COMMUNITY UNITY? PATTERNS IN MOLLUSCS AND FORAMINIFERA

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Abstract: Organisms living together at the same time and place are often referred to as a "community." Few studies, however, have questioned whether changes in abundance by different-size members coincide. Here densities of molluscs and foraminifera in a tropical and a subtropical environment are compared.

Densities of bivalves and foraminifera were sampled monthly over a one-year period in Jamaica at a back-reef flat (less than 1 m depth), and at Discovery Bay (3 m depth). A significant difference in densities existed between the habitats for all species of bivalves. Two species also show periodicity with time. The total number of bivalve species found in the back-reef flat was six, and at Discovery Bay, 23. Of the 19 species of foraminifera analyzed, only six had density differences between habitats and seven had periodicity. The total number of foraminiferal species at the back-reef flat was 115 and at Discovery Bay, 117.

Molluscs were sampled inside and outside of a cage with 12-mm openings in December, 1975, and in February, April, June, 1976 at Linkport, Florida in the Indian River Estuary. Foraminifera were sampled inside and outside of the same cage during January, February, March, April, May, and June, 1976. In the same area, foraminifera were sampled inside and outside a cage with 1-mm openings during March, April, May, and June, 1976.

Of five species of gastropods analyzed, only one had a significant difference inside vs outside the cage, with higher densities inside. Densities of four gastropod species had significant differences with time. The densities of total gastropods had no significant differences inside vs outside or with time. Densities of total bivalves were significantly higher inside the cage and differed significantly with time. The densities of three taxa of foraminifera tested and total foraminifera had no significant differences between inside and outside the 12-mm cage, but differed with time. The densities of all three taxa of foraminifera and total foraminifera were significantly higher inside the cage with 1-mm openings than outside, and differed with time. These results suggest only the cage with 1-mm openings provided an effective exclosure from foraminiferal predators. Foraminiferal densities were much greater inside vs outside-the 1-mm cage than those for molluscs which had differences inside vs outside the 12-mm cage. Differences in foraminiferal densities were synchronous inside and outside of both cages. Molluscan densities differed with time among taxa.

The results suggest little integration in the response of these dominant members of the macro- and meiofauna to abiotic and biotic variables.

ISBN 0-12-751850-9

Introduction

A basic question of concern to ecologists and paleoecologists is whether or not various taxonomic groups react to habitat changes in a similar manner. If groups of organisms are regulated by the same physical-chemical variables, and have the same tolerances, similar patterns of biofacies should result. Similarly, if all organisms respond to the same environmental variables with time, similar periodicities should be observed. Understanding this unified behavior, or unison in time and space, is necessary to determine how "tightly-knit" are communities. Quantitative observations on two widely different-sized taxa made at the same time and place are, however, woefully scant.

In the present study, I examine patterns of density of molluscs and foraminifera in sea grass habitats in (1) Jamaica, West Indies, and (2) the Indian River, Florida. Three situations are analyzed: (1) different habitats, (2) periodicity with time, and (3) inside and outside of cages. The purpose is to see if the two groups act in unison.

I. Jamaica

Methods

Two homogeneous *Thalassia* habitats were sampled in Jamaica. The first, called Pear Tree Bottom, is located between Discovery Bay and Runaway Bay on the northern coast of Jamaica. The site is about 20 m from the mean-high water line on a back-reef flat. The water depth is about 10--15 cm at low tide (Station 1, Jackson, 1972). The second area, in Discovery Bay, is at a depth of 3 m (Station 3, Jackson, 1972). Samples of foraminifera and molluscs were collected simultaneously by Jackson (1972). Foraminiferal samples were taken by inserting plastic core liners into the sediment. Four replicate samples, each consisting of 20 ml of sediment, were taken each month for 12 successive months in 1969 and 1970. Buffered formalin was added to each sample in the field. All samples were washed over a 63 μ sieve and stored in alcohol within a few hours of sampling. In the laboratory samples were stained with rose bengal and floated in a mixture of bromoform-acetone. For laboratory details see Buzas *et al.* (1977).

Four replicate samples each of sizes .25 m^2 and 0.1 m^2 were taken for molluscs monthly for 12 months. The larger samples were sieved over a .64 mm sieve and the smaller ones over a 1 mm mesh sieve. For laboratory details see Jackson (1972).

At each sampling time, Jackson (1972) measured (1) bottom-water temperature, (2) sediment temperature, (3) bottom-water salinity, (4) bottom-water turbidity, (5) bottom-water particulate organic carbon, (6) bottom-water oxygen, (7) bottom-water pH, (8) sediment pH, (9) median sediment size, (10) sediment sorting, (11) sediment silt plus clay weight percent, and (12) dry weight *Thalassia*/ 0.1 m^2.

