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EXPERIMENTS ON PREDATION, SUBSTRATE PREFERENCE, AND COLONIZATION OF BENTHIC FORAMINIFERA AT THE SHELFBREAK OFF THE FT. PIERCE INLET, FLORIDA

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ABSTRACT

Two sets of sediment-filled boxes were placed at a depth of 125 m off the Ft. Pierce Inlet, Florida, on 3 June 1980. Each set contained an uncovered box of mud, an uncovered box of sand, a screened box of mud and a screened box of sand. One set was retrieved on 14 July 1980, the other on 1 October 1980. Sediments from the natural environment were also sampled at these recovery times.

Densities of 14 species of benthic foraminifera were analyzed by two-way ANOVA's. For most species, densities were highest in screened boxes, indicating that predation significantly reduces foraminiferal densities in the uncovered boxes. After six weeks the uncovered box of mud had densities comparable to the natural environment. The uncovered sand-filled boxes had very low densities (poor colonization), causing us to suggest that some mud is necessary to maintain foraminiferal populations. Analysis of the screened boxes retrieved on 1 October 1980 indicates that there was no significant difference between mud and sand substrates for any of the species. This suggests that once colonization had taken place, particle size was not an important influence.

INTRODUCTION

The importance of foraminifera in the food web of benthic marine communities is poorly understood. The ingestion of foraminifera by a wide variety of organisms has been noted by many authors (Buzas, 1978, 1982; Buzas and Carle, 1979; Arnold and others, 1985). One way to evaluate the importance of predators in regulating foraminiferal densities is through predator exclusion experiments, such as those of Buzas (1978, 1982). Buzas showed that foraminiferal densities were significantly higher inside cages with 1-mm mesh screens, which prevented macrofaunal predators from entering the cages. These experiments were conducted in very shallow (1-m depth) water, however, and conducting exclusion experiments in deeper water is much more difficult.

We were given the opportunity to "piggy back" on a macrofaunal experiment called "Wagon Wheels," conducted by R. Virnstein for the Harbor Branch Oceanographic Institution and located off the Ft. Pierce Inlet, Florida, at a depth of 125 m. The experiment allowed us to examine: 1) the effects of open vs screened boxes; 2) the effect of a sand vs mud substrate; 3) the speed of colonization.

METHODS

Each of two "Wagon Wheel" arrays consisted of a circular arrangement of nine boxes attached to a frame bearing vertical struts to facilitate retrieval. The array was designed so that the boxes were open only when on the sea floor. Because the macrofaunal experiment used screens with 4-mm openings, an additional container for the microfaunal experiment (14 × 14 × 10 cm), covered with a screen bearing 1-mm openings, was attached to each "Wagon Wheel" array.

Pure quartz sand was obtained from a deposit near Link Port, Florida, and mud was obtained from the natural environment at the experiment site. The mud was "sterilized" by alternate freezing and drying. For the foraminiferal experiment, each "Wagon Wheel" contained one open sand-filled box, one screened sand-filled box, one open mud-filled box, and one screened mud-filled box.

The "Wagon Wheels" were placed on the bottom (27°28.8′N, and 79°56.6′W, 125 m depth) on 3 June 1980 (Fig. 1). With the aid of a manned submersible, the first "Wagon Wheel" was retrieved on 14 July 1980, the second on 1 October 1980. At each of these times, sediment samples were obtained from the natural environment. All samples (in the statistical sense) consisted of four replicates, taken by inserting 3.5-cm core liners, plugging the top and removing them. Buffered formalin was added aboard ship.

Immediately upon returning to the laboratory, the top 10 ml of sediment were removed, washed over a 63-μm sieve and preserved in 95% ETOH. Rose Bengal was added the day before the samples were prepared for picking. The samples were picked over a period of about six years; all were picked while wet, so that the stained protoplasm could be clearly seen. All stained specimens were mounted on faunal slides and identified using the collection of the National Museum of Natural History, Washington, D.C. The experiment was designed so that the observations could be analyzed by a two-way analysis of variance with interaction.

