Foraminifera as prey for benthic deposit feeders: results of predator exclusion experiments

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ABSTRACT

To assess the importance of predation on foraminifera, a meiofaunal enclosure with openings of 1 mm containing 30 *l* of azoic sand was placed in a subtidal flat at Link Port, Florida in February 1976. During March, April, May, and June 1976, 4 replicate samples were taken inside and outside the cage. Foraminiferal densities were significantly higher inside the cage indicating foraminiferal densities are higher in the absence of macrofaunal predators.

To estimate the importance of larger predators, a cage with 12 mm openings constructed for a macrofaunal enclosure experiment was placed over the natural substrate. A control area with no cage was established nearby. Samples were taken with 4 replicates in January, February, March, April, and May, 1976. Foraminiferal densities inside vs. outside the cage were not significantly different indicating macrofaunal predation was equal inside and outside the cage.

The meiofaunal enclosure experiment was repeated in 1977. Results paralleled those found in 1976.

Examination of gut contents of macrofaunal animals indicates a wide variety of deposit feeders ingest foraminifera. Foraminiferal biomass inside meiofaunal cages in April and May for both years are estimated to be 3 to 12 g/m^2 higher than outside the cages. These experiments indicate foraminiferal densities are substantially reduced by predation and, therefore, foraminifera probably represent an important food source.

1. Introduction

Foraminifera are one of the most abundant constituents of the permanent meiofauna (Olsson and Eriksson, 1974). During the past few years several researchers (Lynts, 1971; Lankford and Phleger, 1973; Buzas *et al.*, 1977) have demonstrated physio-chemical variables often do not account for observed patterns of species densities. Observations of gut contents indicate foraminifera are ingested accidently or purposefully by many marine organisms (Lipps and Valentine, 1970; Lipps and Ronan, 1974), and predation has been suggested as a means of regulating foraminiferal densities (Buzas *et al.*, 1977).

Numerous ecologists have quantitatively demonstrated the importance of predation on regulating macrofaunal densities by means of caging experiments which exclude predators (Blegvad, 1928; Dayton, 1971; Young *et al.*, 1976, Virnstein, 1977).

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The role of the meiofauna in the food web, however, has remained controversial. Some researchers believe few organisms are meiofaunal predators and the major role of the meiofauna is to aid in the recycling of nutrients (McIntyre, 1969; Coull, 1973). To my knowledge, however, no experimental caging has been reported where the macrofauna has been excluded from the meiofauna. Lee (personal communication) has conducted some experiments but the results are not, as yet, available. The present paper summarizes the results of 3 caging experiments in a subtidal sandy flat in the Indian River estuary at Link Port, Florida.

2. Methods

Sediment (sand) was removed from the experimental site (maximum water depth 1m) and after washing with water, the sediment was alternately frozen and sun-dried for a period of 5 weeks to kill all organisms. A meiofaunal cage was constructed from a large (166 *l*) PVC trash can by cutting out 4 windows 35 cm on a side located 15 cm from the bottom. The can measures 79 cm from top to bottom. The sides of the can were strengthened with 4 wooden slats fastened with stainless steel bolts. Replaceable nylon screen with openings of 1 mm were constructed to fit over the openings.

On February 4, 1976 the cage was placed in a 15 cm deep hole and 30 *l* of azoic sand was added making the sediment surface inside and outside the cage approximately level. In March, April, May, and June, 4 replicate samples each 2 cm deep and consisting of 20 ml of sediment were taken inside the cage and outside from a control area a few m away with coring tubes. To prevent fouling and allow easy passage of water, the nylon screen was changed twice a week throughout the experiment.

For macrofaunal experiments Young and Young (1977) constructed a square 2 m cage with openings of 12 mm at the same site. The enclosure extended to a depth of about 5 cm into the sediment. Consequently, only larger macrofaunal organisms were excluded from inside the cage. During the months of January, February, March, April, and May, 1976, the cage was sampled with coring tubes inside and outside in a control area a few m away with 4 replicates, each 2 cm deep and consisting of 20 ml of sediment.

On February 14, 1977 the meiofaunal enclosure experiment was repeated using exactly the same procedures as in 1976 except each replicate was reduced to 5 ml of sediment.

Each biological sample was fixed with neutralized foramlin, washed through a 63 μ sieve, stained with rose bengal, dried, floated with bromoform-acetone, rewetted, and placed in grided petri dishes for counting. In those samples where foraminiferal densities were extremely high the number was estimated by counting randomally selected squares. Usually about 6 squares per dish were counted because

Table 1. Analyses of variance of meiofaunal cage 1976.

