Response of Benthic Diatoms to Removal of Macroconsumers

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Introduction

Changes in community structure and varieties of algae may affect higher organisms in aquatic ecosystems. The fact that changes in populations of higher organisms may exert comparable effects on algae populations is less often recognized (1). Evidence from rocky shore systems suggests that local community structure and diversity is directly related to the number of predators in the system and the efficiency with which predators prevent a few species from monopolizing some limiting resource. Experimentally excluding predators capable of preventing such monopolies resulted in reduction in community diversity. (3, 17, 18, 19). Although the importance of macroconsumers in regulation of microalgal biomass and productivity has been demonstrated for soft mud substrates (2, 5, 16), little data exist concerning the effects of macrofauna on algal community structure. Macroconsumer activities of ingestion, excretion, maceration, and bioturbation may all exert a significant effect on microalgal communities (16).

The present study examines the effect of fish (*Fundulus spp.*) and fiddler crabs (*Uca Pugnax*) on the composition of benthic diatom assemblages in salt marsh creek beds, where light is the major limiting factor (21). The objective of this study was to measure the *net* result of complete macroconsumer removal rather than to determine separate importance values for the various macroconsumer activities.

Materials and Methods

The study was carried out in two tidal salt marsh creeks within the Great Sippewissett Salt Marsh on Buzzard's Bay, Massachusetts. The creeks averaged one to two meters in width and were bordered by *Spartina alterniflora*. Substantial numbers of *Fundulus* occur in these creeks at high tide, while *Uca pugnax* is common in the creek beds throughout the day. The algal community consisted primarily of Bacillariophycae (diatoms), Chlorophyceae (greens), and Cyanophyceae (blue-greens) (26).

Two replicate field experiments, carried out on separate creeks, were designed to assess the effect of macrofauna on the benthic diatom community. Exclusion cages measured 0.5 by 1.0 m with a 5 mm square mesh. One cage was placed in each creek during low tide on July 11, 1981. In addition, one of the creeks (Site 1) contained an identical cage which had been in place for one year. Thirty days later, on August 10, sediment samples were taken from both creeks (Site 1 and Site 2) from grazed and ungrazed plots using a hand-held piston corer 2.5 cm in diameter. With only one sampling date for all areas, shifts in species abundance could be compared between treatments (ungazed and grazed plots) without the added variable of seasonal changes. Two sets of three cores 1.0 cm deep and 5.0 ml in volume were extracted at low tide from: Each 30-day cage (30-day ungrazed plot), the year-old cage located only on Site 1 (year-old ungrazed plot), and surrounding open (grazed) areas. Each 3-core pool was stirred vigorously and 1.0 ml of sediment was removed and preserved in 50 ml of dilute Lugol's solution. This pooling of cores minimized the patchiness characteristic of most benthic communities.

Organic matter was cleared from the specimens using equal volumes of preserved sample and 30% H_2O_2 (2.5 ml of each was usually sufficient). After bubbling ceased 0.1 ml was distributed evenly on a #0 coverslip and dried over low heat. Coverslips were mounted on slides with Hyrax and examined at 1000X using a phase microscope. Replicate slides were made from each of the six pooled core samples. Approximately 600 diatoms in 60 to 70 randomly selected fields were counted and identified per slide. Several taxonomic references were employed (6, 8, 10, 20, 22). Further counting did not significantly alter the proportions of the dominant species in relation to the total diatom counts, a finding also reported by (26, 27). To assess shifts in species composition based on biomass rather than numbers, further counts were made of diatoms with a maximum length of at least 50 μ. Random fields were examined at 600X until 300 of these larger diatoms were counted and identified from each core pool. Size of diatom was also measured as area using a Zeiss videoplan image analyzer.

Sample dilutions, number and area of counted fields, number of diatoms counted and total surface area of each subsample on the coverslip were used to calculate the diatom species in each ml of sediment. The 10 numerically most abundant diatom species, the dominants, were compared between grazed and ungrazed plots with each species abundance calculated as a numerical percent of the total diatoms in the sample. Further comparisons between treatments were made using the Shannon index of general diversity ($\bar{H}$), an evenness index (e) (15), and a similarity index (SIMI) (25). Significant abundance differences between treatments were determined using a one way analysis of variance.