RESULTS

At each of the two sampling times four replicates were taken from each of the four boxes and the natural environment giving us 16 observations for the mud-

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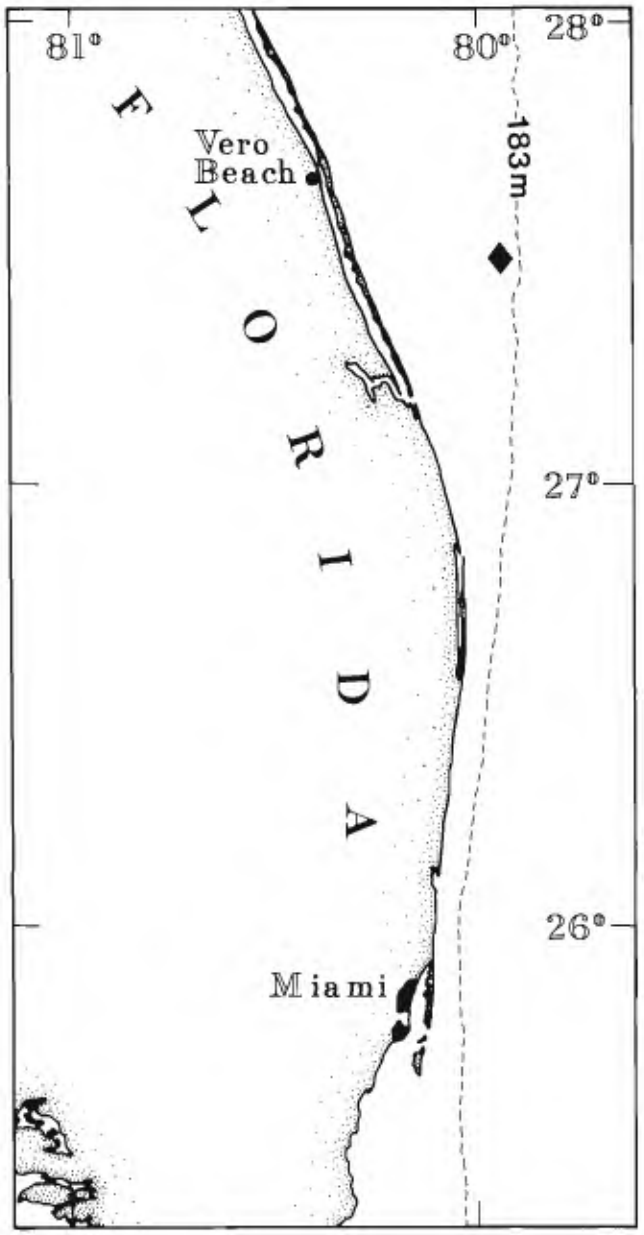

FIGURE 1. Location of "Wagon Wheel" experiment.

filled boxes, 16 for the sand-filled ones and eight for the natural environment. The species diversity in this area is relatively high, but only 14 species were abundant enough to warrant statistical analysis (counts are in Appendices 1–5).

Table 1 shows the mean number of individuals per 10 ml for these species in the mud-filled boxes. Table 2 records the same observations for the sand boxes. Before statistical analyses, the data were transformed to log (x + 1) to normalize the distribution and avoid the problem of "0's."

Two-way analyses of variance were run for each species from the mud-filled boxes, and sand-filled boxes. The model chosen was: density = constant + time + screened vs open + interaction. The hypothesis "time" tests whether or not there is a difference between time 1 and time 2. The hypothesis "screened vs open" tests whether or not there is a difference between boxes covered by a screen and those left open. The hypothesis "interaction" contrasts time 1 (open) and time 2 (screened) against time 1 (screened) and time 2 (open). Because of the experimental design (equal number of replicates), each of these hypotheses is orthogonal or independent.

TABLE 1. Mean number of individuals per 10 ml in the mud-filled boxes.

Species	Time 1 14 July 1980		Time 2 1 October 1980	
	Open	Screened	Open	Screened
Bigenerina irregularis	2.00	4.25	0.50	2.50
Bolivina fragilis	7.25	10.50	10.75	13.25
Bolivina paula	3.50	2.75	10.50	8.25
Bulimina marginata	0.50	2.75	1.75	11.00
Cassidulina carinata	0.75	2.50	3.00	53.75
Cassidulina subglobosa	1.50	3.75	8.50	49.25
Eggerella advena	3.75	12.25	0.75	18.25
Goesella mississippiensis	5.25	8.75	4.00	10.75
Nonionella atlantica	3.25	2.00	2.50	0.75
Nonionella opima	18.75	15.50	12.50	7.25
Rosalina floridana	1.25	5.75	0.50	0.75
Siphotextularia affinis	3.00	8.50	1.50	10.50
Trifarina angulosa	1.00	1.75	14.00	6.00
Uvigerina peregrina	0	2.00	1.00	18.75

Because there are so many ANOVA's, we do not present the traditional ANOVA tables. Instead, we show only the probabilities of the F-ratios for the hypotheses. Table 3 shows these probabilities for the mud-filled boxes. Those hypotheses with a probability of 0.05 or less are considered significant, and are underlined. Table 4 shows the probabilities for the sand-filled boxes.

