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COLONIZATION RATE OF FORAMINIFERA IN THE INDIAN RIVER, FLORIDA

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ABSTRACT

A cage containing azoic sand was placed on the seabed (1 m water depth) at Link Port, Florida on 17 March 1988. Beginning one week after emplacement, four replicate cores were taken inside the cage and outside every week for six weeks. From each of the eight cores 5 ml of sediment was removed from each cm to a depth of three cm. The number of living (stained) individuals for *Quinqueloculina, Ammonia, Elphidium* and *Ammobaculites* were enumerated. These data were analyzed by two-way ANOVA testing for differences between time, cms and their interaction.

Inside, all taxa had significantly lower densities at the first two sampling times and had significantly lower densities in the second and third cms.

Outside, only *Elphidium* had a significant difference with time, the fifth sampling time had lower densities. *Quinqueloculina* had significantly higher densities in the first cm and *Ammobaculites* in the first two cms.

These results indicate that colonization is rapid and occurs in the same rank order as the ambient fauna. Densities stabilize inside within about three weeks after emplacement. The top cm is colonized initially followed by the second and third cms. No density peak was observed after the initial colonization, nor was there any succession of species.

INTRODUCTION

Previous studies have indicated that benthic foraminifera colonize rapidly (Buzas, 1978, 1982; Schafer, 1982, Ellison and Peck, 1983; Buzas and others, 1989). In shallow water (1 m) Buzas (1978, 1982) found densities inside a container originally containing azoic sand were similar to those in the natural environment at the first sampling time which was one month after emplacement. At deeper depths (65 m) on the shelf off New Jersey, Ellison and Peck (1983) found that an azoic substrate was fully colonized by the time of their first observation ten weeks after emplacement. At 125 m off Florida, Buzas and others (1989) found complete colonization of azoic substrate by the time of their first observation six weeks after emplacement.

Clearly, the benthic foraminifera colonize new substrate too rapidly for the earlier sampling plans to track. In an attempt to alleviate this difficulty, the present study evaluates the rate of colonization on a weekly basis. To achieve this goal, a container with azoic sand was placed on the bottom (1 m depth) at Link Port, Florida. The foraminiferal densities were enumerated weekly inside the container and outside in the natural environment over a period of six weeks at one centimeter intervals to a depth of three cm to follow the process of colonization.

METHODS

About 30 liters of sand was dug from a sand pit and placed in a large (166 l) PVC trash can which measured 79 cm from top to bottom. Four windows (35 cm on a side) were cut into the can 15 cm from the bottom. Around these windows, screening with 1 mm openings were fastened with Velcro to exclude any large organisms. To minimize fouling, the screen was changed weekly. In a nearshore area north of the Link Port, Florida jetty (27° 32.1′N; 80° 20.9′W) at a water depth of about 1 m, the can was placed in a 15 cm deep hole dug in the natural environment which consists of 98% sand. The date of emplacement was 17 March 1988. One week thereafter and on each succeeding week for six weeks four cores were inserted and removed from the container. The same procedure was followed outside the can in the natural environment.

In the laboratory, the sediment from each core was extruded a cm at a time by pushing it upward with a pusher (a short broom stick on top of which was fastened a stopper of the same diameter as the core, 3.4 cm). To avoid contamination between cms while using the pusher, 5 ml from the center of each one cm segment (10 ml volume) was removed by means of a calibrated syringe. Each 5 ml sample was washed over a 63 μm sieve and placed in a 90% ethanol solution saturated with rose Bengal. Immediately before examination each sample was floated with sodium polytungstate to concentrate the foraminifera. All samples were enumerated while wet so that the stained protoplasm within the test could be seen easily.

The genera counted were *Quinqueloculina* (mostly *Q. impressa* and some *Q. seminula*), *Elphidium* (mostly *E. mexicanum* and *E. gunteri*), *Ammonia* (*Ammonia beccarii*) and *Ammobaculites* (*A. exiguus*). Illustrations and a taxonomic discussion are given in Buzas and Severin (1982).