Results

A general linear model was constructed to analyze the Jamaican data; de-

tails are given by Buzas *et al.* (1977). In matrix notation the model is written

$$\underset{(N\,X\,1)}{\Omega : \quad x} \quad = \quad \underset{(N\,X\,q)}{Z'} \quad \underset{(q\,X\,1)}{b} \quad + \quad \underset{(N\,X\,1)}{e} \quad .$$

The dependent variable, x, is a vector of N = 96 observed densities. The matrix Z' is composed of columns containing the 12 environmental variables and 10 instrumental variables given below. The vector b has q = 22 parameters to "explain" the observed species densities. The vector e is a vector of "residuals" not accounted for by the model. The composition of Z' is as follows. The vector z_1 is a column of units, and because each of the other z's add to zero, b_1 is the mean of the observations. The vector z_2 gives +1 values to Pear Tree Bottom and −1 to Discovery Bay, thereby contrasting them. The vectors $z_3, \ldots, z_{14}$ are the environmental variables. The vectors z_{15} and z_{16} are $\sin(m \times \frac{\pi}{6})$ and $\cos(m \times \frac{\pi}{6})$ where m = 1, . . ., 12 respectively. The vectors z_{17} and z_{18} are $\sin(m \times \frac{\pi}{3})$ and $\cos(m \times \frac{\pi}{3})$ where m = 1, . . ., 12 respectively. These vectors taken two at a time test for an overall periodicity in the observations. The vectors z_{19} and $z_{20} = z_2 \times z_{15}$ and $z_2 \times z_{16}$ respectively. The vectors z_{21} and $z_{22} = z_2 \times z_{12}$ and $z_2 \times z_{18}$ respectively. These vectors test whether or not the two localities have different periodicities, i.e., interaction.

To construct restricted ω models containing s parameters, chosen b's are equated to zero. In this manner several hypotheses can be tested. To test the significance of an hypothesis the sum of squares of the residual, $\mathcal{L}_\Omega$, of the Ω model is compared with the sum of squares of the residual, $\mathcal{L}_\omega$, of an ω model. It can be shown that

$$\frac{\mathcal{L}_\omega - \mathcal{L}_\Omega \div (q-s)}{\mathcal{L}_\Omega \div (N-q)} = F_{(q-s)\,(N-q)}$$

$F_{(q-s)\,(N-q)}$ is called the F-ratio. Given the proper number of degrees of freedom we seek the probability α that a random variable z distributed as F exceeds the obtained F ratio z_α i.e. Pr $(z > z_\alpha) = \alpha$. In the present paper a value of $\alpha = .05$ was chosen as the significant α level.

The hypotheses tested are (1) sta diff (station differences), $b_2 = 0$, (2) envir var (environmental variables), $b_i = 0$ (i = 3, . . ., 14), (3) $\pi/6$ overin (overall periodicity and interaction of $\pi/6$ type), $b_i = 0$ (i = 15, 16, 19, 20), (4) $\pi/3$ overin (overall periodicity and interaction of $\pi/3$ type), $b_i = 0$ (i = 17, 18, 21, 22), (5) $\pi/6$ inter (interaction of $\pi/6$ type), $b_i = 0$ (i = 19, 20), (6) $\pi/3$ inter (interaction of $\pi/3$ type), $b_i = 0$ (i = 21, 22).

Most of the 143 species of foraminifera identified in Jamaica were relatively rare. Because of the extreme non-normality of species represented by only a few

individuals, only those species with a grand mean of greater than two were statistically analyzed. Only 19 species met this criterion.

Table 1 shows the probability of exceeding the F ratio values for each hypothesis tested. For individual ANOVA's see tables in Buzas *et al.*, 1977. At the 95% (.05) level (values in bold type in Table 1), seven species exhibit periodicity and five a significant difference between localities, and environmental variables are not significant for any of the species. Results of analysis of the total living population (standing crop) are similar to those of the most abundant species, only overall periodicity is significant at the 95% level. Similarly, multivariate analysis (all 19 species considered simultaneously) using the same hypotheses showed only station differences and overall periodicity to be significant (Buzas *et al.*, 1977).

The trend in mean monthly density for the total live population of foraminifera was similar to that for most of the abundant species (Figure 1). May was a month of maximum densities at both stations. Most species had smaller peaks in November, February, August, or September. In summary, at the 95% level, six species, but none of the five most abundant, had significant station differences. An overall periodicity was exhibited by seven of the species studied. In no case were the hypotheses for environmental variables statistically significant. A total of 115 species were found at Pear Tree Bottom and 117 at Discovery Bay.

The same statistical model was used to analyze the bivalves. Table 2 shows the probabilities of exceeding the F ratios for four species of bivalves and the total number of individuals of all infaunal and semi-infaunal bivalves. All four species had significant station differences, two had overall periodicities and one of these also had different periodicities at the two sites. In no case were the hypotheses for environmental variables statistically significant, but the F values were higher than for the foraminifera. The total bivalve assemblage had a significant difference between stations, and periodicity differed between stations. The hypothesis for the set of environmental variables was significant at the 95% level. Figure 2 shows a plot of the mean total number of individuals by month. The maximum occurred in June at both stations. As the significance of the interaction hypothesis indicates, the pattern of minor peaks between stations was not similar. The total number of bivalve species observed is six at Pear Tree Bottom and 23 at Discovery Bay.

All four of the most abundant bivalve species had statistically significant station differences, while for foraminifera only about a third of the species did, and none of these are among the five most abundant. Two of four mollusc species and seven of 19 foraminiferal species had significant periodicities. As Figures 1 and 2 indicate, however, the times of maxima did not coincide. The total number of species observed at the two habitats was drastically different for molluscs while the number of foraminiferal species was quite similar. Evidently, the two habitats present vastly different environments for the molluscs, but were only slightly different for the foraminifera. Environmental variables, while not signficant at the 95% level for any of the molluscs, do have F values in three cases which are

Table 1. Probability that F ratio is exceeded for 19 foraminiferal species and total foraminifera in Jamaica. $\alpha \leq .05$ is in bold type. (See text for explanation of hypotheses.)