Results

Effect of macroconsumer removal on total diatom community

Grazer removal had a significant effect on diatom density in both creeks. Ungrazed plots had higher numerical abundances than corresponding grazed plots (Figure 1). Abundance increased with the length of time the plot remained ungrazed.

The structure of the diatom community appeared to be similar for all samples. Ten species, out of 151 identified, dominated the benthic diatom community in Site 1 for both grazed and ungrazed plots (Table 1). Dominants were identical at Site 2 but occurred in slightly different proportions; shifts in the proportion of these species between treatments at Site 2 were similar to those at Site 1.

The percent frequency of *Achnanthes hauckiana* was less in the year-old ungrazed plot than in the 30-day ungrazed plot. It is a genus which adheres strongly to the substrate. Consequently, it may be less affected by grazing than are other diatoms (14, 23). The actual density of the species (as opposed to the percent of the community) (Table 1) indicated that no significant change occurred in the abundance of *Achnanthes hauckiana*, although its frequency within the community decreased. Slight increases in abundance and percent frequency of the chain-formers (*Melosira nummuloides* and *Fragilaria construens*) occurred after macroconsumer removal. This colonizing morphology may facilitate ingestion by macrofauna. Once an end is caught, the whole chain may be pulled in like spaghetti. (14). Simultaneously, meiofauna grazing may be inhibited by cumbersome size of the chain formers. The smaller species, *Fragilaria shiloi*, *Navicula diserta*, and *N. cryptocephala*, decreased in both percent frequency and total numbers after macroconsumer removal. An increase in meiofauna numbers was observed inside

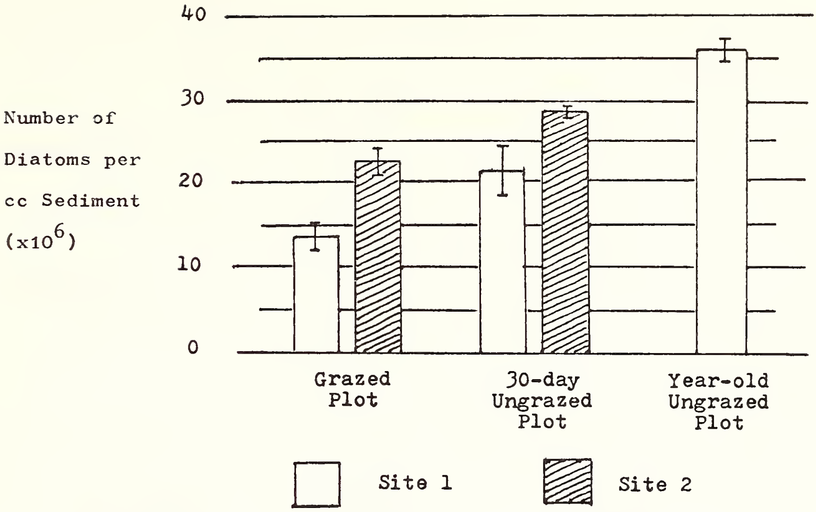

FIGURE 1: *Diatom density ($\bar{x}$ ± SE) in two salt marsh creeks, Site 1 and Site 2, for three different treatments (Site 2 has no year-old ungrazed plot). Samples were taken on August 10, 1981. Differences between treatments (ungrazed nad grazed plots) are significant to the $p < 0.05$ level using a one way ANOVA. Number of diatoms is shown as 10^6 per cc of sediment. Verticle bars above each treatment bar show standard error.*

the cages (pers. obs.). These meiofauna may in turn have been selectively grazing on smaller diatom species. Concomitant increases in the larger species, *Navicula menisculus, N. salinarum* and *N. digito-radiata* with macroconsumer removal support this finding. A significant ($p < 0.05$) increase in percent composition and abun-

TABLE 1: *The ten most numerically abundant species and their percent frequency ($\bar{x}$ ± SE) of the total diatom community in Site 1. All samples were taken on August 10. Significant shifts between treatments (* denotes $p < 0.05$) were tested using the one way ANOVA for each species.*