The number of individuals (x) for each of the four taxa in each 5 ml sample constitute the data (Appendices 1, 2). There are $i = 1, \ldots, 6$ sampling times (24 Mar, 31 Mar, 7 Apr, 14, Apr, 21 Apr and 28 Apr), $j = 1, 2, 3$ one cm depth intervals and $k = 1, \ldots, 4$ replicates. There are, then, $n = 72$ samples inside the can and 72 outside. Before statistical analysis each count was transformed to $\ln(x_{ijk} + 1)$ to stabilize the variance and make the data more normal. The data were analyzed by a two-way analysis of variance with interaction (Scheffe, 1959). SYSTAT version 5.02 was used for the analyses. The hypotheses tested were for time, cm (depth) and their interaction (time × cm).

RESULTS

The results for the ANOVA on *Quinqueloculina* are presented in Table 1 and the means for the replicates at each sampling time and cm depth are plotted in Figure 1. Inside, the hypothesis for time and cm is significant. Figure 1 sug-

TABLE 1. Two-way analysis of variance, *Quinqueloculina*.

INSIDE

Source	Sum of squares	DF	Mean square	F	p(F)
Time	38.626	5	7.725	6.163	0.000
cm	86.685	2	43.343	34.578	0.000
Time × cm	18.044	10	1.804	1.440	0.189
residual	67.687	54	1.253		

mean cm 1 = 129.92	mean Time 1 = 23.08	mean Time 4 = 82.08
mean cm 2 = 28.04	mean Time 2 = 39.08	mean Time 5 = 54.25
mean cm 3 = 20.50	mean Time 3 = 88.08	mean Time 6 = 70.33

OUTSIDE

Source	Sum of squares	DF	Mean square	F	p(F)
Time	4.356	5	0.871	1.003	0.425
cm	33.858	2	16.929	19.489	0.000
Time × cm	8.555	10	0.855	0.985	0.468
residual	46.907	54	0.869		

mean cm 1 = 119.46	mean Time 1 = 65.58	mean Time 4 = 60.75
mean cm 2 = 49.88	mean Time 2 = 84.00	mean Time 5 = 60.42
mean cm 3 = 31.54	mean Time 3 = 40.25	mean Time 6 = 90.75

gests that at sampling times one and two there were very low densities inside the can. A contrast of sampling times 1 and 2 against the rest indicates a statistically significantly lower density during the first two sampling times. The mean for times 1 and 2 was 31 and for times 3, . . . , 6 74 (Table 1). Figure 1 also indicates much higher means in the first cm than in the second and third. A contrast of cm 1 and 2, 3 also is highly significant. The mean in the first cm is 130 and in cms 2 and 3, 28 and 20, respectively (Table 1). For the natural environment, outside, there is no significant difference with time. There is, however, a significant difference with depth (cm). Figure 1 suggests cm 1 has higher densities than cms 2 and 3, and a contrast indicates that this difference is statistically significant. The mean square for cm in the outside analysis is much smaller than for the inside analysis (Table 1) suggesting smaller differences with depth outside. This is indeed the case (Table 1).

The results for the ANOVA on *Ammonia* are shown in Table 2 and the mean densities are plotted in Figure 2. Inside all three hypotheses are significant. Figure 2 again suggests that the first two sampling times inside had lower densities and a contrast of time 1 and 2 vs the rest is statistically significant. Figure 2 also shows that except for 14 April, mean densities were higher in the first cm. The contrast 1 vs 2 and 3 is statistically significant indicating higher mean densities in cm 1 (Table 2). On 14 April the densities at cm 2 and 3 were greater than at cm 1 and on 21 April the densities greatly decreased at cm 2 and 3 while they increased at cm 1 (Figure 2). This probably accounts for the significance of the interaction hypothesis. Contrasts indicate no significant difference between 14 and 21 April at cm 1, but a significant difference between 14 and 21 April at cms 2 and 3. For the analysis of the outside none of the hypotheses are statistically significant. Although not significant, the mean densities at cm 2 and 3 were, however, higher than in cm 1 (Table 2).