Species	Hypotheses					
	$\pi/3$ inter	$\pi/6$ inter	$\pi/3$ ovrin	$\pi/6$ ovrin	envir var	sta diff
Bolivina striatula	.99	.73	.73	**.02**	.11	.54
Bolivina subexcavata	.29	.62	.14	.07	.30	.69
Trifarina occidentalis	.22	.78	.47	.06	.16	.71
Ammonia beccarii	.33	.24	.62	.09	.93	.49
Rosalina globularis	**.02**	.72	.08	**.001**	.57	.19
Discorbis mira	.29	.08	.35	.11	.33	**.0005**
Rosalina subaraucana	.47	**.03**	.32	**.002**	.69	.10
Rosalina floridana	.29	.31	.52	.57	.40	**.03**
Amphistegina gibbosa	.66	.09	.82	.11	.65	**.0002**
Cymbaloporetta squammosa	**.01**	.25	**.05**	.19	.73	.78
Cymbaloporella tobagoensis	.36	.25	.28	.40	.09	.50
Cymbaloporetta atlantica	.20	**.02**	.06	**.0003**	.12	**.02**
Asterigerina carinata	.41	**.004**	.57	**.0008**	.22	.70
Bolivina doniezi	.99	.86	.97	.80	.66	.21
Planorbulinella acervalis	.22	.46	.35	.80	.40	.12
Nonionella auricula	.40	.82	.72	.42	.41	.08
Cyclogyra planorbis	.41	.15	.72	.10	.34	.21
Discorbis murrayi	.36	.98	.70	.77	.20	**.04**
Fursenkoina pontoni	.08	.16	**.05**	.27	.78	**.02**
Total Foraminifera	.24	.15	.57	**.002**	.07	.89

much higher than for the foraminifera. These analyses coupled with the great difference in species diversity between the habitats for the molluscs indicate that the molluscs were more abiotically controlled in these habitats than the foraminifera.

II. Indian River

Methods

Several square wire cages (12 mm mesh) 2 m on a side, were set up at Linkport for various experimental treatments in a seagrass bed of *Halodule wrightii.* The cages were placed in a subtidal flat and had no tops or bottoms. The present analyses utilized data from a plain cage (no treatment) and a nearby control area (no cage). Of the many Phyla collected (Young and Young, 1977) only the molluscs and foraminifera are treated here.

