Great Sippewissett Marsh, Massachusetts, U.S.A. Tidal elevations of creek bottoms were +52 to +64 cm M.L.W.; mean tidal range was 122 cm. Each creek bisected a circular plot of salt marsh 10 m in radius used for long-term nutrient enrichment studies. Since spring 1974, two plots have received 2.6 g N m<sup>-2</sup>wk<sup>-1</sup> urea plus 1.56 g P m<sup>-2</sup>wk<sup>-1</sup> phosphate fertilizer on one half and urea fertilizer only on the other half. Fertilizer was applied biweekly from late April to early November. Two untreated plots served as controls. The fertilization treatment increases the biomass and nitrogen content of

Table 1. Sequence of treatments and data collected in tidal creeks at Great Sippewissett Marsh.

Dates	Treatments	Measurements
4/74	Fertilization began	
4/74–11/74, 5/75	Control creeks	Density of macrofauna
5/75–10/75	Control & fertilized creeks	Sediment carbon & nitrogen
5/79–9/79	Control & fertilized creeks	Macrofauna density & biomass
	Exclusion and partial cages	
9/79	Control & fertilized creeks	Sediment chlorophyll <i>a</i>
	Exclusion and partial cages	
6/80–8/80	Control & fertilized creeks	Sediment chlorophyll <i>a</i>
	Exclusion cages	
7/81–8/81	Control & fertilized creeks	Sediment grain size, organic matter
	Exclusion cages	

marsh grasses (Valiela *et al.*, 1981) which senesce and fall into creeks each autumn. The resulting detritus provides nitrogen-enriched food for benthic deposit feeders. Enhanced production of benthic algae, cyanobacteria, and chemosynthetic bacteria is another important consequence of fertilization (Van Raalte *et al.*, 1976).

Predators on benthic macrofauna in creeks include marsh killifish (*Fundulus heteroclitus* and *F. majalis*), green crabs (*Carcinus maenas*), and grass shrimp (*Palaemonetes pugio* and *P. vulgaris*). Fish concentrate in creeks at mid-tides and feed on benthic animals, algae, and detritus (Werme, 1981). Abundant fiddler crabs (*Uca pugnator*) ingest and disturb surface sediments in creeks. Migrating shorebirds may be major consumers of tidal flat invertebrates in New England (Whitlatch, 1982), but were rarely observed feeding in the experimental creeks at Great Sippewissett Marsh and are probably less important there than other consumers.

*b. Sequence of data collection.* Because this experiment was part of a long-term study of salt marsh fertilization, we include data taken from several years that relate to the predator and food manipulations (Table 1). These data are ancillary to the main experiment in 1979. In presenting the data taken in 1974–1981, we assume that contrasts among treatments were consistent from year to year.

*c. Macrofauna.* To study seasonal abundance patterns, we sampled the benthic macrofauna of the two control creeks from April to November 1974 and in May 1975. Two Van Veen grab samples (144 cm<sup>2</sup>) per creek were taken monthly, sieved through a 0.5 mm screen, and preserved in buffered formalin containing Rose Bengal stain. All organisms retained by the sieve were identified and counted.

Caging experiments were initiated on 29 May 1979. One cage that excluded fish, crabs, shrimp and birds was placed in each of the four experimental creeks. Cage dimensions were 1.0 m long by .5 m wide by .3 m high. Plastic netting (4 mm diagonal openings) covered all surfaces except the bottoms. Cages were pushed downward,

without disturbing the enclosed sediment, until the bottom of the netting was approximately 10 cm below the sediment surface. A partial cage was placed in one control and one fertilized creek. Partial cages had two adjacent sides open, one (1 m) parallel and one (0.5 m) perpendicular to water flow. These partial cages served as a control for cage artifacts because they produced hydrodynamic and physical environments similar to exclusion cages, but allowed access to fish, shrimp, and crabs.

To sample organisms in our experimental areas we took cores  $33.2 \text{ cm}^2 \times 5 \text{ cm}$  deep. Two or three replicate cores were taken inside and outside cages after 0, 2, 5, 9 and 15 weeks (30 May to 13 September). Samples were gently stirred and a 20 cc subsample removed for examination of meiofauna, which will be considered in a subsequent paper. The remaining mud was sieved through a 0.5 mm screen, and the retained macrofaunal fraction was preserved.

Macrofauna were identified, counted, and measured. Each taxon was evenly divided into 3–10 size categories. Representatives of each size category were dried for 48 hr at  $60^\circ\text{C}$  and weighed. Regressions of length vs. dry weight were calculated for abundant species to estimate biomass. Average weights per individual were used if regressions were nonsignificant or too few individuals were found.

Density and biomass values were tested for homogeneity of variances using Bartlett's test (Zar, 1974). Where variances were heterogeneous, all values were transformed by  $X = \log(X + 1)$  before making comparisons by analysis of variance.