Taxa	Effect	Sum of Squares	Mean Square	*df*	*F*	*P*(*F*)
Ammonia beccarii	Time	22.71	7.57	3	25.19	0.00
	in vs. out	8.22	8.22	1	27.34	0.00
	interaction	3.35	1.12	3	3.71	0.02
	residual	41.46	.30	24		
Elphidium mexicanum	Time	25.26	8.42	3	22.87	0.00
	in vs. out	9.44	9.44	1	26.65	0.00
	interaction	1.71	.57	3	1.55	0.23
	residual	8.84	.37	24		
miliolids	Time	16.12	5.37	3	11.57	0.00
	in vs. out	19.57	19.57	1	42.13	0.00
	interaction	2.19	.73	3	1.57	0.22
	residual	11.15	.46	24		
Total living foraminifera	Time	16.76	5.59	3	14.66	0.00
	in vs. out	12.76	12.76	1	33.46	0.00
	interaction	2.21	.74	3	1.93	0.15
	residual	9.15	.38	24		

a plot of the mean number of individuals vs. number of squares becomes asymptotic at this value.

3. Results

The study was designed for analysis by a two-way analysis of variance with interaction. The hypotheses considered were: an overall difference in density inside vs. outside; an overall difference in density with time; interaction (changes in density with time are different inside vs. outside). After transforming the original counts to ln x to stabilize the variance and make the data more normally distributed, ANOVA's were calculated for the abundant taxa *Ammonia beccarii, Elphidium mexicanum*, miliolids (largely *Quinqueloculina seminula* and *Q. impressa*) and total foraminifera. The results for the meiofaunal cage in 1976 are shown in Table 1. In all cases, the hypotheses time and inside vs. outside are significant. For *Ammonia beccarii* the interaction hypothesis is also significant, but the mean square is relatively small compared to the others. Figure 1 plots the mean densities for the total living population inside and outside the meiofaunal cage in 1976. Variation in densities of the other taxa are similar and are not shown here. Note, at the first sampling time, one month after placement of the cage the densities inside are already higher than outside. Densities were always higher inside than outside, generally by about 4 or 5 times.

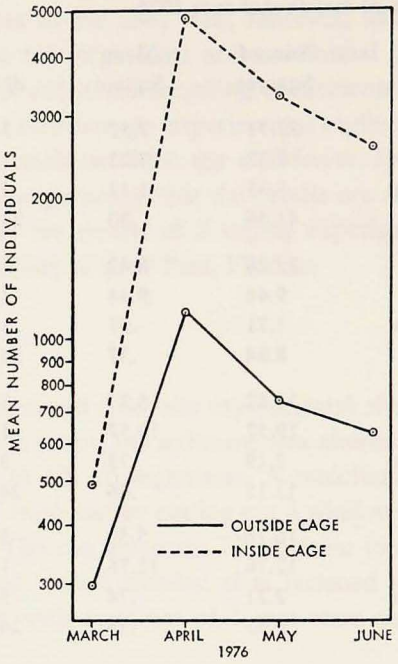

Figure 1. Mean densities of total living population inside and outside meiofaunal cage 1976 (20 ml replicates).

Table 2. Analyses of variance of macrofaunal cage 1976.

Taxa	Effect	Sum of Squares	*df*	Mean Square	*F*	*P*(*F*)
Ammonia beccarii	Time	4.23	4	1.06	6.96	0.00
	in vs. out	0.53	1	0.53	3.47	0.07
	interaction	0.34	4	0.08	0.56	0.69
	residual	4.55	30	0.15		
Elphidium mexicanum	Time	7.03	4	1.76	11.43	0.00
	in vs. out	0.49	1	0.49	3.22	0.08
	interaction	0.20	4	0.05	0.32	0.86
	residual	4.62	30	0.15		
miliolids	Time	6.52	4	1.63	8.63	0.00
	in vs. out	0.09	1	0.09	0.48	0.49
	interaction	0.14	4	0.03	0.18	0.95
	residual	5.67	30	0.19		
Total living foraminifera	Time	5.57	4	1.39	14.87	0.00
	in vs. out	0.07	1	0.07	0.78	0.38
	interaction	0.24	4	0.06	0.64	0.63
	residual	2.81	30	0.09		

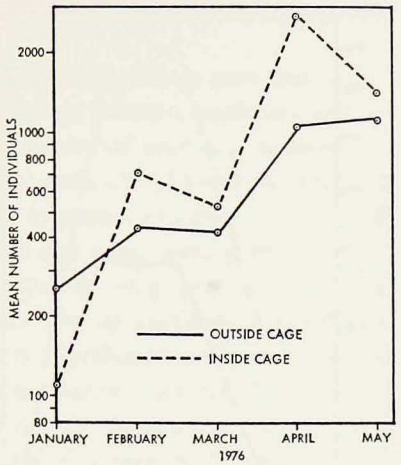

Figure 2. Mean densities of total living population inside and outside macrofaunal cage 1976 (20 ml replicates).

