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REGULATION OF FORAMINIFERAL DENSITIES BY PREDATION IN THE INDIAN RIVER, FLORIDA

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ABSTRACT

In 1976 and 1977 screened cages with sterile sand and an outside control area were sampled in replicate during March, April, May and June in a subtidal flat at Link Port, Florida (Buzas, 1978). In both years foraminiferal densities were significantly higher inside the screened cages than in the outside area. The higher densities were attributed to exclusion of predators from inside the cage.

During these experiments no attempt was made to assess the effect, if any, of sterile sand or the cages on the experiments. In 1978 and 1979 experiments were conducted to alleviate this difficulty and to repeat the experiments at different times of the year.

In 1978 sterile sand was placed in a screenless cage and a screened cage. The cages and a nearby outside control area were sampled in replicate monthly during July, August, September, October, and November. The densities inside the screenless cage were significantly lower than outside for all taxa. The densities inside the screened cage were significantly higher than outside for all taxa except one.

In 1979 the experiment was repeated using sediment from which the macrofauna was removed by sieving. Replicate samples were taken biweekly during May, June, July, and August. For all taxa, except one, no significant differences in densities were observed inside the screenless cage versus outside. Densities inside the screened cage were significantly higher than outside for all taxa except one.

These experiments demonstrate and reconfirm that predators play an important role in regulating foraminiferal densities.

INTRODUCTION

In 1976 and 1977 experiments using screened cages and a nearby outside control area were carried out at Link Port, Florida (Buzas, 1978). The cages consisted of polyvinyl chloride (PVC) trash cans with openings cut into the sides, permitting the fastening of 1 mm mesh nylon screens around them. Each year in February a screened cage was placed in an excavation so that the 30 L of sterile sand placed inside the cage was essentially level with the surrounding substrate. Each year the cage and a nearby control area were sampled for foraminifera in replicate during March, April, May, and June. The results for both years showed that significantly higher densities occurred inside the cages. Although densities remained higher inside the cages than in the control area, each year in May and June they decreased. Observations of gut contents from macrofaunal organisms which had gotten inside the cage and from other macrofaunal organisms in the Indian River, Florida, indicated that a variety of deposit feeders ingest foraminifera (Buzas and Carle, 1979). Consequently, the significantly higher densities inside the cages were attributed to lack of predation, and the decrease in densities during May and June to predation by organisms which had gotten into the cages as larvae, and to unmeasured other variables influencing overall periodicity in the Indian River.

Two aspects of the experiments, however, were

bothersome. Perhaps the foraminifera entered the cage and multiplied rapidly on the sterile substrate until resources (food? space?) were exhausted, after which densities decreased, or the cage itself provided some sort of favorable but unforeseen environment suitable for the maintenance of large foraminiferal populations.

To investigate these possibilities and replicate the original experiments at different seasons, two sets of simultaneous experiments were carried out in 1978 and 1979. Each year one cage with a screen and one without a screen were implanted as before. In the first year 30 L of sterile sand was added to each cage, and in the second year sediment from which the macrofauna was removed by sieving was added. In both years, samples were taken in replicate during the course of the experiments from each cage and a nearby uncaged control area. The results of these experiments are reported herein.

METHODS

Two identical cages were constructed by cutting large windows into the sides of large (166 L) PVC trash cans (see Buzas, 1978, for details of construction). On 19 June 1978, the cages were placed on the bottom at a depth of about 1 m at Link Port, Florida. Around one cage replaceable nylon screen with a 1 mm mesh was fastened (screened cage). The second cage was left open (screenless cage). Into each, 30 L of sand, sterilized by alternate freezing and drying, was added. To prevent fouling, the screen was changed twice a week. On 18 July, 17 August, 20 September, 18 October and 14 November, four replicate samples of 5 ml each were taken from the screened cage, screenless cage and a nearby uncaged control area. The cages were removed on 15 November and the sand sieved for macrofaunal organisms.

On 7 May 1979 the same two cages were placed into approximately the same area. For each cage, 30 L of nearby sediment was sieved to retain particles larger than 28 μm and smaller than 1 mm. About 6 L of sediment outside of this size range was discarded and sterile sand was added to bring the volume up to 30 L. The screened cage, screenless cage, and outside control area were sampled with 4 replicates of 5 ml each on 8 May, 21 May, 4 June, 18 June, 2 July, 16 July, 30 July, and 13 August. The cages were removed on 13 August and their sediment was sieved for macrofaunal organisms.