*d. Chlorophyll.* On 17 Sept 1979, 16 weeks after the cages were set out, sediment samples were collected from the creeks for chlorophyll measurements. Two replicate samples (each consisting of 3 pooled  $5.3 \text{ cm}^2 \times 1 \text{ cm}$  deep cores) were taken from inside and outside each cage and one sample was taken from each partial cage. The pooled sediment in each sample was stirred thoroughly and a 5 cc subsample was withdrawn and frozen ( $-20^\circ\text{C}$ ). All samples were extracted within 1 month. The frozen sediment was dropped into a suspension of 30 ml cold 90% acetone and 0.1 g  $\text{MgCO}_3$ , then homogenized for 2 min in a Virtis homogenizer in a dimly lit room. The homogenized sediment was transferred to a large test tube with a 5 ml rinse of cold acetone and allowed to extract at  $4^\circ\text{C}$  in the dark for 8–12 hr. Then an aliquot of this suspension was centrifuged and about 3 ml of the supernatant was pipetted into a 1 cm cuvette and assayed for chlorophyll *a* by the spectrophotometric method of Lorenzen (1967).

On 16 June 1980 cages like those used in 1979 were placed in the four experimental creeks to make additional measurements of chlorophyll *a* concentrations. Two replicate samples were taken from inside and outside each cage immediately after cages were emplaced, and after 2.5 and 10 wks. Analytical and sampling methods were identical to those used in 1979.

*e. Sediments.* A sediment sample was taken from each control and fertilized creek approximately monthly from May to October 1975. Samples contained pooled surface ( $< 1 \text{ cm}$  deep) mud taken from 3 locations within each creek. Visible animals and plant

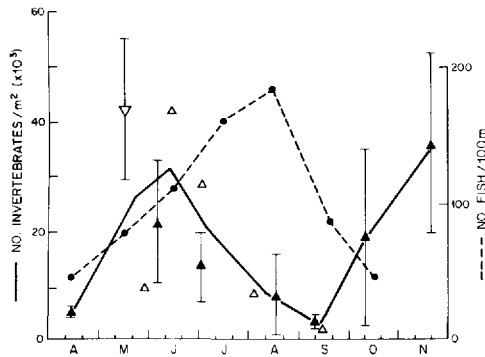


Figure 1. Density of macro-invertebrates in control creeks in 1974 (▲), May 1975 (▽), and May–Sept. 1979 (Δ—these data are also shown in Figure 2, upper left). Mean  $\pm$  1 S.E. of 4 samples (2 creeks, 2 replicates) are shown for 1974–75. The solid line connects the average invertebrate density of all years for each month. The fish abundances (*Fundulus heteroclitus* and *F. majalis*) are taken from Werme (1981).

fragments were removed. The muds were dried at 60°C for 48 hr and ground. Percent carbon and nitrogen were determined in these sediment samples using a Perkin-Elmer Elemental Analyzer.

In July 1981, exclusion cages were again placed in 3 creeks to assess changes in sediment characteristics caused by cage structures. After 6 wks sediment samples were collected from inside and outside cages. Three 5.3 cm<sup>2</sup>  $\times$  3 cm deep cores were pooled for each sample and mixed thoroughly. A 5 cc sample was weighed, dried at 60°C for 48 hr and reweighed to determine percent water. The salinity of filtered pore water was measured and used to correct the dry weight of sediment for salt content. Percentages of sand, silt, clay and organic material were determined in 10 cc subsamples. Each subsample was rinsed through a 63  $\mu$ M sieve. Sediments retained by the sieve were dried and weighed, then ashed and reweighed to determine percents sand and organic matter, respectively. An aliquot of the finer material that passed through the sieve was centrifuged using Milliman and Barretto's (1975) method to separate silt (>2  $\mu$ M) and clay (<2  $\mu$ M) fractions. The silt fraction was dried and weighed, then ashed and reweighed. Clay weights were estimated by subtracting the dry weight of sand and silt from the dry weight of whole sediment, corrected for salt content. The weight lost during ashing of sand and silt fractions was summed to estimate the weight of organic material in the sediment.

### 3. Results

Our surveys of macroinvertebrate abundance during 1974, 1975, and 1979 show a seasonal pattern in which the density of infauna in the control creeks was high in early summer, declined to low levels in late summer, and increased in fall (Fig. 1). The decline in density from June to September coincided with the season when *Fundulus*

Table 2. Comparison of densities of 7 major taxa inside and outside of cages in 1979. Shown are *t*-values from comparison of densities inside and outside cages. Mean densities are given in Tables 7 and 8. In all cases where significant differences occurred, densities inside cages were greater than outside. C = control creeks, F = fertilized creeks, \* =  $P < 0.05$ , \*\* =  $P < 0.01$ .