The results for the ANOVA on *Elphidium* are presented in Table 3 and the mean densities with time and cm depth are plotted in Figure 3. Inside the can the hypotheses for time and cm are significant. Figure 3 suggests the first two sampling times had lower densities than the rest and a contrast of times 1 and 2 vs 3, . . . , 6 is significant. Figure 3 also suggests that cm 1 has higher densities than cms 2 and 3, and a contrast indicates that this difference is statistically

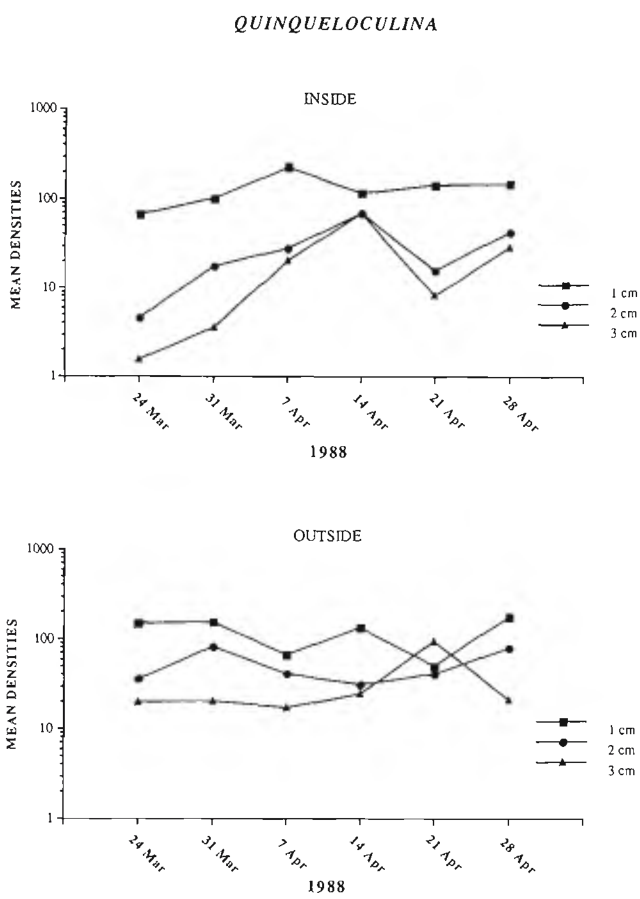

FIGURE 1. Mean (4 replicates) number of living (stained) individuals per 5 ml of sediment.

TABLE 2. Two-way analysis of variance, *Ammonia*.

INSIDE

Source	Sum of squares	DF	Mean square	F	p(F)
Time	35.151	5	7.030	7.759	0.000
cm	59.136	2	29.568	32.634	0.000
Time × cm	23.388	10	2.339	2.581	0.012
residual	48.926	54	0.906		

mean cm 1 = 40.67	mean Time 1 = 7.92	mean Time 4 = 39.75
mean cm 2 = 19.96	mean Time 2 = 12.83	mean Time 5 = 19.42
mean cm 3 = 9.46	mean Time 3 = 29.17	mean Time 6 = 31.08

OUTSIDE

Source	Sum of squares	DF	Mean square	F	p(F)
Time	1.118	5	0.224	0.569	0.724
cm	2.333	2	1.167	2.969	0.060
Time × cm	7.541	10	0.754	1.919	0.062
residual	21.220	54	0.393		

mean cm 1 = 62.38	mean Time 1 = 57.67	mean Time 4 = 82.67
mean cm 2 = 86.79	mean Time 2 = 76.75	mean Time 5 = 68.92
mean cm 3 = 88.54	mean Time 3 = 101.25	mean Time 6 = 88.17