Species	Grazed Plot	30-day Ungrazed Plot	Year-old Ungrazed Plot
Melosira nummuloides	2.72 ± .501	5.62 ± 1.56	3.16 ± .382
Fragilaria construens	30.7 ± 1.44	29.6 ± 1.25	33.7 ± .450
F. shiloi	7.25 ± .092	4.39 ± 1.22	3.07 ± .315
Achanthes haukiana	13.2 ± .944	11.4 ± 1.30	6.56 ± .460
Navicula diserta*	8.19 ± .378	7.02 ± .396	5.29 ± .117
N. cryptocephala	2.61 ± .534	4.94 ± 1.07	2.42 ± .407
N. menisculus	3.62 ± .185	3.15 ± .884	5.92 ± .290
N. salinarum	1.46 ± .120	1.85 ± .442	2.50 ± .070
N. aigito-radiata	.620 ± .120	1.46 ± .357	1.93 ± .251
Amphora no. 152c	2.42 ± .032	4.47 ± .470	1.49 ± .311

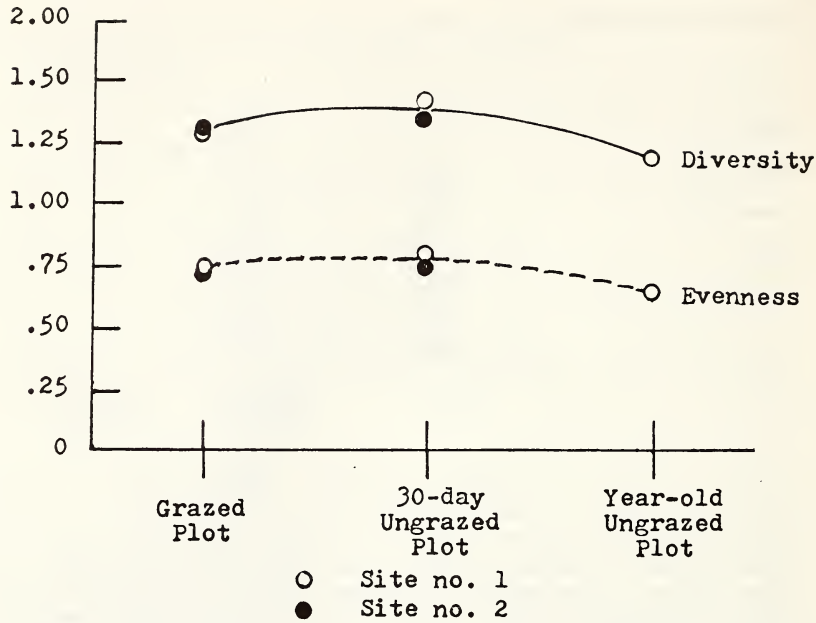

FIGURE 2: *Diversity ($\bar{H}$) and evenness ($\bar{e}$) ($\bar{x}$ ± SE) of the total diatom community at two sites. Differences between treatments are not significant to the $p < 0.10$ level using a one way ANOVA.*

dance occurred in the genus *Amphora* in 30-day ungrazed plots, followed by a sharp decline in the year-old ungrazed plot. The cause of this trend is unknown.

Diversity and evenness indices did not change significantly over a 30-day period in ungrazed plots. However, both indices decreased after one year of macroconsumer removal (Figure 2). Further computations based on the similarity of diatom communities between treatments (Table 2) disclosed slight differences between grazed and 30-day ungrazed, and also between 30-day ungrazed and year-old ungrazed plots, with the largest dissimilarity occurring between the grazed and year-old ungrazed plots.

Effect of macroconsumer removal on population of larger diatoms

A net increase in the abundance and percent frequency of species over 50 μ in length was observed in all ungrazed areas and reached a peak in the 30-day plot

TABLE 2: *Values of similarity between treatments (range 0-1) both for the total diatom community and for populations of diatoms above 50 μ in Site 1.*

Diatom Community	SIMI between Grazed and 30-day Ungrazed	SIMI between 30-day Ungrazed and year-old Ungrazed	SIMI between year-old Ungrazed and Grazed
Total Community	.93	.95	.90
Diatoms above 50 μ	.76	.69	.58