Each foraminiferal replicate was washed over a 63 μm sieve upon return to the laboratory, stored in 95% ethanol, stained with rose Bengal, dried, floated with bromoform-acetone, rewetted, and placed in petri dishes for enumeration.

To enumerate macrofaunal animals present at the end of the experiments, all the sediment in the cages was sieved over a 1 mm sieve. Sediment and animals larger than 1 mm were treated with 15% propylene phenoxytol in seawater, fixed with 5–10% formalin, and stored in 75% ethanol with rose Bengal.

Estimates of wet-weight biomass of foraminifera were calculated using the procedures given by Saidova (1967), Murray (1968), Wefer and Lutze (1976), and Buzas (1978).

RESULTS

As in previous experiments (Buzas, 1978), the experimental design anticipated evaluation of the data by a two-way analysis of variance with interaction. All observations (counts) were transformed to $ln(x + 1)$ to normalize the data and stabilize the variances. The hypotheses considered are: an overall difference in densities inside versus outside; an overall difference in densities with time; interaction (changes in density with time are different inside versus outside).

Because of the difficulty involved in identifying some of the species, only *Ammonia beccarii* (Linné) was identified to species. The group called miliolids consists mainly of *Quinqueloculina impressa* (Reuss) and to a lesser extent of *Q. seminula* (Linné). The *Elphidium* group is made up of *E. mexicanum* (Kornfeld), *E. gunteri* (Cole) and *Haynesina germanica* (Ehrenberg).

Table 1 records the analyses of the 1978 experiment using sterile sand inside the screened cage. All hypotheses except inside versus outside for *Elphidium* were significant. The *Elphidium* group accounts for less than 5% of the total living population. The grand mean inside for total living foraminifera was 1,485.20 and outside 293.30. Most of these were miliolids that had a grand mean of 1,298.80 inside and 201.65 outside. *Ammonia beccarii* had a grand mean of 83.94 inside and 33.15 outside. The *Elphidium* group had a grand mean of 18.70 inside and 16.05 outside. Figure 1 shows that the total living foraminifera inside the cage were often an order of magnitude higher than outside in the control area. The decrease in density outside from July to August while densities were increasing inside probably accounts for the significance of the interaction hypothesis.

Table 2 records the analyses of the 1978 experiment using sterile sand inside the screenless cage. All the hypotheses considered were significant. As Fig. 1

TABLE 1

Two-way analysis of variance of screened cage vs outside control, 1978.

Taxa	Effect	Sum of squares	df	Mean square	F	P (F)
Ammonia beccarii	time	22.52	4	5.63	12.72	.00
	in vs out	7.59	1	7.59	17.15	.00
	interaction	9.10	4	2.28	5.14	.00
	residual	13.27	30	.44		
Miliolids	time	26.66	4	6.67	17.22	.00
	in vs out	21.09	1	21.09	54.45	.00
	interaction	12.51	4	3.13	8.07	.00
	residual	11.62	30	3.39		
Elphidium	time	10.36	4	2.59	5.72	.00
	in vs out	1.15	1	1.15	2.54	.12
	interaction	6.29	4	1.57	3.46	.02
	residual	12.61	30	.45		
Total living foraminifera	time	13.83	4	3.46	9.88	.00
	in vs out	18.15	1	18.15	51.85	.00
	interaction	10.26	4	2.57	7.33	.00
	residual	10.50	30	.35		

TABLE 2

Two-way analysis of variance of screenless cage vs outside control, 1978.