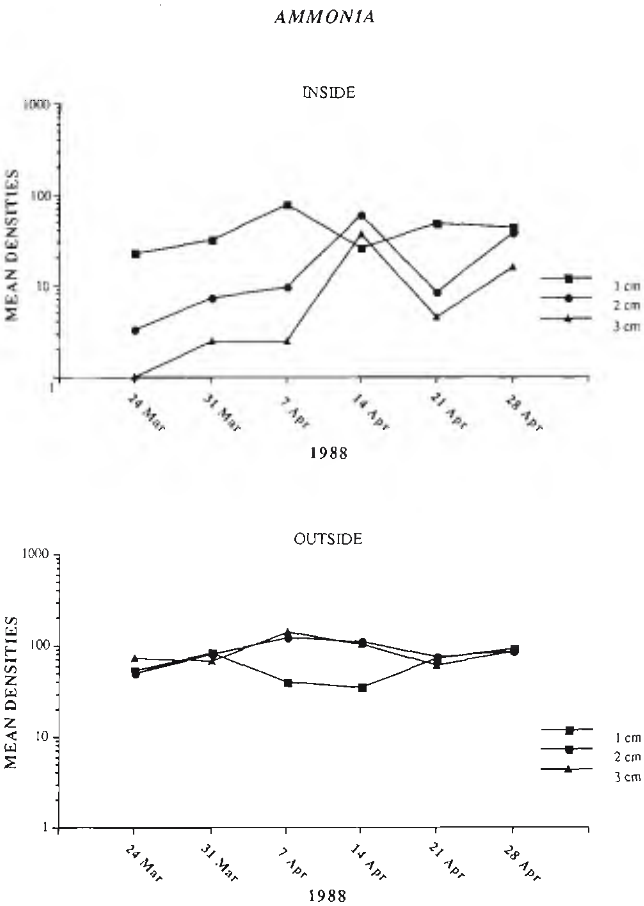

FIGURE 2. Mean (4 replicates) number of living (stained) individuals per 5 ml of sediment.

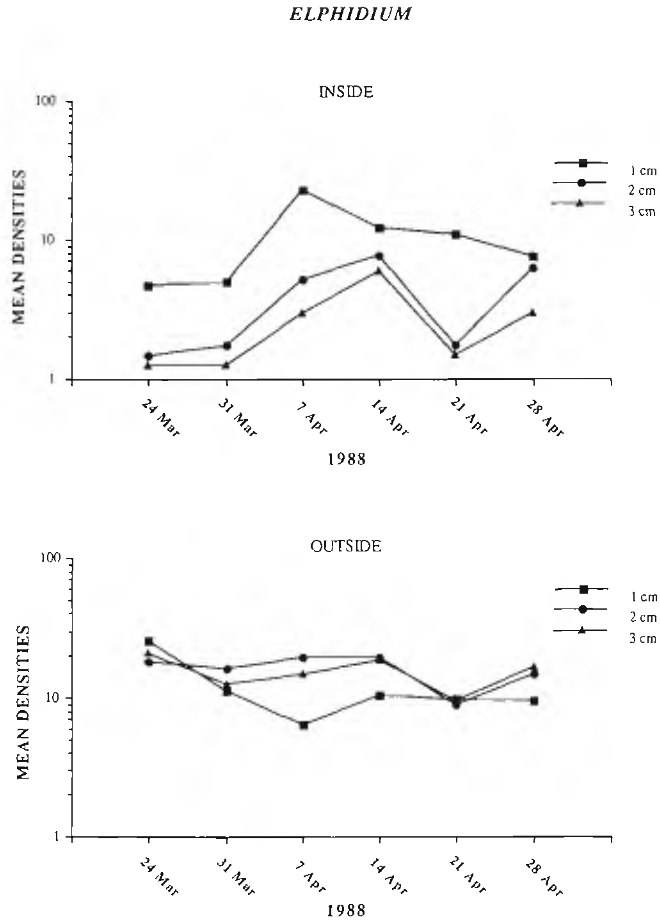

FIGURE 3. Mean (4 replicates) number of living (stained) individuals per 5 ml of sediment.

significant. The mean density in cm 1 is 10 while cms 2 and 3 are 3 and 2, respectively (Table 3). Outside, only the hypothesis for time is significant, and this barely so. Figure 3 suggests that the 5th sampling time (21 April) is a time of

TABLE 3. Two-way analysis of variance, *Elphidium*.