		<i>t</i> -values				
		May	Jun.	Jul.	Aug.	Sept.
<i>Paranais litoralis</i>	C	0.91	1.70	1.55	1.75	2.65*
	F	1.38	2.04*	2.46*	2.71*	4.33**
<i>Streblospio benedicti</i>	C	2.05*	0.45	1.02	2.11*	3.91**
	F	0.99	1.47	1.55	4.33**	3.26**
Amphipods¶	C	0.14	0.48	0.73	0.46	1.18
	F	1.81	0.73	1.34	0.00	1.12
<i>Hydrobia</i> sp.	C	3.05*	0.69	3.36**	2.57*	3.65**
	F	0.5	0.34	1.81	1.63	1.76
<i>Nematostella vectensis</i>	C	0.00	1.45	0.44	2.52*	2.16*
	F	0.00	1.15	1.15	1.15	1.72
<i>Hobsonia florida</i>	C	0.50	1.15	0.25	1.22	1.29
	F	1.45	1.06	1.92	1.90	1.52
<i>Capitella</i> spp.	C	1.06	1.15	2.00*	1.81	2.22*
	F	1.17	1.19	0.38	1.68	3.75**
Total no. individuals	C	0.40	0.73	2.10*	2.91*	4.65**
	F	1.36	2.08*	2.33*	6.12**	4.78**
No. species	C	0.87	0.93	0.47	2.17*	3.01*
	F	0.96	0.00	1.47	3.01*	4.18**

¶*Leptocheirus plumulosus* and *Jassa falcata*

*heteroclitus* and *F. majalis*, the numerically dominant marsh fishes, were most abundant and actively feeding in marsh creeks. This suggests that fish can reduce the density of macrofauna.

When cages were first placed in creeks in May 1979, samples taken inside and outside cages did not differ in total density or number of species of macrofauna (Table 2). During the first two weeks of the caging experiment, the density of macrofauna inside cages increased by 480% in control creeks and 180% in fertilized creeks (Fig. 2, top graphs). Macrofaunal abundance in cages remained high throughout the experiment. Outside cages, densities were highest during the first 5 wks, then declined in all creeks. By September, the number of animals in uncaged areas had declined to 7% (control) and 5% (fertilized) of the average density found during the first 5 wks. Significant differences in total density due to increases inside and declines outside cages were detected in June (fertilized) and July (control) and persisted through the experiment (Table 2).

Initially (May) only *Streblospio benedicti* and *Hydrobia* sp. in control creeks had significantly higher densities inside than outside cages (Table 2). In September, samples from cages contained significantly higher densities of the oligochaete *Para-*

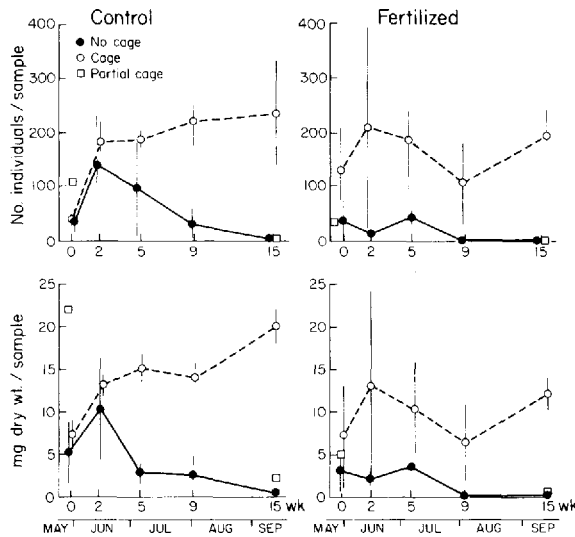


Figure 2. Average densities ( $\pm 1$  S.E.) of macrofauna inside and outside cages (top graphs) and the corresponding mean biomass ( $\pm 1$  S.E.) (bottom graphs) of two replicate control and two replicate fertilized creeks during the caging experiment in 1979. Where vertical S.E. lines are not shown, S.E. was too small to illustrate. Density and biomass are significantly correlated ( $r = +0.89$ ).

*nais litoralis*, polychaetes *S. benedicti* and *Capitella* sp., snail *Hydrobia* sp., anemone *Nematostella vectensis*, higher total numbers of individuals, and numbers of species than samples outside cages.

The abundance of macrofauna within partial cages initially resembled or exceeded that inside cages (Fig. 2). In contrast to the caged areas, densities inside partial cages declined during summer to levels comparable to those in uncaged areas. In September, densities and numbers of species in partial cages did not differ from those outside cages

Table 3. Comparison of sediment characteristics outside and inside exclusion cages after cages were in place for 6 wks in 1981. Means  $\pm 1$  S.D. are given. A paired-sample *t*-test was used to compare data taken outside and inside cages in 3 creeks (2 control, 1 fertilized). (n.s. = not significant).

	Percent of dry weight		
	Outside	Inside	Paired-sample <i>t</i>
Sand	47.7 $\pm$ 5.3	39.8 $\pm$ 3.2	2.79 n.s.
Silt	47.6 $\pm$ 6.4	51.6 $\pm$ 3.9	1.44 n.s.
Clay	4.7 $\pm$ 3.7	8.7 $\pm$ 0.9	1.50 n.s.
Water††	87.2 $\pm$ 2.0	86.7 $\pm$ 1.2	0.74 n.s.
Organic matter	32.9 $\pm$ 8.8	30.5 $\pm$ 12.9	0.70 n.s.

††Water data are available for 2 creeks only.



Table 4. Chlorophyll *a* concentrations ( $\mu\text{g Chl } a/\text{cc}$  sediment) from inside and outside cages in 1979 and 1980. Mean value of all 4 creeks, and ratio of chlorophyll concentration inside cages to chlorophyll concentration outside cages is shown for each date sampled.