Taxa	Effect	Sum of squares	df	Mean square	F	P (F)
Ammonia beccarii	time	19.52	4	4.88	12.67	.00
	in vs out	11.39	1	11.39	29.55	.00
	interaction	11.45	4	2.86	7.43	.00
	residual	11.56	30	.39		
Miliolids	time	25.73	4	6.43	19.90	.00
	in vs out	14.19	1	14.19	43.90	.00
	interaction	10.56	4	2.65	8.18	.00
	residual	9.70	30	.32		
Elphidium	time	12.99	4	3.25	11.76	.00
	in vs out	11.90	1	11.90	43.09	.00
	interaction	6.38	4	1.59	5.77	.00
	residual	8.29	30	.28		
Total living foraminifera	time	19.62	4	4.91	14.62	.00
	in vs out	13.35	1	13.35	39.76	.00
	interaction	12.05	4	3.01	8.98	.00
	residual	10.07	30	.34		

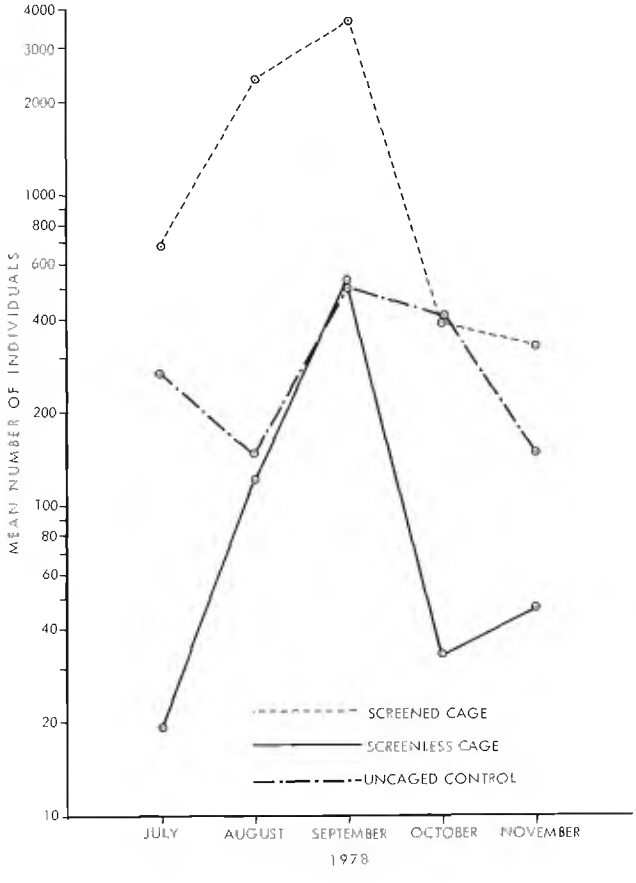

FIGURE 1

Total living foraminifera in 5 ml of sediment at Link Port, Florida.

shows, however, the densities inside the screenless cage were generally lower than in the control area. The grand mean for the total living population was 149.45 inside and 293.30 outside. Again, the miliolids accounted for most of these with a grand mean of 104.25 inside and 201.65 outside. *Ammonia beccarii* had a grand mean of 12.70 inside and 33.15 outside. The *Elphidium* group had a grand mean of 6.85 inside and 16.05 outside. Figure 1 shows densities inside the screenless cage were always an order of magnitude lower than inside the screened cage.

Table 3 records the analyses of the 1979 experiment using sieved sediment inside the screened cage. In 1979, sampling times were every other week instead of once a month and sampling was begun a day after implacement rather than a month after. This was done because the experiments began with a live meiofauna. All hypotheses considered were significant except in versus out and interaction for *Elphidium*. The total living population had a grand mean of 455.69 inside and 92.81 outside. The miliolids had a grand mean of 318.15 inside and 52.56 outside. *Ammonia beccarii* had a grand mean of 73.00 inside and 16.53 outside. The *Elphidium* group had a mean of 25.88 inside and 22.19 outside. Figure 2 shows densities inside the screened cage were always much higher than outside. Densities inside and outside were generally lower than in 1978.

Table 4 records the analyses of the 1979 experiment using sieved sediment inside the screenless cage. The

TABLE 3

Two-way analysis of variance of screened cage vs outside control, 1979.

Taxa	Effect	Sum of squares	df	Mean square	F	P (F)
Ammonia beccarii	time	11.59	7	1.66	5.78	.00
	in vs out	20.79	1	20.79	72.62	.00
	interaction	11.65	7	1.66	5.81	.00
	residual	13.74	48	.29		
Miliolids	time	22.21	7	3.17	14.81	.00
	in vs out	38.62	1	38.62	180.30	.00
	interaction	11.82	7	1.69	7.88	.00
	residual	10.28	48	.21		
Elphidium	time	21.60	7	3.09	17.55	.00
	in vs out	.20	1	.20	1.15	.29
	interaction	2.36	7	.34	1.92	.09
	residual	8.44	48	.18		
Total living foraminifera	time	18.92	7	2.70	17.48	.00
	in vs out	25.87	1	25.87	167.24	.00
	interaction	7.52	7	1.07	6.94	.00
	residual	7.43	48	.15		

TABLE 4

Two-way analysis of variance of screenless cage vs outside control, 1979.