Table 2 shows the results of the ANOVA's on the same foraminiferal taxa from the macrofaunal cage in 1976. The hypothesis for time is significant in all cases, but none of the others are. Figure 2 plots the mean densities for the total population inside vs. outside the macrofaunal cage. Although densities are usually larger inside

Table 3. Analyses of variance of meiofaunal cage 1977.

Taxa	Effect	Sum of Squares	*df*	Mean Square	*F*	*P*(*F*)
Ammonia beccarii	Time	2.68	3	0.89	12.55	0.00
	in vs. out	0.67	1	0.67	9.42	0.00
	interaction	0.18	3	0.06	0.84	0.48
	residual	1.70	24	0.07		
Elphidium mexicanum	Time	1.60	3	0.53	3.56	0.03
	in vs. out	0.84	1	0.84	5.62	0.03
	interaction	0.30	3	0.10	0.66	0.58
	residual	3.59	24	0.15		
Miliolids	Time	2.79	3	0.93	21.17	0.00
	in vs. out	0.34	1	0.34	7.84	0.01
	interaction	0.04	3	0.02	0.35	0.79
	residual	1.06	24	0.04		
Total living foraminifera	Time	0.85	3	0.28	8.30	0.00
	in vs. out	0.23	1	0.23	6.88	0.01
	interaction	0.12	3	0.04	1.14	0.35
	residual	0.82	24	0.03		

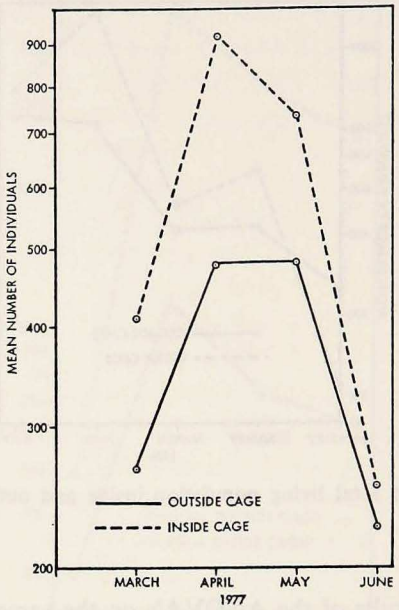

Figure 3. Mean densities of total living population inside and outside meiofaunal cage 1977 (5 ml replicates).

the cage, the statistical analyses indicate they are not significantly so. The pattern of densities in March, April, and May is similar to the one obtained for the meiofaunal cage (Fig. 1).

Results of the ANOVA's for the meiofaunal cage in 1977 are shown in Table 3. The hypotheses time and inside vs. outside are significant for all taxa, just as they were in 1976. Figure 3 plots the mean densities (per 5 ml) for the total living population. Although differences between inside and outside the cage were not as large as in 1976, they are statistically significant, and show the same pattern.

The foraminiferal densities observed inside the meiofaunal cages were among the highest ever recorded for foraminifera (maximum about 5000 per 20 ml in April 1976), and are similar to average densities in the east Mississippi Delta (Lankford, 1959) and those recorded from a single sample in the tail of the Grand Banks (Sen Gupta, 1971).

4. Discussion

No significant difference in densities exists inside vs. outside the macrofaunal cage. This is not surprising because many of the invertebrates reported to ingest foraminifera (Lipps and Valentine, 1970) were inside the cage when it was built (azoic

sediment was not used inside the macrofaunal cage) and could easily fit through 12 mm openings.

At the outset no macrofaunal organisms were inside the meiofaunal cage, and the very large difference in densities between inside and outside is most easily explained by the inability of adult macrofaunal predators to enter the cage. There is, however, the possibility that the azoic sediment allowed the foraminifera to undergo exponential growth before limiting resources caused a decline. This does not seem likely in this case because both food and space were plentiful at maximum densities. Diatom counts indicate a large standing crop present both inside and outside the cage throughout the experiment and at maximum densities the foraminifera occupied less than 1% of the volume of sediment inside the cage. An experiment is underway using azoic sediment in a can without screens, but results are not yet available.