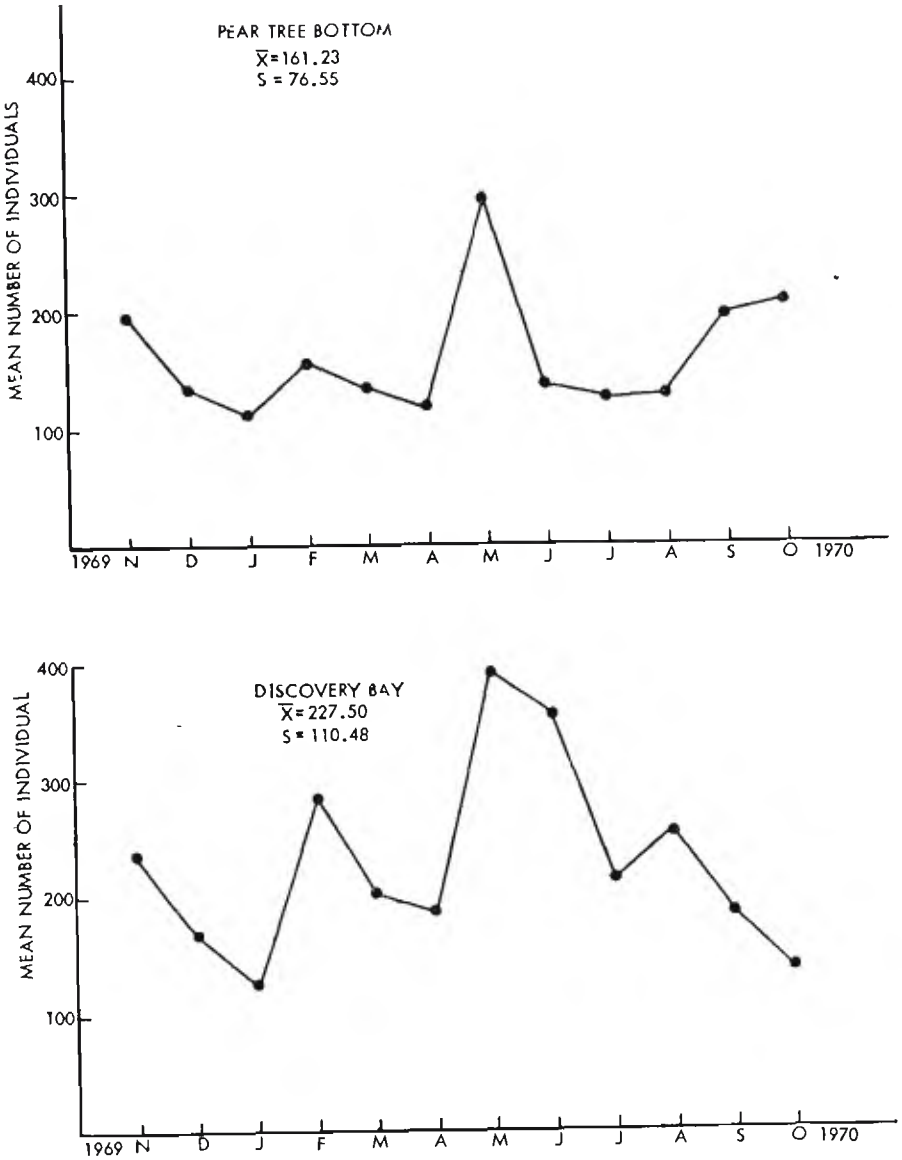

Figure 1. Monthly variations in density of foraminifera at Jamaica.

Macrofaunal sampling consisted of four replicate box cores (15 cm x 15 cm x 20 cm) taken inside and outside the cage during the months of December, 1976, and February, April, June, 1977.

The samples were washed through a 1 mm screen, narcotized, fixed, and

preserved for later enumeration. For details see Young and Young (1977).

The foraminifera were sampled by inserting Phleger core liners into the sediment and removing the top 2 cm (20 ml) of sediment. The sediment was immediately fixed with neutralized formalin, washed over a 63 μ sieve, stored in alcohol, stained with rose bengal, floated in bromoform-acetone, rewetted, and enumerated while wet. Four replicates were taken inside the macrofaunal cage and four outside in the control area during the months of January, February, March, April, May, and June, 1976.

In addition to the macrofaunal cage, a foraminiferal cage was constructed by cutting four windows of 35 cm on a side 15 cm from the bottom of a large PVC trash can. The windows were covered with 1 mm nylon mesh screens to exclude predators. The screens were replaced about twice a week to prevent fouling. In February, the cage was placed in a 15 cm hole and 30 l of "sterile" sand was placed inside. Four replicate (20 ml) samples were taken inside and four outside the cage in an undisturbed area in March, April, May, and June, 1976. The samples were treated in the same manner as the foraminiferal samples from the macrofaunal cage.

Results

All of the experiments were designed to analyze differences in mean densities by a two-way analysis of variance with interaction. The three hypotheses are (1) an overall difference with time, (2) an overall difference between inside and outside the cage, and (3) interaction (differences inside and outside the cage with time). Only the more abundant species were analyzed. A minimum grand mean of about two was used as a cutoff (see Jackson, 1972; Young *et al.*, 1976). The original counts were transformed to $\ln (x + 1)$ to normalize the data and to stabilize the variance.

Table 3 gives the probability of a random variable distributed as F exceeding the calculated F ratio for five species of gastropods, total gastropods, and total

Table 2. **Probability that F ratio is exceeded for four bivalve species and total bivalves in Jamaica. $\alpha \leq .05$ is in bold type. (See text for explanation of hypotheses.)**

	Hypotheses					
Species	$\pi/3$ inter	$\pi/6$ inter	$\pi/3$ ovrin	$\pi/6$ ovrin	envir var	sta diff
Codakia orbicularis	.96	**.03**	.69	**.05**	.07	**.001**
Ctena orbiculata	.56	.17	.31	.39	.14	**.0000**
Diplodonta punctata	.16	.73	**.05**	.90	.16	**.05**
Parvalucina costata	.65	.81	.52	.75	.60	**.005**
Total Bivalves	.93	**.03**	.74	.09	**.03**	**.04**