Date	June 80	July 80	August 80	September 79
Time caged	initial	2 weeks	10 weeks	16 weeks
Outside cages	20.3	23.8	8.0	5.0
Inside cages	22.5	31.4	24.7	21.8
Ratio	1.1	1.3	3.1	4.6
Paired <i>t</i> -test	1.79	3.30	11.73	3.63
	n.s.	$P < .05$	$P < .005$	$P < .05$

in the same creek (*F*-test, all  $P > 0.15$ ), indicating that cage artifacts did not significantly affect macrofaunal abundance.

Cages in our experimental marsh creeks did not foul, scour, collect drift algae, or contain predatory decapods. No cages were damaged or lost. The physical characteristics of the sediment were not measurably altered by cages (Table 3). Sediments within cages did not differ from those outside cages (all  $P > 0.1$ ) in sand, silt, clay, water or organic matter content, even after cages had been in place 6 weeks. The organic matter content of creek sediments was high (20–48% dry weight). Most of the organic material occurred in the sand fraction as fragments of decomposing *Spartina alterniflora*.

The concentration of chlorophyll *a* in sediments was initially the same inside and outside of cages, but became significantly ( $P < 0.05$ ) higher inside cages after the cages had been in place for 2 weeks (Table 4). Chlorophyll *a* remained higher inside cages in samples taken 16 wks (1979) and 10 wks (1980) after caging. Chlorophyll *a* concentrations in sediments of partial cages in September 1979 (5.9–6.4  $\mu\text{g Chl } a \text{ cc}^{-1}$  sediment) were within the range of values for uncaged sediments on the same date. These results indicate that the high chlorophyll *a* concentrations inside cages are not

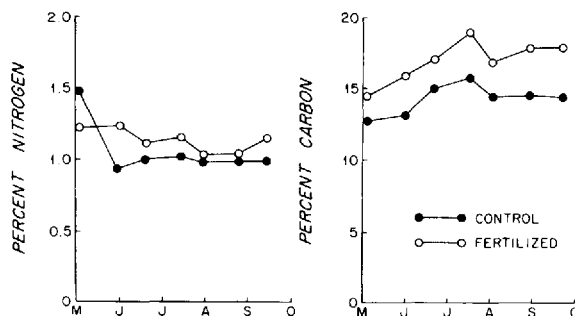


Figure 3. Nitrogen (N) and carbon (C) content of sediments from experimental creeks in 1975. Fertilized sediments have significantly higher percent N (Wilcoxon paired sample test,  $P < 0.05$ ) and percent C ( $P < 0.01$ ) than controls.

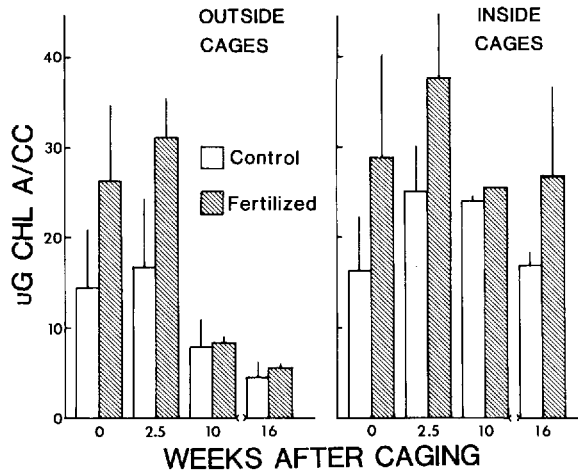


Figure 4. Chlorophyll *a* concentrations in sediments of control and fertilized creeks. Data are means  $\pm$  1 S.E. of chlorophyll levels in two replicate creeks taken in June, July, August 1980 (0, 2.5, 10 wks after caging) and in September, 1979 (16 weeks after caging). Paired comparisons at each date showed that chlorophyll concentrations in fertilized creeks were significantly greater than in controls (sign test,  $P < 0.008$ ).

due to physical or chemical modifications caused by cage structures. Grazing and sediment disturbance reduced chlorophyll *a* concentrations outside cages during summer; exclusion of large grazers by cages allowed benthic microalgae and cyanobacteria to accumulate inside cages.

The percentage of nitrogen and carbon was consistently greater in fertilized than in control sediments (Fig. 3). Chlorophyll *a* concentrations were higher in sediments from fertilized creeks in all 1979–80 samples, both inside and outside cages (Fig. 4). The mean chlorophyll concentration was 51% higher in fertilized creeks than in controls,

Table 5. Comparison of macrofaunal density and biomass in control vs. fertilized creeks in 1979 (see Fig. 4). Shown are *F*-values determined by linear comparison (Sokal and Rohlf, 1969) of control vs. fertilized creeks following one-way ANOVA on 4 individual creeks. For all significant differences ( $* = P < 0.05$ ), control was higher than fertilized.