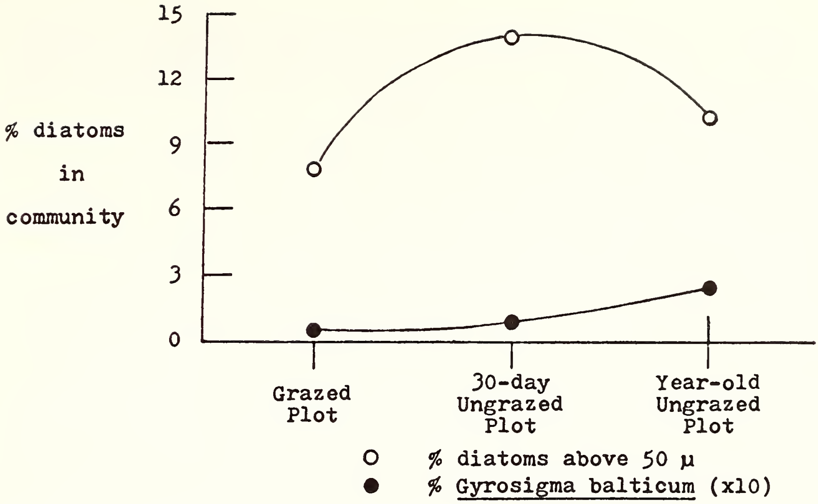

FIGURE 3: *Percent of diatoms larger than 50 µ ($\bar{x}$ ± SE) and percent of one larger dominating species, Gyrosigma balticum, in the total community for Site 1. Concentrations of G. balticum were multiplied by one order of magnitude for comparison. Differences between treatments were significant at $p < 0.10$ level for the concentration of G. balticum but not for the percent of diatoms larger than 50 µ using a one way ANOVA.*

(Figure 3). This result was anticipated and supports previous observations of food partitioning between macrofauna and meiofauna based on diatom cell-size (13, 24). The reason for the peak at 30-days rather than one year is not readily apparent, although it may be due to a more even distribution of certain species. The one-year ungrazed community was heavily dominated by three species. One is *Gyrosigma balticum*, averaging 420 µ in length (Figure 3).

Some significant shifts ($p < 0.05$) in the population structure of these larger diatoms were observed between grazed and ungrazed plots. Because there was no year-old ungrazed plot at Site 2 and there was variability in species composition between sites on other plots, analysis of the populations of large diatoms from Site 2 was not attempted. Table 3 lists the species which occurred most frequently in the three treatments on Site 1. The causes for the changes in percent frequency for particular species did not appear to be size-related. For example, *Gyrosigma peisonis* is half the size of *Pleurosigma angulatum*, but it increased in frequency in ungrazed areas while *P. angulatum* decreased. Similar phenomena occurred with some larger species becoming abundant in ungrazed areas while smaller species decreased in numbers. A trend towards dominance by *Navicula digito-radiata*, *Gyrosigma balticum* and *G. peisonis* was observed at 30 days and reached its maximum in the year-old ungrazed plot where these three species comprised 50% of the large diatoms.

Significant ($p < 0.05$) decreases in diversity and evenness after macroconsumer removal (Table 4) further support the observed trend towards monopolization by a few species. The similarity values obtained for these larger diatoms between treatments (Table 2) indicated substantial differences between grazed,

TABLE 3: *The eleven most numerically abundant species of larger diatoms ($\bar{x}$ ± SE) as percent of the community of species larger than 50 μ in Site 1. Significant shifts between treatments (* denotes $p < 0.05$: ** denotes $p < 0.01$) were tested using the one way ANOVA for each species.*

Species	30-day Ungrazed Grazed Plot	Year-old Plot	Ungrazed Plot
Synedra fasiculata*	2.63 ± .520	8.53 ± .156	4.43 ± .064
Amphiprora no. 29	5.21 ± 1.54	2.83 ± .117	1.35 ± .270
Navicula digito-radiata**	9.84 ± .548	11.1 ± .560	33.1 ± 1.14
Gyrosigma peisonis**	.335 ± .169	.545 ± .130	7.28 ± .580
G. balticum*	.470 ± .283	2.21 ± 1.02	8.49 ± .707
Pleurosigma angulatum	2.48 ± .145	1.66 ± .099	.630 ± .241
P. strigosum	1.43 ± .064	1.02 ± .453	0.00 ± 0.00
Stauroneis sp.	2.86 ± .124	3.02 ± .318	2.11 ± .350
Amphora no. 152*	1.22 ± .325	6.60 ± .438	2.34 ± .633
Amphora sp.**	7.44 ± .435	10.8 ± .131	3.78 ± .396
Nitschia sigma	6.66 ± .912	8.38 ± .527	4.51 ± 1.04

30-day ungrazed, and year-old ungrazed plots. The largest dissimilarity occurred between grazed and year-old ungrazed populations, as would be expected. A simple comparison between similarity values of the total diatom community and the species over 50 μ (Table 2) made clear that the larger species changed most after macroconsumer removal. The total diatom community exhibited some shifts in population structure in ungrazed areas, but the larger species changed markedly.