The data in Table 2 indicate that at time 1, relatively few foraminifera occupied the sand-filled boxes. Consequently, in comparing the mud-filled with the sand-filled boxes we considered only time 2. This analysis also avoids the potential difficulty posed by the fact that the same boxes could not be sampled at times 1 and 2. The model chosen was density = constant +

TABLE 2. Mean number of individuals per 10 ml in sand-filled boxes.

Species	Time 1 14 July 1980		Time 2 1 October 1980	
	Open	Screened	Open	Screened
Bigenerina irregularis	0	1.00	0.25	4.50
Bolivina fragilis	1.50	1.50	1.50	10.75
Bolivina paula	0	0.25	1.25	5.00
Bulimina marginata	0	0.75	0.75	6.25
Cassidulina carinata	1.50	6.00	0.50	53.75
Cassidulina subglobosa	0.75	3.25	2.25	87.75
Eggerella advena	0.25	1.75	0	13.50
Goesella mississippiensis	0.25	0.75	0.25	3.00
Nonionella atlantica	0	0.25	0	0.25
Nonionella opima	0	0.75	1.50	4.75
Rosalina floridana	0.50	2.75	0.25	3.25
Siphotextularia affinis	0.75	21.50	0.25	4.00
Trifarina angulosa	0	0.50	0.25	7.25
Uvigerina peregrina	0.25	0	0.50	12.75

TABLE 3. Probabilities of F-ratios for two-way ANOVA's for mud-filled boxes. Significant (.05) hypotheses are underlined.

Species	Time	Open vs screened	Interaction
Bigenerina irregularis	.071	.092	.673
Bolivina fragilis	.211	.274	.959
Bolivina paula	.016	.388	.923
Bulimina marginata	.062	.036	.348
Cassidulina carinata	.001	.001	.009
Cassidulina subglobosa	.002	.020	.120
Eggerella advena	.262	.000	.040
Goesella mississippiensis	.675	.047	.280
Nonionella atlantica	.354	.082	.936
Nonionella opima	.406	.934	.616
Rosalina floridana	.001	.092	.092
Siphotextularia affinis	.624	.005	.324
Trifarina angulosa	.002	.717	.132
Uvigerina peregrina	.042	.006	.421

TABLE 4. Probabilities of F-ratios for two-way ANOVA's for sand-filled boxes. Significant (.05) hypotheses are underlined.

Species	Time	Open vs screened	Interaction
Bigenerina irregularis	.012	.000	.061
Bolivina fragilis	.014	.031	.022
Bolivina paula	.000	.002	.012
Bulimina marginata	.001	.002	.073
Cassidulina carinata	.025	.000	.003
Cassidulina subglobosa	.000	.000	.000
Eggerella advena	.009	.000	.003
Goesella mississippiensis	.196	.035	.196
Nonionella opima	.005	.026	.378
Rosalina floridana	.640	.013	.874
Siphotextularia affinis	.007	.000	.038
Trifarina angulosa	.008	.002	.027
Uvigerina peregrina	.000	.000	.000

mud vs sand + screened vs open + interaction. These results are shown in Table 5.

In the mud-filled boxes, six species had significantly different densities between times 1 and 2 (Table 3). Table 1 shows the nature of these differences. *Bolivina paula* had higher densities at time 2 in both the screened and open boxes. *Cassidulina carinata* and *C. subglobosa* had an order of magnitude higher densities at time 2 in the screened box. *Trifarina angulosa* had its highest density at time 2, and *Uvigerina peregrina* was abundant in the screened box at time 2. In contrast, *Rosalina floridana* had its highest density at time 1.

In the mud experiment, seven species had significant differences between screened and open boxes (Table 3). Three of these had their greatest densities in the screened box at time 2, giving a significant F-ratio for time as noted above. Another of the seven species, *Bulimina marginata,* also had its highest densities in the screened box at time 2. Although the hypothesis for time was not significant, it was nearly so, supporting the data of Table 1. The remaining species, *Eggerella advena, Goesella mississippiensis* and *Siphotextularia affinis,* all had their highest densities in screened boxes at both times 1 and 2.