Month	<i>F</i> -values				
	May	Jun.	Jul.	Aug.	Sept.
Weeks after caging	0	2	5	9	15
<b>Density</b>					
Outside cages	0.4	10.2*	0.0	20.8*	0.9
Inside cages	0.4	6.8	0.4	1.7	0.8
<b>Biomass</b>					
Outside cages	2.2	13.3*	0.0	8.9*	0.5
Inside cages	1.9	1.8	7.2	1.9	2.3

Table 6. Frequency of occurrence of major taxa in all control ( $N = 41$ ) and fertilized ( $N = 41$ ) creek samples taken from May to September 1979. Taxa that occurred in less than 5% of all samples are omitted.

Taxon	Percent of Total Samples	
	Control	Fertilized
Cnidaria		
<i>Nematostella vectensis</i>	59	10
Mollusca		
<i>Hydrobia</i> sp.	83	63
Oligochaeta		
<i>Paranais litoralis</i>	76	73
Unidentified sp.	17	0
Polychaeta		
<i>Capitella</i> spp.	39	37
<i>Haploscoloplos robustus</i>	22	0
<i>Hobsonia florida</i>	46	27
<i>Manyunkia aestuarina</i>	41	24
<i>Nereis succinea</i>	24	5
<i>Polydora ligni</i>	15	10
<i>Streblospio benedicti</i>	80	61
Insecta		
<i>Culicoides</i> larva	32	12
Crustacea		
<i>Edotea trilobita</i>	12	2
<i>Leptocheirus plumulosus</i>	51	17

Table 7. Mean densities (no./core) of major taxa and species richness outside cages in control and fertilized creeks during 1979. Data are means of 2 control (C) or 2 fertilized (F) creeks. A statistical test of control vs. fertilized was made by linear comparison (Sokal and Rohlf, 1969) after performing a one-way ANOVA on data for each date from 4 individual creeks (\* =  $P < 0.05$ ).

Taxa	Outside cages									
	May		Jun.		Jul.		Aug.		Sept.	
	C	F	C	F	C	F	C	F	C	F
<i>Paranais litoralis</i>	19.5	33.8*	14.3	9.8	16.0	23.0	3.0	0.3	0.7	0.5
<i>Streblospio benedicti</i>	3.8	3.8	104.3*	1.3	56.5	10.0	17.0	0.3	1.5	0.5
Amphipods¶	2.5	0.5	10.0	1.5	6.5	4.5	6.3	0.0	0.3	0.0
<i>Hydrobia</i> sp.	1.8	1.5	5.8	1.8	2.3	0.8	1.5	0.3	0.5	0.3
<i>Nematostella vectensis</i>	0.5	0.0	2.5	1.3	4.0	0.8	1.0	0.5	0.7	0.0
<i>Hobsonia florida</i>	0.5	0.3	1.0	0.5	6.0*	1.0	1.0	0.0	0.3	0.0
<i>Capitella</i> spp.	0.3	0.3	0.0	0.8	0.0	4.8*	0.3	0.0	0.2	0.2
No. species/core	6.8	5.5	7.8	4.8	7.8	6.3	3.5	1.3	3.2	1.2

¶*Leptocheirus plumulosus* and *Jassa falcata*

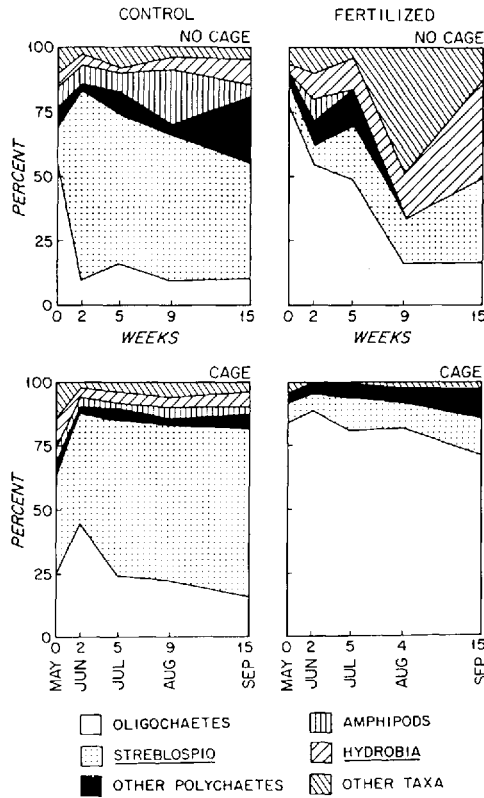


Figure 5. Percent taxonomic composition of macrofauna in treatments of 1979 caging experiment. Data are averages for the two replicate creeks of each treatment.

averaging  $23.7 \mu\text{g cc}^{-1}$  sediment in samples from the fertilized creeks and  $15.6 \mu\text{g cc}^{-1}$  sediment in the control creeks. However, fertilization did not increase the density or biomass of macrofauna, even inside cages (Table 5). The only significant differences between control and fertilized creeks occurred outside cages in June and August when density and biomass were higher in control creeks.