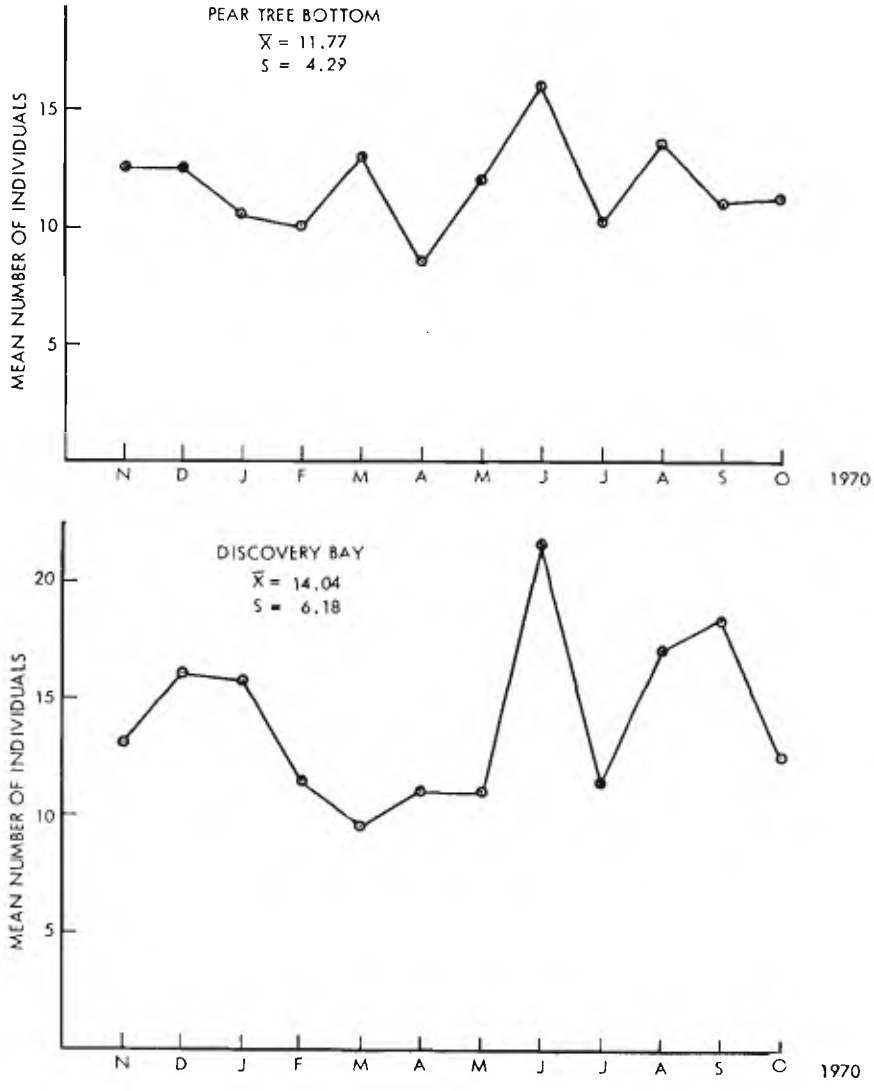

Figure 2. Monthly variations in density of bivalves at Jamaica.

bivalves (no bivalve species was abundant enough to be included in an individual analysis).

The mean numbers of individuals of *Diastoma varium* showed litttle difference inside and outside of the cage for the four sampling times. The only statistically significant hypothesis was for differences with time; maximum densities occurred in February (Figure 3).

The mean number of individuals of *Mitrella lunata* inside and outside of

Table 3. Probability that F ratio is exceeded for molluscs at Linkport. $\alpha \leq .05$ is in bold type.

	Hypotheses		
Species	time	in vs out	interaction
Diastoma varium	**.02**	.66	.06
Mitrella lunata	.09	**.005**	.20
Crepidula fornicata	**.02**	.67	.43
Cerithium muscarum	**.0001**	.12	.19
Modulus modulus	**.0000**	.06	.19
Total Gastropods	.06	.35	.29
Total Bivalves	**.01**	**.005**	.49

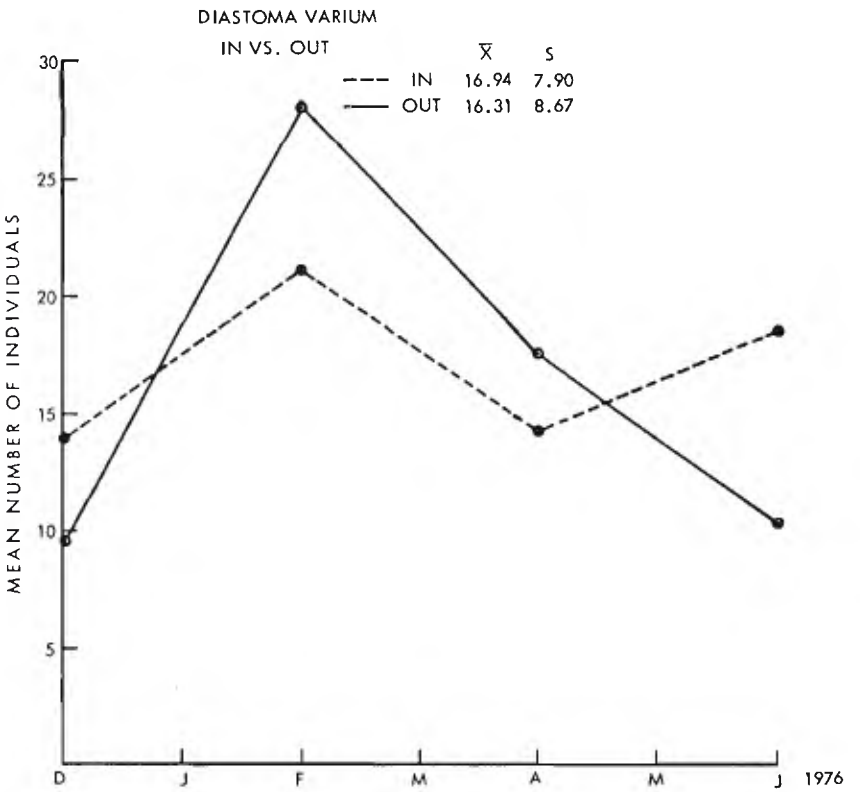

Figure 3. Variation in density of Diastoma varium *inside vs outside cage at Linkport, Florida.*

the cage for the four sampling times is shown in Figure 4. Table 3 indicates a significant difference between inside and outside, which is apparent in the plot for the months February, April, and June. This species was the only one tested that lacked a statistically significant difference with time.

The mean number of individuals of *Crepidula fornicata* inside and outside of the cage at the sampling times is shown in Figure 5. Little difference was observed inside vs outside of the cage, but as Table 3 indicates, there was a significant difference with time. The maximum density was in December.