For the mud experiment only two species have a significant interaction F-ratio (Table 3). Table 1 does not show why this is so. Other species with no significant interaction F-ratio appear to have a similar pattern. For example, whereas *Cassidulina carinata* and *C. subglobosa* exhibit similar patterns, one has a significant interaction F-ratio, and the other does not.

In the sand experiment, all the time hypotheses are significant except for two (Table 4). This is not surprising because the densities were very low at time 1 (Table 2). No analysis was possible for *Nonionella atlantica* because only one individual was found in the screened box at time 1, and one at time 2, resulting in a sum of squares of 0.

All the screened vs open box hypotheses are significant for sand (Table 4). The high densities inside the screened box at time 2 account for this. The only exception is *Siphotextularia affinis,* which has a high density inside the screened box at time 1 (Table 2).

In contrast to the mud experiment, eight hypotheses for interaction are significant for sand. This is so because the interaction contrasts time 1 (open) and time 2 (screened) against time 1 (screened) and time 2 (open). Because time 1 (screened) and time 2 (open) boxes had such low densities, the interactions are significant.

Six of 14 species have a significant mud vs sand F-ratio (Table 5). For these six species, in all cases, except one, densities were higher in the mud (Tables 1, 2). Nine species showed significant differences between open vs screened (Table 5). Only two of these, *Bolivina fragilis* and *Goesella mississippiensis,* also showed significant differences between sediment types (the highest densities were in mud). For *Cassidulina carinata, C. subglobosa, Eggerella advena* and *Uvigerina peregrina,* the differences of open vs screened were especially large (Tables 1, 2). Three interaction hypotheses were significant, but, as with the mud experiment (Table 3), it is difficult to determine why from examining Tables 1 and 2. All five species showing no significant differences between open and screened boxes did likewise in the mud experiment (Table 3).

DISCUSSION

The results of our study at a depth of 125 m parallel, in some ways, those conducted previously in the shallow water of the Indian River, Florida (Buzas, 1978, 1982). Overall densities increase significantly when the foraminifera are protected from predators. In the shallow-water experiments, the densities were one to two orders of magnitude larger, but species diversity was much lower than in the offshore site. Gut contents of macrofaunal animals in the Indian River indicated that decapods, shrimp, gastropods, bivalves, polychaetes and fish ingest foraminifera (Buzas and Carle, 1979). Any deposit feeder would have difficulty not ingesting

TABLE 5. Probabilities of F-ratios for two-way ANOVA's for time 2, 1 October 1980. Significant (.05) hypotheses are underlined.

Species	Mud vs sand	Open vs screen	Interaction
Bigenerina irregularis	.402	.002	.153
Bolivina fragilis	.002	.002	.012
Bolivina paula	.004	.182	.029
Bulimina marginata	.406	.003	.916
Cassidulina carinata	.247	.000	.297
Cassidulina subglobosa	.791	.000	.099
Eggerella advena	.381	.000	.816
Goesella mississippiensis	.010	.011	.856
Nonionella atlantica	.019	.125	.348
Nonionella opima	.019	.333	.135
Rosalina floridana	.444	.214	.214
Siphotextularia affinis	.084	.003	.505
Trifarina angulosa	.005	.156	.005
Uvigerina peregrina	.879	.001	.659

TABLE 6. Mean number of individuals per 10 ml in the natural habitat.

Species	14 July 1980	1 October 1980
Bigenerina irregularis	1.75	1.75
Bolivina fragilis	1.75	1.25
Bolivina paula	1.00	4.00
Bulimina marginata	1.50	1.00
Cassidulina carinata	0	0.50
Cassidulina subglobosa	0.75	4.50
Eggerella advena	2.75	0.50
Goesella mississippiensis	5.50	1.00
Nonionella atlantica	1.25	1.00
Nonionella opima	35.00	17.75
Rosalina floridana	1.00	3.50
Siphotextularia affinis	1.00	0.25
Trifarina angulosa	1.50	1.50
Uvigerina peregrina	0	0.50

foraminifera. Indeed, they may even be ingested secondarily. Williamson (1858) recorded a single species of *Elphidium* in the gut contents of a shelldrake (a feathered biped, his term) which had ingested a crustacean believed to be feeding on the foraminifera. Unfortunately, the macrofaunal phase of the "Wagon Wheel" experiment was terminated, and we have no data about potential predators at the offshore site.