The 1 mm openings of the meiofaunal cage not only allow members of the meiofauna to enter, but also larval stages of the macrofauna. After an undetermined period of time, therefore, the cage could act as an enclosure instead of an exclosure. Consequently, the decline in foraminiferal densities inside the meiofaunal cage during the last two months of the experiment could be due to predation inside the cage. At the conclusion of the experiment in 1976, a sample of about 6 *l* was taken with a post-hole sampler (Young and Young, 1977) to examine the macrofauna inside the cage. The densities and species composition of polychaetes, crustacea, gastropods, bivalves, and a sipunculid were similar to what might be expected from such a single sample from the site, however, numerous species known to inhabit the site were not recorded. Young and Young (1977) give a complete listing of macrofaunal organisms at the site. Examination of the guts of 71 animals revealed 1 foraminiferal test. Little is known about the feeding habits of macrobenthos encountered and foraminiferal tests might have been crushed by species having jaw structures or dissolved by low pH in the guts of others. On the other hand, the synchronous decline in densities inside and outside during May and June at both the meiofaunal and macrofaunal sites might represent an overall seasonal cycle at the Link Port site. Such an overall periodicity does not mean that predation is not important in regulating densities, but would indicate other variables are also important unless the activity of predators can be demonstrated to be cyclic.

The lack of success in identifying foraminiferal predators in 1976 prompted a repeat of the meiofaunal caging experiment in 1977 and examination of gut contents from a variety of organisms inhabiting the Indian River. The only change in the 1977 experiment consisted of taking 5 ml samples instead of 20 ml samples. This change was necessitated because densities in 20 ml were so high in 1976 that enumeration became exceedingly time-consuming. As Table 3 and Figure 3 show, the results in 1977 paralleled those obtained in 1976. For purposes of statistical analyses the experiment was concluded in June; however, densities inside and outside the cage were monitored until December. During these months densities inside

the cage were generally slightly lower than outside. In December the entire cage was removed and the sediment was examined for its macrofaunal contents. The total number of macrofaunal organisms found was 827, and of these 224 were dissected to examine gut contents. A total of 213 foraminifera were found in the guts of 43 individuals. A complete listing of the taxa found inside the cage and their gut contents are given by Buzas and Carle (in press). None of the animals fed solely on foraminifera but were instead generalized deposit feeders. Taxonomically the 43 individuals belonged to species of crabs, shrimp, gastropods, the bivalve *Tellina tampanensis*, and an assortment of polychaetes. In addition two species of gastropods belonging to the genus *Acteocina* and a small fish *Gobionellus boleosoma* not found inside the cage, but occurring commonly in the Indian River, often contain foraminifera in their guts. These data indicate predation is important in regulating foraminiferal densities, and failure to find foraminifera in guts of invertebrates during 1976 was most likely due to inadequate sampling. Whether the synchronous decline in densities inside and outside all cages observed in 1976 and 1977 was due to predation pressure alone or in combination with other environmental variables cannot be determined from the present set of data.

The data presented here suggest foraminifera are an important food source for a variety of organisms, and some estimate of the amount of biomass available for utilization is desirable. Because of the small size of individuals, biomass cannot be measured directly, so the approach used here (Sadovia, 1967; Murray, 1968) measures the dimensions of average individuals, calculates the volume of similar geometric form (right circular cylinder), multiplies by the estimated number of individuals to obtain total volume, and estimates the biomass because the density of protoplasm is very close to 1 g/ml (Beams and King, 1941). The estimates presented here are probably very conservative because living foraminifera occur with similar densities to a depth of about 6 or 7 cm in this area (Buzas, 1977) and these estimates are for only the top 2 cm. The estimates are wet-weights of protoplasm only and do not take into account the weight of the foraminiferal tests. In 1976 the wet-weight estimates for inside the meiofaunal cage varied from 2 to 15 g/m^2, and outside from 1 to 3 g/m^2. In 1977 inside estimates range from 3 to 11 g/m^2 and outside from 3 to 6 g/m^2.

Although the estimates vary widely, they indicate foraminifera are much more important contributors to the standing crop of the benthos than has been previously thought (Mare, 1942; Thorson, 1966). Differences between inside and outside during April and May for both years range from 3 to 12 g/m^2. This difference represents the amount of food cropped by predators and suggests the foraminifera are an important, but overlooked, food source.

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