The mean numbers of individuals of *Cerithium muscarum* per sampling time is shown in Figure 6. Little difference was observed between inside and outside, and a maximum density occurred in December. Table 3 indicates a statistically significant difference in density with time. The maximum density occurred in December.

The mean number of individuals per sampling time for *Modulus modulus* is shown in Figure 7. Again, the hypothesis for time is significant (Table 3). The maximum density occurred in April.

In summary, only *Mitrella lunata* was affected by the cage, having higher densities inside, and this was the only species showing no difference with time.

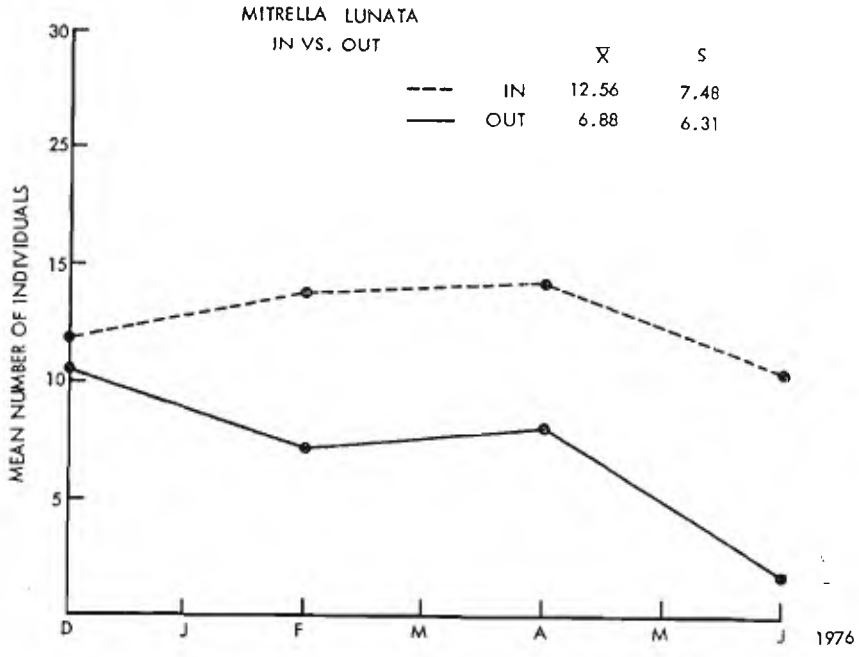

Figure 4. Variation in density of Mitrella lunata *inside vs outside cage at Linkport, Florida.*

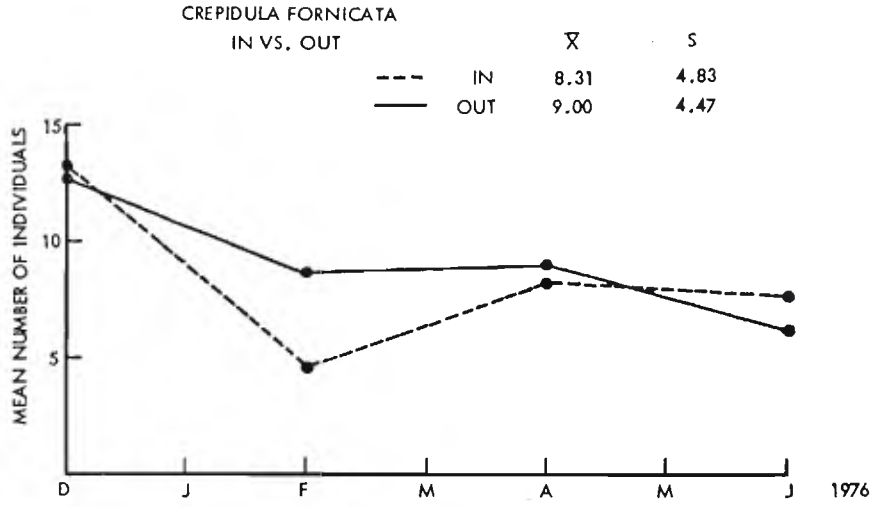

Figure 5. Variation in density of Crepidula fornicata *inside vs outside cage at Linkport, Florida.*