In the shallow-water studies, the rank order of abundance in a control area and inside the screened cage remained the same. In the offshore study, this is not true. Table 6 gives the densities of the 14 species from a control area near the "Wagon Wheels" at sampling times 1 and 2. *Nonionella opima* is the numerically dominant species, as it is in the open mud-filled boxes. At time 2 the two species of *Cassidulina* dominate the screened-sand and mud-filled boxes. *Nonionella* does not appear to derive any advantage from living in a screened box. A similar situation developed with *Elphidium* in the shallow-water experiments of Buzas. In his 1978 and 1979 experiments there was no significant difference between open and screened, but in 1976 and 1977 there was. Unfortunately, because of the cost, we will probably not be able to repeat the "Wagon Wheels" experiment.

A spin-off of the exclosure study is that we can use the open boxes as a colonization study. Ellison and Peck (1983) performed such an experiment at a depth of 60 m off New Jersey. They found that within 10 weeks, the foraminiferal community inside the boxes was the same as the natural community, although densities were greater in the boxes. Our first recovery took place six weeks after deployment. The assemblage in the open mud-filled box, and in the natural environment is the same. The mean density for the total living population is 96.00 in the natural habitat and 95.25 in the mud-filled box. The sand-filled box clearly did not support as abundant a population. The mean density for the total living population was only 18.00, and the numerically dominant species of the natural environment, *Nonionella opima,* was not present. The second set of boxes was recovered 13 weeks after deployment. Once again, the species composition of the natural environment and the mud-filled box was similar. The total living mean density in the natural setting was 115.50, whereas in the open mud-filled box, it was 173.75. A one-way ANOVA indicated that there is a significantly higher density in the box, corroborating the results obtained by Ellison and Peck (1983). Again the total live mean density for the open sand-filled box was low, only 22.00.

Studies on the effects of substrate on foraminifera are numerous, but controversial; summaries are given by Phleger (1960), Boltovskoy and Wright (1976), Sen Gupta (1982) and Culver (1987). Here we are concerned only with the effects of mud vs sand. At time 1 the mud-filled boxes were well-occupied while the sand-filled boxes had few occupants. At time 2, the open sand-filled box still had relatively few individuals. The significant difference between mud- and sand-filled boxes at time 2 for six species (Table 5) is due to the low densities in the open sand-filled box (Tables 1, 2). We calculated one-way ANOVA's for species densities in the screened mud-filled box, and the screened sand-filled box for time 2. No significant differences were found for any of the species.

The low densities in the open sand-filled boxes might be produced if foraminiferal predators preferred sand, but it may also be due to the lack of mud. The relationship between organic matter and mud is well known (Trask, 1939), and some organic matter must be present to provide a food source, either directly or indirectly. While sampling at time 2, one of us (K.P.S.) noted a small amount of mud on the surface of the screened sand-filled box. Evidently, the screened sand-filled box acted as a sediment trap. Parker (1952), Phleger (1960), Buzas (1965) and Akpati (1975) compared the distribution and densities of species from areas in close proximity to one another with different particle sizes. In general, they found no relationship between these properties, but Buzas (1965) pointed out that

where silt-clay was less than 2% by weight, there were no foraminifera. Consequently, we believe that the high densities in the screened sand-filled box at time 2 are due to lack of predation as well as the addition of some mud. We did not, however, measure the amount of mud or the organic content.

CONCLUSIONS

1. Predation limits benthic foraminiferal densities at the shelfbreak (125 m depth) off the Ft. Pierce Inlet, Florida.

2. Providing a small amount of mud (organic matter) is present, particle size is not important in determining foraminiferal species composition or densities.

3. Within six weeks after deployment, colonization (in the open mud-filled box) was complete, with densities comparable to the natural environment.

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APPENDIX 1

NUMBER OF INDIVIDUALS IN MUD REPLICATES 14 JULY 1980

Species	Open				Screened			
	1	2	3	4	1	2	3	4
Bigenerina irregularis	2	2	1	3	2	7	7	1
Bolivina fragilis	7	6	8	8	9	14	15	4
Bolivina paula	1	3	4	6	5	5	0	1
Bulimina marginata	1	1	0	0	1	1	9	0
Cassidulina carinata	0	1	0	2	7	3	0	0
Cassidulina subglobosa	2	2	2	0	8	5	2	0
Eggerella advena	4	2	5	4	14	25	7	3
Goesella mississippiensis	5	7	7	2	8	18	5	4
Nonionella atlantica	4	4	2	3	0	4	4	0
Nonionella opima	26	21	0	28	19	19	17	7
Rosalina floridana	1	1	3	0	3	7	11	2
Siphotextularia affinis	0	4	3	5	6	18	7	3
Trifarina angulosa	4	0	0	0	1	3	3	0
Uvigerina peregrina	0	0	0	0	2	3	2	1