Most species occurred in both fertilized and control creeks (Table 6), but their relative abundances differed. In May, the oligochaete *P. littoralis* was the most abundant species outside cages, and its density was significantly higher in fertilized than control sediments (Table 7). In June, large numbers of the polychaete *S. benedicti* recruited into control creeks where it predominated throughout the summer. The only other differences in density between control and fertilized treatments outside cages occurred in July when *Hobsonia florida* and *Capitella* spp. were more abundant in controls. No significant differences in species richness were detected, although the mean number of species was higher in control creeks on all 5 dates. Densities of all taxa

Table 8. Mean densities (no./core) of major taxa and species richness inside cages in control and fertilized creeks during 1979. Data are means of 2 control (C) or 2 fertilized (F) creeks. A statistical test of control vs. fertilized for each month was made by linear comparison (Sokal and Rohlf, 1969) after performing one-way ANOVA on 4 individual creeks. Probabilities from separate *F*-tests were combined using Fisher's technique (Sokal and Rohlf, 1969, p. 623) to test overall significance. C or F in the far right column indicates which treatment had significantly higher density for that taxon (\* =  $P < 0.05$ , n.s. = not significant).

Taxa	Inside cages												Overall significance (combined <i>P</i> )
	May		Jun.		Jul.		Aug.		Sept.		Overall significance (combined <i>P</i> )		
	C	F	C	F	C	F	C	F	C	F			
<i>Paranais litoralis</i>	9.0	98.0	83.0	187.5	22.5	76.0*	50.3	88.5	48.7	130.4	F*		
<i>Streblospio benedicti</i>	15.3*	9.3	79.5*	13.8	57.5	12.5	137.0	11.0	150.7*	32.4	C*		
Amphipods <sup>†</sup>	2.3	2.0	6.5*	0.5	1.8	0.0	10.0	0.0	4.0	0.2	C*		
<i>Hydrobia</i> sp.	4.8*	2.0	7.5*	1.0	4.0*	0.0	10.0*	0.8	9.7*	1.2	C*		
<i>Nematostella vectensis</i>	0.5	0.0	1.0	0.0	3.0*	0.0	10.8*	0.0	8.2*	0.3	C*		
<i>Hobsonia florida</i>	0.8	1.5	2.3	2.8	5.0	3.5	2.8	1.8	3.2	0.2	n.s.		
<i>Capitella</i> spp.	0.8	1.3	0.5	3.3	1.0	6.5	1.0	5.0	6.3	23.5	n.s.		
No. species/core	8.0	6.0	9.0*	4.8	9.0*	4.3	8.8*	5.0	8.7*	5.8	C*		

<sup>†</sup>*Leptocheirus plumulosus* and *Jassa falcata*

Table 9. Mean number of species per core and evenness inside cages in 1979. *F*-value, from one-way ANOVA on all 5 dates, compared changes over time within individual cages. \* =  $P < 0.05$ , n.s. = not significant.

Treatment	Replicate no.	No. species					<i>F</i> -value	Evenness <sup>¶</sup>					<i>F</i> -value		
		M	J	J	A	S		M	J	J	A	S			
Control	1	8.0	10.5	10.5	10.5	11.0	0.44	n.s.	.57	.30	.39	.38	.43	2.53	n.s.
	2	8.0	7.5	7.5	7.0	6.3	0.38	n.s.	.39	.24	.21	.27	.28	0.39	n.s.
Fertilized	1	4.5	3.0	4.0	3.0	4.0	0.38	n.s.	.14	.10	.32	.29	.24	3.75	n.s.
	2	7.5	6.5	4.5	7.0	7.7	1.16	n.s.	.12	.11	.16	.15	.40	5.41*	

<sup>¶</sup>Measured by scaled standard deviation (Fager, 1972) where evenness =  $[(N - S) / \sqrt{S - SD}] / [(N - S) / \sqrt{S}]$ ,  $N$  = no. of individuals,  $S$  = no. of species, and  $SD$  = standard deviation.

decreased after July. In September, total densities in uncaged sediments averaged only 3.3 individuals core<sup>-1</sup>, but most major taxa were represented.

In uncaged sediments the relative abundance of species changed through time, particularly in fertilized creeks (Fig. 5, top graphs). This was due mainly to a decline in the dominance of oligochaetes when overall mortality was high. By August, *P. littoralis* comprised <17% of the total individuals.

Inside cages *S. benedicti* predominated in control creeks throughout the experiment and was significantly more abundant in control than in fertilized creeks (Table 8). *Paranais littoralis* was the most abundant species in fertilized cages on all dates and its density was significantly higher overall in fertilized than control creeks. *Hydrobia* sp., *N. vectensis*, and amphipods all had consistently higher densities in control than fertilized cages. *Capitella* spp. and *H. florida* showed no significant differences between control and fertilized cages.

The number of species did not differ in May between control and fertilized cages, but control cages averaged significantly more species per core on all subsequent dates (Table 8). Initially, cages in fertilized creeks showed significantly lower ( $F = 22$ ,  $P < 0.003$ ) species evenness than controls, due to the strong dominance of oligochaetes, but in September evenness was similar ( $F = 0.3$ ,  $P > 0.5$ ) in control and fertilized cages (Table 9).

Inside cages the relative abundance of taxa changed little during the experiment (Fig. 5), showing that competitive exclusion did not occur. The mean number of species in cages did not change significantly, and species evenness did not decrease through time (Table 8).