INSIDE Source	Sum of squares	DF	Mean square	F	p(F)
Time	15.866	5	3.173	5.531	0.000
cm	19.685	2	9.842	17.155	0.000
Time × cm	7.200	10	0.720	1.255	0.279
residual	30.981	54	0.574		

mean cm 1 = 9.58	mean Time 1 = 1.50	mean Time 4 = 7.67
mean cm 2 = 3.04	mean Time 2 = 1.67	mean Time 5 = 3.75
mean cm 3 = 1.67	mean Time 3 = 9.42	mean Time 6 = 4.58

OUTSIDE Source	Sum of squares	DF	Mean square	F	p(F)
Time	8.023	5	1.605	2.417	0.048
cm	2.964	2	1.482	2.231	0.117
Time × cm	5.922	10	0.592	0.892	0.547
residual	35.859	54	0.664		

mean cm 1 = 11.25	mean Time 1 = 20.75	mean Time 4 = 15.25
mean cm 2 = 15.21	mean Time 2 = 12.42	mean Time 5 = 8.41
mean cm 3 = 14.54	mean Time 3 = 14.25	mean Time 6 = 12.58

lower density. A contrast of time 5 vs 1, . . . , 4, 6 is statistically significant.

The results of the ANOVA for *Ammobaculites* are shown in Table 4 and the mean densities are plotted in Figure 4. Inside, the hypothesis for time is significant and a contrast of time 1, 2 vs 3, . . . , 6 is significant. The hypothesis for cm is also significant and the contrast cm 1 vs 2 and 3 is significant. Outside, the hypothesis for cm is significant. In this case the mean for cm 2 is almost the same as for cm 1 (Table 4) and a contrast of cms 1, 2 vs 3 is significant.

DISCUSSION

Inside the cage, which was protected from larger organisms by a 1 mm mesh screen and which began the experiment with azoic sand, the hypothesis for time was significant for all four taxa. In all cases the first two weeks of sampling had lower densities than the remaining four weeks. Evidently, the foraminifera require about three weeks to colonize the substrate and stabilize their density. These results are in agreement with Buzas (1978, 1982) who found, in the same location, that at the beginning of initial sampling one month after emplacement of a container, foraminiferal densities were as high or higher than in the outside control area. At deeper localities, Ellison and

TABLE 4. Two-way analysis of variance, *Ammobaculites*.

Source	Sum of squares	DF	Mean square	F	p(F)
INSIDE					
Time	22.096	5	4.419	7.666	0.000
cm	27.834	2	13.917	24.140	0.000
Time × cm	8.652	10	0.865	1.501	0.165
residual	31.131	54	0.576		

mean cm 1 = 10.42 mean Time 1 = 1.58 mean Time 4 = 8.83
mean cm 2 = 4.17 mean Time 2 = 2.75 mean Time 5 = 6.83
mean cm 3 = 2.29 mean Time 3 = 5.83 mean Time 6 = 7.67

Source	Sum of squares	DF	Mean square	F	p(F)
OUTSIDE					
Time	3.811	5	0.762	1.734	0.142
cm	2.882	2	1.441	3.279	0.045
Time × cm	5.825	10	0.583	1.325	0.241
residual	23.732	54	0.439		

mean cm 1 = 31.38 mean Time 1 = 32.67 mean Time 4 = 29.42
mean cm 2 = 32.83 mean Time 2 = 33.67 mean Time 5 = 19.58
mean cm 3 = 22.83 mean Time 3 = 33.25 mean Time 6 = 24.92

Peck (1983) from 65 m depth and Buzas and others (1989) from 125 m retrieved sediment boxes which were initially azoic after 10 weeks and 6 weeks, respectively. In both instances, colonization of boxes were complete at the retrieval times. In the present study, a substantial number of foraminifera are present within the initially azoic sediment within a week, and densities in the first cm are comparable to those outside within three weeks.

Outside, three of the taxa had no significant differences with time. The only exception was *Elphidium* which had a significantly lower density at time 5 (21 April). The lack of significance for the time hypothesis in the outside samples indicates that the low densities observed inside during the first two weeks was due to colonization rather than to a low point in seasonal periodicity.

Inside, all taxa exhibited significantly different densities between the first and second-third cms. Although the cage was protected from the activity of larger organisms, sediments at such a shallow (1 m) depth were undoubtedly disturbed by water turbulence. Nevertheless, the data indicate, as expected, that the foraminifera occupy the surface first and then proceed to occupy the lower levels. Whether or not they do so of their own volition or are forced to by turbulence is open to question. Ellison and Peck (1983) also sampled every cm to a depth of 3 cm, but found no differences between levels after ten weeks. The taxa in their study were, of course, quite different and, perhaps more mobile. On the other hand, ten weeks may be required instead of six.