Taxa	Effect	Sum of squares	df	Mean square	F	P (F)
Ammonia beccarii	time	5.35	7	.76	1.69	.13
	in vs out	.24	1	.24	.54	.47
	interaction	6.77	7	.97	2.14	.06
	residual	21.66	48	.45		
Miliolids	time	29.44	7	4.21	16.03	.00
	in vs out	1.78	1	1.78	6.08	.02
	interaction	5.03	7	.72	2.74	.02
	residual	12.59	48	.26		
Elphidium	time	26.67	7	3.18	17.00	.00
	in vs out	.08	1	.08	.35	.56
	interaction	3.88	7	.55	2.47	.03
	residual	10.76	48	.22		
Total living foraminifera	time	15.67	7	2.24	12.96	.00
	in vs out	.30	1	.30	1.73	.19
	interaction	5.00	7	.71	4.14	.00
	residual	8.29	48	.17		

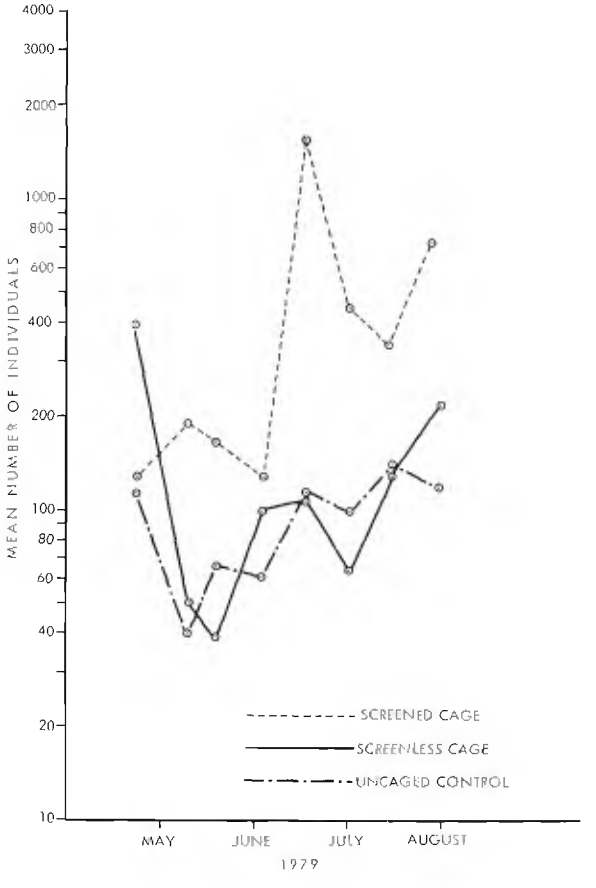

FIGURE 2

Total living foraminifera in 5 ml of sediment at Link Port, Florida.

hypothesis for time is significant for all groups except *Ammonia beccarii*. The in versus out hypothesis is significant only for the miliolids. The grand mean for the total living population was 134.97 inside and 92.81 outside. For the miliolids the grand mean inside was 92.64 and outside 52.66. *Ammonia beccarii* had a grand mean of 18.29 inside and 16.53 outside. The *Elphidium* group had a grand mean of 22.54 inside and 22.19 outside.

After five months on the bottom, on 14 November 1978 the cages were removed and all organisms larger than 1 mm were enumerated. In all, 5,000 macrofaunal organisms were recorded in the screened cage; of these, over 4,000 were polychaetes. The screenless cage contained only 155 macrofaunal organisms.

After three and one-half months on the bottom, the 1979 experiment cages were removed on 13 August and macrofaunal organisms were enumerated. In the screened cage 343 macrofaunal organisms were counted and in the screenless cage 242.