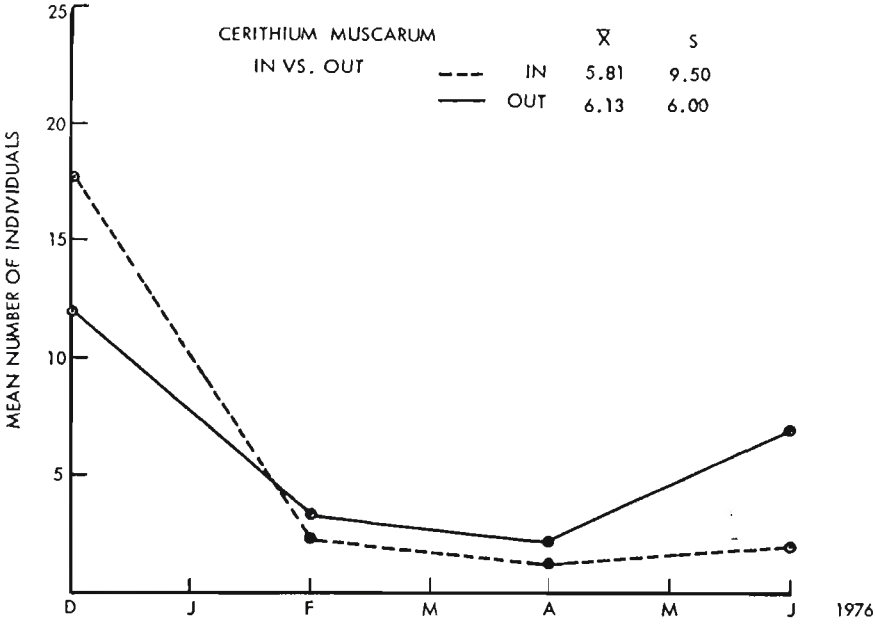

Figure 6. Variation in density of Cerithium muscarum *inside vs outside cage at Linkport, Florida.*

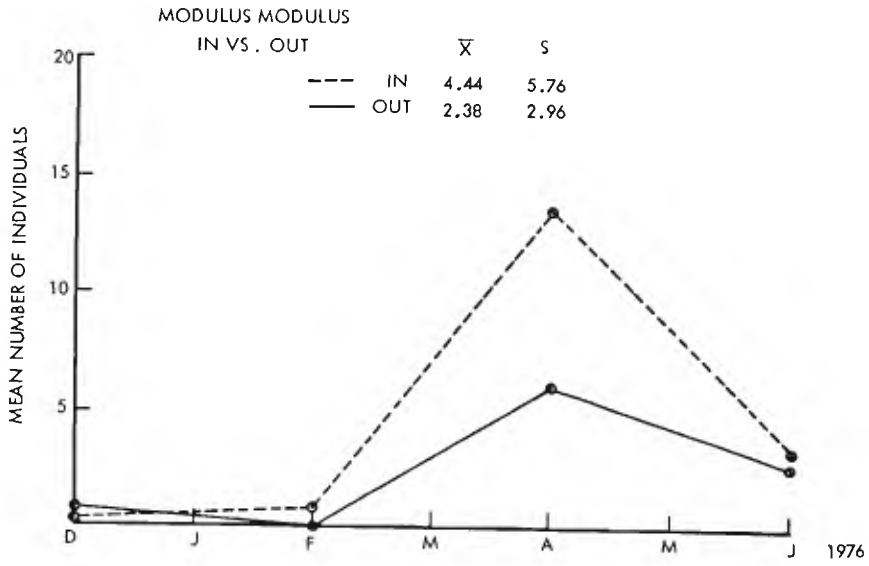

Figure 7. Variation in density of Modulus modulus *inside vs outside cage at Linkport, Florida.*

Cerithium muscarum and *Crepidula fornicata* both had maximum densities in December. *Diastoma varium* had a maximum in February and *Modulus modulus* in April. The pattern of densities inside and outside was similar for all species. As Table 3 indicates, no significant difference exists inside vs outside with time (interaction hypothesis).

Because species of gastropods do not have the same pattern of densities with time, we cannot expect the total number of gastropods to reflect the differences cited above. None of the hypotheses were significant for total gastropods (Figure 8).

As stated above, no species of bivalve was abundant enough to warrant statistical analysis. Consequently, only the total number of bivalves was tested. Table 3 shows that the hypothesis for inside vs outside and time was significant while interaction was not. Bivalves were always more abundant inside the cage and were most abundant in December and April (Figure 9).

The foraminiferal taxa *Ammonia beccarii, Elphidium mexicanum,* miliolids (mostly *Quinqueloculina impressa* and *Q. seminula*), and total foraminifera were enumerated at the same macrofaunal macrocage as the molluscs. The statistical summary is shown in Table 4. The hypothesis for time is highly significant for all four taxa. No other hypothesis is significant. Examination of plots of density against time indicates similar patterns for all taxa. Consequently, only the total foraminiferal densities are shown here (Figure 10). Densities of all taxa of foraminifera have maxima in April. As one would expect, the lack of a large differ-

ence between inside and outside indicates that a cage with 12 mm openings does not exclude predators of the foraminifera.

The hypotheses for time and inside vs outside are statistically significant for all taxa (Table 5). In addition, the interaction hypothesis is significant for *Ammonia beccarii*. As observed with the macrofaunal cage and control treatments, foraminifera had a maximum density in April. Figure 11 shows the pattern of density for the total living population. The differences between inside and outside are most striking with a maximum mean of about 5,000 individuals per 20 ml of sediment inside and 1,000 outside in April. Foraminiferal density patterns inside and outside were similar at the macrofaunal and meiofaunal sites (Figures 10 and 11). The synchrony observed is further assurance of adequate sampling and demonstrates that foraminifera respond to an overall rhythm at the Linkport site which, at present, is unexplainable.