Outside, *Quinqueloculina* and *Ammobaculites* had significant differences with depth. The former had significantly higher densities in the first cm. In a previous study, at the same locality Buzas (1977) found no significant difference in the density of this taxa in 10 cm of sediment. The majority of *Quinqueloculina* in this study belong to *Q. impressa* and Wetmore (1988) showed that this species has a preference, at least in the dark, to move upward when buried in sediment. Perhaps, this organism prefers the surface and the lack of significant difference in the 10 cm of sediment previously examined is due to displacement by larger organisms. *Ammobaculites* had significantly higher densities in the top 2 cm in the outside samples. The same species *A. exiguus* had no significant differences in the top 10 cms of the muddy sediments from the Chesapeake Estuarine system (Ellison, 1972; Buzas, 1974). However, in the above comparisons, we must keep in mind that testing for density differences in 10 cm of sediment is not equivalent to testing for differences in 3 cm.

Unlike the dramatic succession of species observed for macrofaunal organisms during colonization (Grassle and Grassle, 1974; Rhoads and others, 1978), the foraminifera colonize in proportions similar to those in the natural environment. During the observations made here, outside the cage species proportions were *Quinqueloculina* 0.35, *Ammonia* 0.42, *Ammobaculites* 0.15 and *Elphidium* 0.07. Inside the cage the proportions were 0.65, 0.25, and 0.06 and 0.05. Thus, while *Quinqueloculina* and *Ammonia* were codominants outside, *Quinqueloculina* dominated species proportions inside. During the 1978 and 1979 experiments in the same area (Buzas, 1982) *Quinqueloculina* also became relatively more dominant inside. Thus, among these foraminifera, *Quinqueloculina* might be regarded as the most opportunistic of the species examined, but it does not exclude substantial numbers of other species. These results are

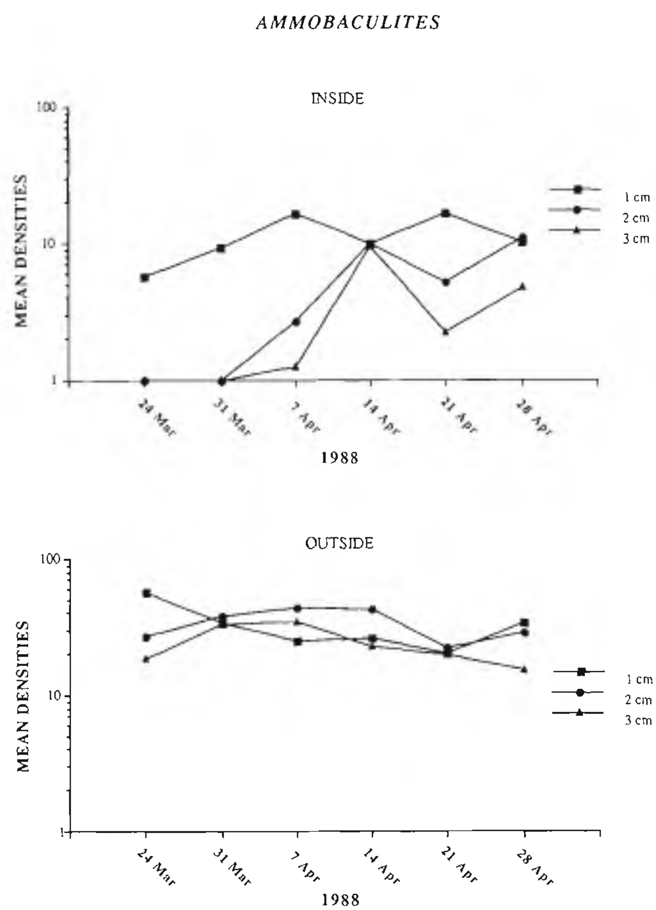

FIGURE 4. Mean (4 replicates) number of living (stained) individuals per 5 ml of sediment.

in complete agreement with offshore colonization experiments by Ellison and Peck (1983) and Buzas and others (1989). In these experiments changes in species proportions between boxes and the natural environment were also observed, but in general the ambient population colonized the azoic sediment in proportions similar to their natural ones.