#### 4. Discussion

Where predator/disturbance were excluded, the density of benthic macroinvertebrates increased or remained constant during the summer. In contrast, dramatic declines occurred in the density of macrofauna living in uncaged or partially caged

areas of the creeks which were exposed to fish, crabs and shrimp. These animals appear to control the benthic macrofaunal populations of natural creek bottoms in summer by feeding and by disturbing surface sediments.

Three criteria are used to conservatively specify taxa that were controlled by predation/disturbance: significantly higher density inside than outside cages in September, a decline in density in uncaged sediments during the experiment, and an increase or no change in density inside cages. Taxa meeting all these criteria are *Paranais litoralis* and *Streblospio benedicti* in both control and fertilized creeks, *Hydrobia* sp. and *Nematostella vectensis* in control, and *Capitella* spp. in fertilized creeks. Densities of amphipods and *Hobsonia florida* did not appear to be influenced by predator/disturbers.

Before August, *P. litoralis* and *S. benedicti* were the 2 most abundant species both inside and outside cages. The high reproductive rates of these opportunists enabled them to remain common during May, June, and July despite the activity of fish, crabs and shrimp. Other macrofauna exhibited low densities at all times. All of the major taxa of macrofauna in marsh creeks live at the sediment surface and are potentially vulnerable to predation and disturbance. This is unlike Virnstein's (1979) findings in Chesapeake Bay where species not susceptible to predation were numerically dominant in the natural community. He found that different, opportunistic species predominated inside predator exclusion cages.

Results from caging experiments must be interpreted cautiously because cages placed over soft sediments may alter many factors in addition to access by predators (Virnstein, 1977, 1978; Dayton and Oliver, 1980; Hulberg and Oliver, 1980). The most difficult problem is in separating the effects of reduced predation or disturbance from those caused by modification of water flow due to the cage structures (Hulberg and Oliver, 1980). Cages may alter patterns of larval settlement (Woodin, 1974) and increase sedimentation (McCall, 1977; Virnstein, 1977; Hulberg and Oliver, 1980). No significant cage artifacts were detected in our experiments. If subtle or undetected changes in sediment quality or larval settlement due to "cage effects" were important, these would be reflected in the density and composition of fauna within partial cages. At the conclusion of the caging experiment, data from partially caged areas were comparable to those in uncaged areas. Habitat modifications due to cages are probably less severe in our narrow marsh creeks than in mudflats, sandflats, and unvegetated subtidal areas because marsh grasses and peat banks normally produce turbulence and slow water flow.

The diet and growth of fish and shrimp at Great Sippewissett Marsh provide additional evidence that predation and related disturbance account for the large decline of macrofaunal density in uncaged sediments. Werme (1981) found that several fish species (*Fundulus heteroclitus*, *F. majalis*, *Tautoga onitis*, *Centropristes striatus*, *Pseudopleuronectes americanus*, and *Anquilla rostrata*) fed on benthic invertebrates in tidal creeks at Great Sippewissett Marsh. The omnivores *F. heterocli-*

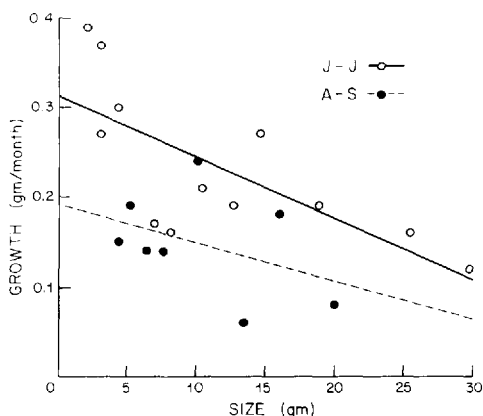


Figure 6. Growth rate of 3–30 g *Fundulus heteroclitus* at Great Sippewissett Marsh in June–July and in August–September. Data adapted from Valiela et al. (1977). *F*-values for regressions are 10.6,  $P < 0.02$ , for June–July and 1.2,  $P > 0.5$ , for August–September.

*tus* (av. = 111 individuals sighted while swimming a 100 m transect) and *F. majalis* (av. = 12 individuals per 100 m transect) were the most abundant, especially in muddy creeks. From May to June benthic invertebrates comprised 40% and 85% of the diets of *F. heteroclitus* and *F. majalis*, respectively. Carnivory dropped to 6–27% in July–September when fish ate more algae and detritus. This dietary shift corresponded with low densities of benthic animals and reduced growth rates of fish (Fig. 6). Prinslow et al. (1974) found that a diet of detritus alone could not sustain the growth of *F. heteroclitus*.

Similarly, the percentage of grass shrimp (*Palaemonetes pugio*) at Great Sippewissett Marsh with guts containing annelids and nematodes declined from 23–55% in March and April to 0–5% during June, July and August (Chambers, 1982). Growth of adult shrimp ceased during summer when their diet was mostly filamentous algae and *Spartina* detritus.

These observations on the diet and growth of fish and shrimp suggest that they prey on benthic invertebrates in marsh creeks until these prey are depleted, then shift to less desirable plant or detrital food. Depletion of the benthos may be common in marsh creeks and channels during summer. The amount of food available in subtidal channels of a North Carolina marsh was also insufficient to support normal growth of the *F. heteroclitus* population (Weisberg and Lotrich, 1982).