Effect of macroconsumer removal on size within species

Differences in mean frustule length were observed in some species between treatments. Also, careful measurements indicated a significant increase ($p < 0.01$) in length and surface area of *Gyrosigma balticum* and *Pleurosigma angulatum* after macroconsumer removal in both Site 1 and 2 (Figures 4 and 5). In addition, two other species showed a similar narrowing of the range of size classes and an increase in size through time, possibly indicating that a larger optimal size was being selected for in ungrazed areas.

TABLE 4: *Diversity and evenness calculations ($\bar{x}$ ± SE) for the populations of diatoms larger than 50 μ in Site 1. Shifts between treatments for both diversity and evenness calculations were significant for $p < 0.05$ level using a one way ANOVA.*

	Grazed Plot	30-day Ungrazed Plot	Year-old Ungrazed Plot
Diversity ($\bar{H}$)	1.48 ± .01	1.35 ± .04	1.17 ± .01
Evenness (e)	.87 ± .02	.83 ± .02	.71 ± .01

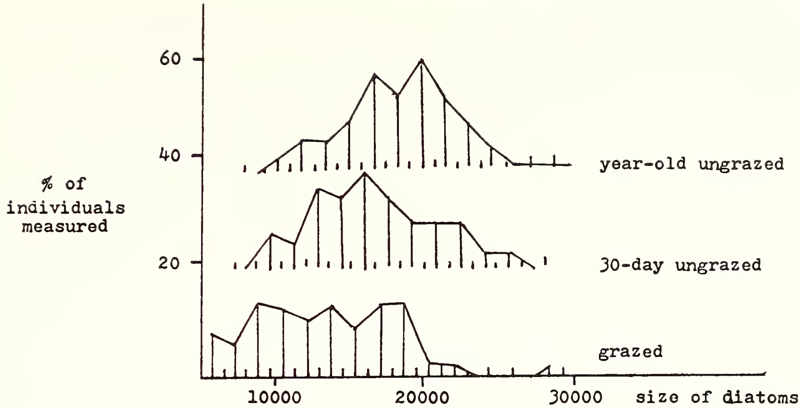

FIGURE 4: *Distribution of size within Gyrosigma balticum for the three treatments in Site 1. Shifts are significant ($p < 0.01$) according to a paired t test. Size of diatom was measured as area on the slide (μ^2).*

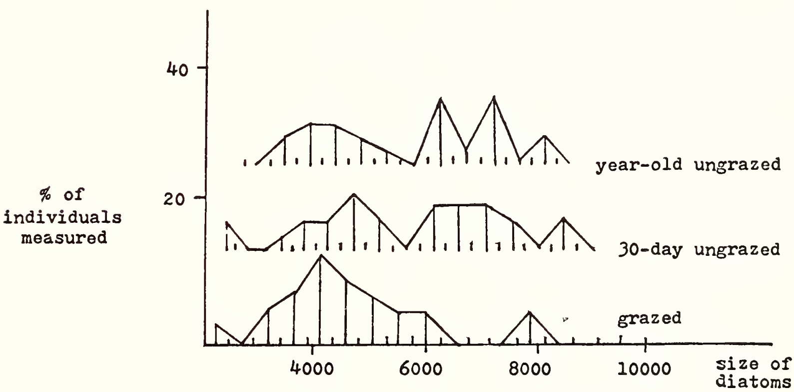

FIGURE 5: *Distribution of sizes (area) within the species Pleurosigma angulatum for the three treatments in Site 1. Shifts are significant ($p < 0.01$) according to a paired test. Size of diatom was measured as area on the slide (μ^2).*