In addition to the succession of species observed during recolonization by marcofaunal species, there is often a very large increase in density during the initial stages of colonization (Grassle and Grassle, 1974; Rhoads and others, 1978). The colonization pattern shown in this study does not exhibit any large increase in density. Instead, the density increased in a moderate fashion until stabilization, and during the six week period of observation of this study the density inside was usually lower than outside. During previous observations in 1978 and 1979 lasting five and four months, respectively, very large increases in density were observed in screen cages after two or three months (Buzas, 1982). These, however, were attributed to the exclusion of predators because identically prepared cages without screens during the same experiments showed no such increase (Buzas, 1982). Ellison and Peck (1983) also found no large increase in densities within their offshore recolonization boxes and speculated that if the foraminifera exhibited a very large increase in density during the initial stages, it occurred prior to their first retrieval which was ten weeks after emplacement. In a similar experiment, Buzas and others (1989) made a retrieval after six weeks with the same result. Based on the data presented here, it seems more likely that no initial large increase in density ever occurred in the offshore experiments either.

The observations presented here indicate a rather orderly and rapid colonization by the foraminifera. The ambient fauna colonizes the azoic sediment in proportions similar to the natural environment and stabilizes in about three weeks. The top cm is colonized first followed by the second and third.

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APPENDIX 1

Inside, Number of Living (Stained) Individuals Observed per 5 ml of Sediment.

Time 1988	cm	Replicate	*Quinqueloculina*	*Ammonia*	*Elphidium*	*Ammobaculites*
24 Mar	1	1	31	14	3	3
24 Mar	1	2	72	18	3	5
24 Mar	1	3	22	9	0	5
24 Mar	1	4	136	45	9	6
24 Mar	2	1	3	0	0	0
24 Mar	2	2	5	3	0	0
24 Mar	2	3	0	3	0	0
24 Mar	2	4	6	3	2	0
24 Mar	3	1	2	0	0	0
24 Mar	3	2	0	0	0	0
24 Mar	3	3	0	0	0	0
24 Mar	3	4	0	0	1	0
31 Mar	1	1	8	3	2	0
31 Mar	1	2	46	16	1	1
31 Mar	1	3	103	22	1	7
31 Mar	1	4	236	82	12	25
31 Mar	2	1	3	1	0	0
31 Mar	2	2	11	0	1	0
31 Mar	2	3	26	7	0	0
31 Mar	2	4	26	17	2	0
31 Mar	3	1	0	1	0	0
31 Mar	3	2	1	0	0	0
31 Mar	3	3	1	0	0	0
31 Mar	3	4	8	5	1	0
7 Apr	1	1	404	84	54	35
7 Apr	1	2	39	32	4	3
7 Apr	1	3	186	100	14	7
7 Apr	1	4	246	93	16	17
7 Apr	2	1	71	19	13	4
7 Apr	2	2	6	5	2	2
7 Apr	2	3	22	8	2	0
7 Apr	2	4	6	3	0	1
7 Apr	3	1	3	0	4	0
7 Apr	3	2	6	3	3	0
7 Apr	3	3	4	2	0	0
7 Apr	3	4	64	1	1	1
14 Apr	1	1	278	58	35	26
14 Apr	1	2	111	24	6	3
14 Apr	1	3	34	15	4	3
14 Apr	1	4	28	6	0	4
14 Apr	2	1	89	99	7	19
14 Apr	2	2	51	32	16	3
14 Apr	2	3	52	34	1	2

14 Apr	2	4	76	69	3	12
14 Apr	3	1	47	16	3	2
14 Apr	3	2	80	64	8	22
14 Apr	3	3	29	22	2	2
14 Apr	3	4	110	41	7	8
21 Apr	1	1	93	49	11	9
21 Apr	1	2	139	51	13	16
21 Apr	1	3	257	57	9	27
21 Apr	1	4	76	32	7	11
21 Apr	2	1	15	13	0	5
21 Apr	2	2	23	15	1	4
21 Apr	2	3	20	1	2	5
21 Apr	2	4	0	1	0	0
21 Apr	3	1	0	0	0	0
21 Apr	3	2	13	13	2	1
21 Apr	3	3	6	0	0	1
21 Apr	3	4	9	1	0	3
28 Apr	1	1	222	50	7	9
28 Apr	1	2	28	25	8	5
28 Apr	1	3	90	30	3	10
28 Apr	1	4	233	64	8	13
28 Apr	2	1	2	2	2	1
28 Apr	2	2	7	5	3	2
28 Apr	2	3	133	128	13	33
28 Apr	2	4	20	11	3	4
28 Apr	3	1	1	0	1	1
28 Apr	3	2	13	12	2	7
28 Apr	3	3	95	45	5	7
28 Apr	3	4	0	1	0	0