DISCUSSION

Numerous researchers have demonstrated that a wide variety of organisms ingest foraminifera (Hurst, 1965; Lipps and Valentine, 1970; Lipps and Ronan, 1974; Burn and Bell, 1974; Shonman and Nybakken, 1978; Buzas and Carle, 1979). While the list of organisms ingesting foraminifera continually grows, we still know very little of how important the foraminifera are

as a food source and how much of their density regulation can be attributed to predation.

The experiments I conducted in 1976 and 1977 demonstrated that foraminiferal densities were much higher in the absence of predators. The experiments conducted in 1978 and 1979 were designed to investigate whether or not these observations might be influenced to some degree by the effects of sterile sediment or the cages themselves. At the same time, these experiments permitted replication of the earlier experiments at different times of the year.

In 1978 and 1979, except for the *Elphidium* group, densities were significantly higher inside screened cages than in the outside control area (Tables 1, 3). These experiments substantiate the results obtained from experiments conducted from February until June in 1976 and 1977. The 1978 experiment was conducted from June until November, and the 1979 experiment from May until August. The experiments of 1976, 1977, and 1978 had monthly sampling, while the 1979 experiment was sampled fortnightly. Regardless of sampling frequency, time of year, or year, the results are remarkably similar; when protected from predation, foraminiferal densities soar.

The results of the experiments using screenless cages indicate that cages (the structure itself) and sediment type have either a deleterious or no effect. In 1978, densities were significantly lower inside the screenless cage with sterile sediment than in the outside control area (Table 2). In 1979, except for the miliolids, there were no significant differences in densities inside the screenless cage with sieved sediment and in the outside control area (Table 4). Screenless cages are evidently frequented by predators who keep the foraminiferal population as low as or lower than in the outside control area.

Fewer macrofaunal organisms were enumerated inside screenless cages than inside screened cages at the end of the experiments. Predators visiting screenless cages evidently reduce the macrofaunal population, especially polychaetes, as well. The large difference in the number of macrofaunal organisms, mostly polychaetes, recorded inside screened cages between 1978 and 1979 is probably due to the different times of implacement (Young and others, 1976). The very large number of polychaetes, over 4,000, observed inside the screened cage in 1978 also indicates that these polychaetes, mostly *Polydora* sp. and capitellids, do not greatly regulate foraminiferal densities. Buzas and Carle (1979) list a variety of deposit feeders which ingest foraminifera.

In the 1978 and 1979 experiments the hypothesis for interaction was significant for almost all analyses. In the 1976 and 1977 experiments this was not so. In 1978, as Fig. 1 shows, there was a decrease in density outside from July to August while densities were increasing inside the cages. This probably accounts for the significance of the interaction hypothesis. In 1976 and 1977, densities were simultaneously increasing inside and outside of the cages at the outset of the experiment. The pattern for the 1979 experiments is not so clear (Fig. 2). The first sampling times are difficult to interpret because the sediment within the cages was disturbed by the sieving procedure. Had samples been taken monthly instead of biweekly, the 3rd, 5th and 7th means would have been recorded, and the data would not be so dissimilar.

The hypothesis for overall difference in densities with time was significant for almost all the analyses made over the four years the experiments were conducted. This is not surprising because many studies have shown that foraminiferal densities exhibit periodicities over relatively short periods of time (for example, Buzas, 1965, 1969; Boltovskoy and Lena, 1969; Wefer, 1976; Buzas and others, 1977). The experiments conducted at Link Port demonstrate the importance of predation on regulating species densities, but do not prove that predation alone is responsible for the observed periodicities. The interplay of abiotic and biotic variables makes the relative importance of each difficult to evaluate (Buzas, 1969; Buzas and others, 1977). Most likely, abiotic and biotic variables acting in concert are responsible for the observed periodicities.

The difference in wet-weight biomass (excluding the weight of tests) between screened cages and outside control areas was calculated at times of maximum foraminiferal densities inside the cages. In 1976 this amounted to about 12 g/m^2, in 1977 about 5 g/m^2, in 1978 about 39 g/m^2, and in 1979 about 17 g/m^2. If even a portion of this biomass is utilized as food, then the foraminifera are an important food source. These results support other recent studies (Barber and De Groot, 1973; Sibert and others, 1977; Bell and Coull, 1978) indicating that meiofaunal densities are regulated by predation.

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