Discussion

Exclusion of macrofauna by cages resulted in significant changes in the structure and abundance of the diatom community. Much controversy surrounds caging experiments, however, and it is important to resolve any errors which might have resulted from experimental design. Effects of shading by cages on the benthic algal community appears to have been negligible, as the tall *Spartina alterniflora* growth bordering the narrow creek banks already shaded the benthic communities. Cages may also act as partial sediment traps by consolidating the creek bottom and allowing algae to grow in denser mats (7) and may cause differences in the structure of the benthic diatom community (25). The absense of bioturbation by macroconsumers could account for these dense algal mats inside cages, although in an experiment simulating consumer activity, algal productivity appeared to be unchanged (16). In addition to increased algal growth, meiofauna numbers also appeared to be higher in ungazed areas (pers. obs.). Cages may serve as partial refuges from predation, although it is generally accepted that meiofauna are utilized only to a small extent by macrofauna in salt marsh creeks (4, 11, 12). Meiofauna are probably immigrating to these ungrazed areas to take advantage of increased epibenthic algal productivity.

These results indicate that any effects attributable to errors in experimental design are probably minimal or reinforce those caused by macroconsumer removal. Such undesirable stress caused by cages would probably favor certain species, rather than morphological features. Major shifts occurring within the diatom community in this experiment appear to be largely size related and consequently not the result of experimental error. Clearly, macrofauna regulated the populations of larger diatoms, while meiofauna grazed more heavily on smaller species. The extent to which macrofauna ingested the smaller cells is difficult to assess, but past studies indicate that biomass is an equally or more important selective factor than quality of food in the nutrition of many benthic organisms (13, 24). Macrofauna grazing appears then to be a passive type of selection based largely on differences in diatom morphology and accessibility rather than on species—specific picking and choosing (14). Bethic diatoms seem to have evolved to surmount such selective predation by having rapid reproductive rates or by becoming too large to be ingested by most consumers (5, 9). In regards to the effects of grazing on the specific composition of benthic diatom assemblages, Mullin (13) suggests that even a slight preferential removal of certain species could have a considerable effect if maintained for any length of time. Consequently, macroconsumer grazing, however slight, is at a level sufficient to produce considerable shifts in the diatom populations.

Changes in the diatom community after larger grazers were removed closely parallels a procession of events observed by Paine and Vadas (19) in a study on macroscopic algal communities on rocky shores after sea urchin removal; 1.) an immediate increase in abundance and numbers of species present, 2.) establishment of larger "canopy-species", 3.) a succession with the majority of biomass vested in a few species, and 4.) establishment of many smaller species under the "canopy". (The data were not analyzed completely enough to be certain of this last point.) Paine and Vadas′ (1969) findings indicate that selective cropping by sea urchins leads to more algal heterogeneity through the reduction of competition. Data on diatom diversity from this experiment leads to a similar conclusion; Macroconsumers may be maintaining diversity by grazing out those species (canopy) which would tend to dominate at the expense of others.

The increase in size observed within several larger species may be attributed to similar competitive interactions in which large size is an advantage both in escaping predation and in maximizing photosynthetic potential in a light-limited system. Similar size shifts within species have been reported by Wimpenny (28) and attributed entirely to grazing pressure. In this study, 30 μ shifts in the mean size of species averaging 420 μ were observed. Most meiofauna ingest diatoms averaging 20-30 μ in length and, consequently, cannot handle such large cells. Competition between species for light in ungrazed areas, which contained up to three times the natural diatom density, may have been a more important factor in controlling intraspecific sizes. This hypothesis is supported by the observed increase in abundance of larger species in ungrazed areas, followed by the eventual dominance of the larger diatom community by several species of *Gyrosigma* and

Navicula, which have well-developed raphe systems thus allowing them to glide upward through the sediment towards light.

Feeding studies show that microalgae are an important food resource for macroconsumers living in the salt marsh (16), but the impact of the consumer on the producer is often neglected. Results from this experiment indicate that the density, community structure, and interspecific interactions of benthic diatoms were significantly affected by the activities of macroconsumers. Size-selective predation by the larger grazers may act further to maintain diversity and reduce competition in the diatom community. Findings from this experiment could have an important impact on future studies of interactions. between different trophic levels in estuarine ecosystems.

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