APPENDIX 2

OUTSIDE, NUMBER OF LIVING (STAINED) INDIVIDUALS OBSERVED PER 5 ML OF SEDIMENT.

Time 1988	cm	Replicate	*Quinqueloculina*	*Ammonia*	*Elphidium*	*Ammobaculites*
24 Mar	1	1	229	50	18	59
24 Mar	1	2	184	61	30	61
24 Mar	1	3	58	56	20	51
24 Mar	1	4	108	45	32	48
24 Mar	2	1	32	37	6	37
24 Mar	2	2	37	69	16	26
24 Mar	2	3	23	50	40	29
24 Mar	2	4	43	39	7	11
24 Mar	3	1	0	89	23	33
24 Mar	3	2	30	74	28	22
24 Mar	3	3	34	59	13	6
24 Mar	3	4	9	63	16	9
31 Mar	1	1	176	116	10	49
31 Mar	1	2	206	121	19	46
31 Mar	1	3	148	68	3	29
31 Mar	1	4	82	27	9	7
31 Mar	2	1	93	91	5	27
31 Mar	2	2	89	78	16	39
31 Mar	2	3	33	47	8	35
31 Mar	2	4	106	100	32	44
31 Mar	3	1	19	51	6	20
31 Mar	3	2	21	40	4	28
31 Mar	3	3	9	93	10	29
31 Mar	3	4	26	89	27	51
7 Apr	1	1	74	40	10	22
7 Apr	1	2	41	27	3	15
7 Apr	1	3	10	8	0	9
7 Apr	1	4	135	82	9	49
7 Apr	2	1	33	111	15	48
7 Apr	2	2	29	123	21	32
7 Apr	2	3	33	163	19	42
7 Apr	2	4	64	96	19	49
7 Apr	3	1	21	186	22	54
7 Apr	3	2	25	159	23	44
7 Apr	3	3	6	131	27	28
7 Apr	3	4	12	89	3	7
14 Apr	1	1	123	36	13	44
14 Apr	1	2	300	62	22	38
14 Apr	1	3	58	28	2	11
14 Apr	1	4	37	11	1	7
14 Apr	2	1	39	84	22	33
14 Apr	2	2	19	34	7	46
14 Apr	2	3	32	85	16	43
14 Apr	2	4	28	239	29	45
14 Apr	3	1	12	170	20	14
14 Apr	3	2	8	65	16	24
14 Apr	3	3	68	86	16	27
14 Apr	3	4	5	92	19	21
21 Apr	1	1	129	112	14	34
21 Apr	1	2	15	121	15	29
21 Apr	1	3	33	39	3	8
21 Apr	1	4	19	19	0	6
21 Apr	2	1	84	122	10	30
21 Apr	2	2	14	44	4	8
21 Apr	2	3	46	106	16	32
21 Apr	2	4	12	25	2	14
21 Apr	3	1	18	79	12	16
21 Apr	3	2	330	87	14	45
21 Apr	3	3	22	55	5	9
21 Apr	3	4	3	18	0	4
28 Apr	1	1	133	76	12	40
28 Apr	1	2	115	97	4	17
28 Apr	1	3	245	102	9	45
28 Apr	1	4	209	93	9	29
28 Apr	2	1	78	107	19	36
28 Apr	2	2	4	18	3	6
28 Apr	2	3	28	37	9	33
28 Apr	2	4	198	178	24	36
28 Apr	3	1	29	116	17	26
28 Apr	3	2	9	98	13	12
28 Apr	3	3	8	13	2	1
28 Apr	3	4	33	123	30	18