We cannot distinguish between the effects of disturbance and direct predation (Woodin, 1978, 1981; Wiltse, 1980; Brenchley, 1981). Furthermore, we do not know whether fish, crabs, or shrimp are primarily responsible for depleting the benthos. The impact of shrimp (*P. pugio*) may be reduced by large fish that feed on grass shrimp (Kneib and Stiven, 1982). However in a natural assemblage where mixed sizes of fish



and shrimp co-occur, both predators could contribute to the depletion of benthic macrofauna.

Despite large increases in density within cages, no significant shift in the relative abundance of species occurred (Fig. 5), indicating that no one species was able to exclude others or increase its dominance through time. The lack of competitive exclusion by dominant species within predator exclusion cages in soft-sediment benthic communities has been attributed to the absence of rapid mortality from adult-adult competitive interactions, intense adult-larval interactions that keep densities below the carrying capacity (Peterson, 1979), or increased predation by infauna within cages (Ambrose, 1984). In salt marshes, the abundant predator/disturbers such as shrimp, crabs, and fish are actually omnivores, ingesting detritus and algae, as well as macrofauna and meiofauna. Exclusion of these large omnivores resulted in higher chlorophyll *a* concentrations and diatom densities (Wagner and Foreman, 1981) inside cages. Benthic microalgae, including diatoms and flagellates, are food for benthic infauna (Davis and Lee, 1983; Bianchi and Levinton, 1984) as well as for the larger omnivores. We suggest that the accumulation of microalgae inside cages lessened competition for food and allowed coexistence of many species of macrofauna at high densities.

Higher chlorophyll *a* concentrations and percent nitrogen and carbon in fertilized than in control creek sediments demonstrate that fertilization increased the quantity and quality of food available to deposit feeders. In spite of this, no increase in benthic biomass or density was detected in fertilized relative to control creeks. Higher secondary production due to increased food may not be reflected in the standing crop of macroinvertebrates where predators are active. However, if fertilization increased production of macrofauna, higher densities should have accumulated inside cages of fertilized creeks. The fact that this did not occur indicates that food does not limit the abundance of macrobenthos in this habitat.

Fertilization did markedly alter the taxonomic composition of the macrofauna. There were fewer species present in fertilized salt marsh creeks than in controls due to reductions in the abundance of rare and moderately common species (Tables 7 and 8). This decrease in total number of species and a trend toward lower biomass and density in fertilized creeks (Fig. 2) suggest that the macrofaunal community was stressed (*sensu* Gray, 1979), rather than stimulated, by fertilization (see review by Pearson and Rosenberg, 1978). This may be due to altered redox conditions, with lower oxygen and increased hydrogen sulfide in fertilized sediments.

Another response to fertilization was a change of dominant species from *S. benedicti* (control) to *P. littoralis* (fertilized). The polychaete *S. benedicti* is well known as an opportunistic species (Grassle and Grassle, 1974; Pearson and Rosenberg, 1978), but the oligochaete *P. littoralis* is rarely included among species typical of polluted and disturbed sediment. *Paranais littoralis* is widely distributed, has rapid asexual reproduction, and is tolerant of polluted sediments. This oligochaete was more abundant than *S. benedicti* and *Capitella* spp. in the urea-fertilized creeks and in six nearby

creeks fertilized with sewage sludge (unpublished data). Gray (1976) also found *P. littoralis* to be the most common species in unstable sediments of the polluted river Tees estuary in England. Other studies have probably undersampled *P. littoralis* by using sieves with  $>0.5$  mm mesh or failed to distinguish it from other oligochaetes or *Capitella* spp. Our findings suggest that dominance by *P. littoralis* may indicate sediments which are severely stressed by enrichment.

In a similar study Dauer *et al.* (1982) simultaneously manipulated predation and food availability in a subtidal area of Chesapeake Bay. As in our study, densities were higher inside than outside predator exclusion cages and organic enrichment had no effect on density in uncaged sediments. Results of both studies indicate that the main process governing density of benthic infauna during summer was the activity of predators, not food-limitation.

Their results also differed from ours in other ways. In Chesapeake Bay during summer, cages treated with organic fertilizer had higher densities and more species of macrofauna than control cages. The results suggest that enrichment stimulated the productivity of macrofauna inside cages in Chesapeake Bay, and stressed the macrofauna in marsh creeks. In subtidal Chesapeake Bay, the input of organic matter to sediments and *in situ* primary production were probably lower than in marsh creeks. The Chesapeake Bay sediments were well-sorted medium sands, with silt-clay content  $<14\%$ , and our marsh sediments averaged  $>52\%$  silt-clay with an organic matter content of 20–48%. Because organic matter content of sediments is often inversely related to grain size (Sanders, 1958; Dale, 1974), their coarser sediments were probably lower in organic carbon content than our sediments. The high input of marsh detritus and microalgal production appear to provide ample food for the macrobenthos of marsh creeks, even where densities were very high in the absence of predators.

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