APPENDIX 2

NUMBER OF INDIVIDUALS IN MUD REPLICATES 1 OCTOBER 1980

Species	Open				Screened			
	1	2	3	4	1	2	3	4
Bigenerina irregularis	0	1	1	0	4	0	5	1
Bolivina fragilis	7	6	18	12	16	12	18	7
Bolivina paula	9	18	11	4	15	9	7	2
Bulimina marginata	1	0	1	5	17	8	18	1
Cassidulina carinata	3	0	1	8	35	64	82	34
Cassidulina subglobosa	0	9	8	17	49	64	67	17
Eggerella advena	0	0	3	0	37	5	20	11
Goesella mississippiensis	0	10	1	5	20	7	8	8
Nonionella atlantica	2	0	4	5	2	0	0	1
Nonionella opima	5	2	27	16	9	3	9	8
Rosalina floridana	0	1	0	1	0	0	0	3
Siphotextularia affinis	0	1	0	5	12	8	19	3
Trifarina angulosa	9	12	31	4	10	6	6	2
Uvigerina peregrina	1	0	2	1	27	15	33	0

APPENDIX 3

NUMBER OF INDIVIDUALS IN SAND REPLICATES 14 JULY 1980

Species	Open				Screened			
	1	2	3	4	1	2	3	4
Bigenerina irregularis	0	0	0	0	1	0	1	3
Bolivina fragilis	1	1	0	4	0	3	3	0
Bolivina paula	0	0	0	0	0	1	0	0
Bulimina marginata	0	0	0	0	0	1	2	0
Cassidulina carinata	4	0	1	1	3	9	12	0
Cassidulina subglobosa	0	1	1	1	2	5	4	2
Eggerella advena	0	0	0	1	1	1	5	0
Goesella mississippiensis	1	0	0	0	1	0	2	0
Nonionella atlantica	0	0	0	0	0	1	0	0
Nonionella opima	0	0	0	0	1	2	0	0
Rosalina floridana	2	0	0	0	2	4	4	1
Siphotextularia affinis	0	2	0	1	26	11	18	31
Trifarina angulosa	0	0	0	0	0	0	1	1
Uvigerina peregrina	1	0	0	0	0	0	0	0

APPENDIX 4

NUMBER OF INDIVIDUALS IN SAND REPLICATES 1 OCTOBER 1980

Species	Open				Screened			
	1	2	3	4	1	2	3	4
Bigenerina irregularis	0	0	1	0	6	5	2	5
Bolivina fragilis	0	2	2	2	13	5	11	14
Bolivina paula	0	3	1	1	7	3	6	4
Bulimina marginata	1	1	1	0	14	4	3	4
Cassidulina carinata	1	0	1	0	47	66	81	21
Cassidulina subglobosa	0	2	5	2	100	44	89	118
Eggerella advena	0	0	0	0	8	14	6	26
Goesella mississippiensis	1	0	0	0	5	4	0	3
Nonionella atlantica	0	0	0	1	0	0	0	0
Nonionella opima	0	3	3	0	3	5	2	9
Rosalina floridana	0	1	0	0	0	2	1	10
Siphotextularia affinis	0	0	1	0	9	4	0	3
Trifarina angulosa	0	0	0	1	17	1	5	6
Uvigerina peregrina	1	0	1	0	18	7	8	18

APPENDIX 5

NUMBER OF INDIVIDUALS IN REPLICATES FROM THE NATURAL ENVIRONMENT

Species	14 July 1980				1 October 1980			
	1	2	3	4	1	2	3	4
Bigenerina irregularis	3	0	3	1	0	0	4	3
Bolivina fragilis	2	0	4	1	2	0	3	0
Bolivina paula	2	0	1	1	7	1	2	6
Bulimina marginata	2	0	3	1	2	0	1	1
Cassidulina carinata	0	0	0	0	0	0	0	2
Cassidulina subglobosa	0	0	1	2	2	2	5	9
Eggerella advena	3	0	5	3	0	0	2	0
Goesella mississippiensis	13	0	1	8	0	0	3	1
Nonionella atlantica	3	1	1	0	7	11	3	8
Nonionella opima	70	9	28	33	13	16	19	25
Rosalina floridana	0	0	3	1	5	2	5	2
Siphotextularia affinis	1	0	3	0	0	0	1	0
Trifarina angulosa	0	1	2	3	7	3	0	0
Uvigerina peregrina	0	0	0	0	0	0	1	1