Discussion

The results of this study indicate that densities of foraminifera and molluscs are not controlled in different habitats or with time in similar fashion. In Jamaica,

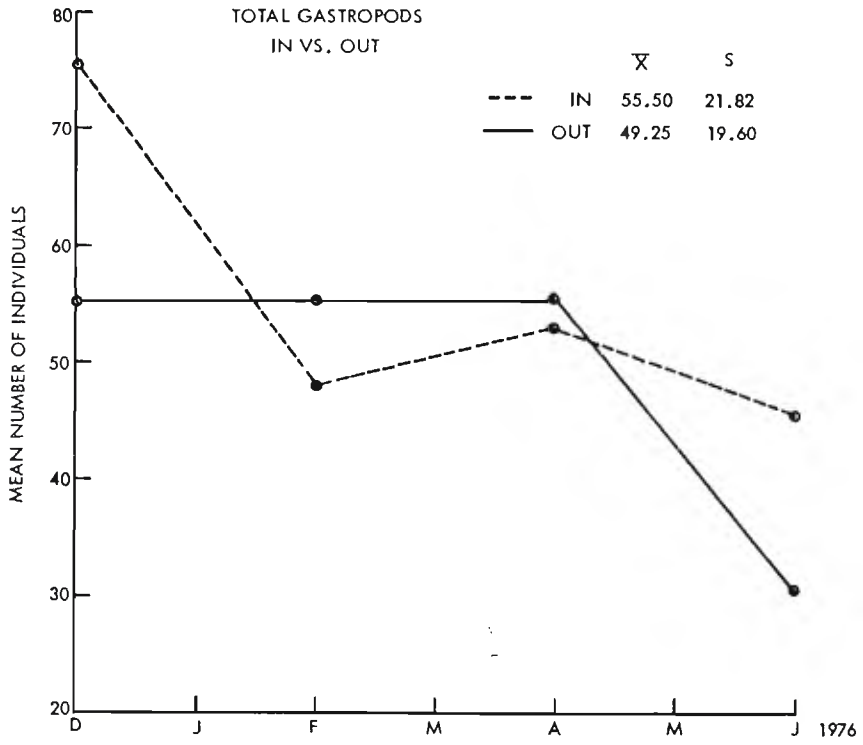

Figure 8. Variation in density of total gastropods inside vs outside cage at Linkport, Florida.

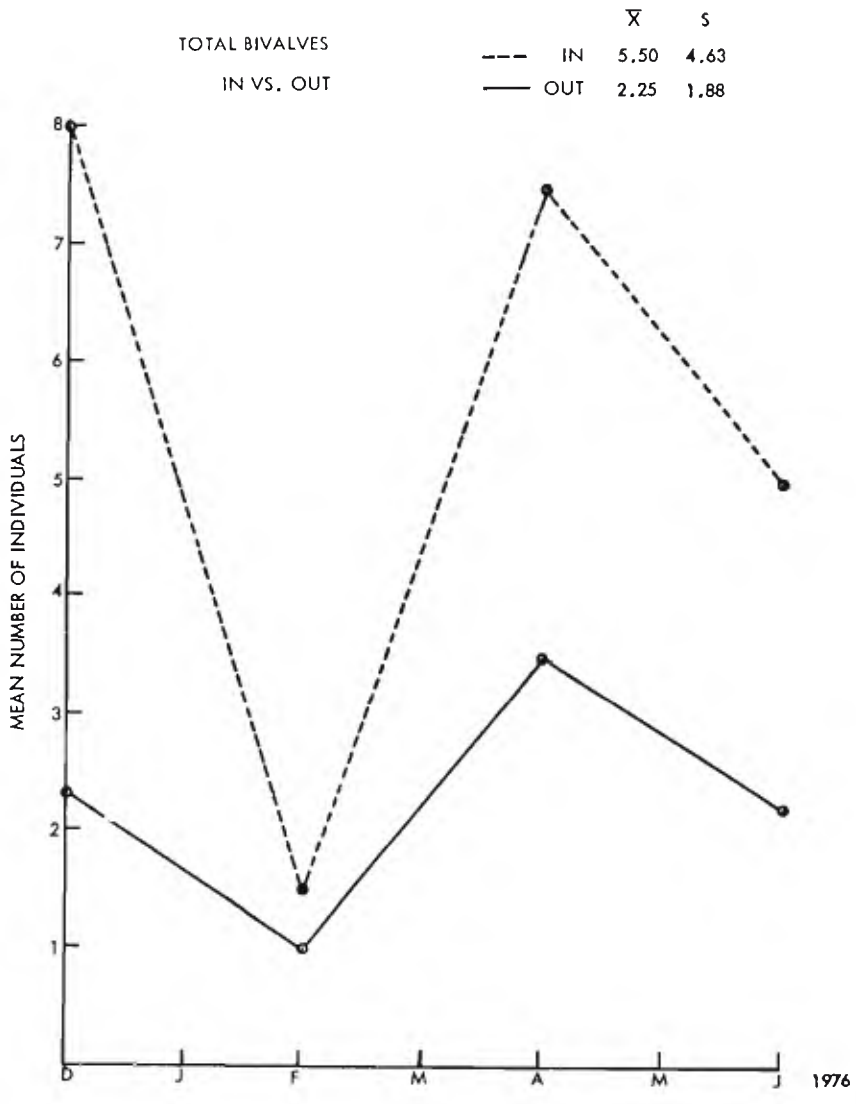

Figure 9. Variation in density of total bivalves inside vs outside cage at Linkport, Florida.

density differences of animals collected from a shallow subtidal habitat and one at 3 m are dramatic for bivalves, but not so for foraminifera. Similarly, periodicities of bivalves and foraminifera are not synchronous. Subtidal bivalve species also live in the deeper habitat, but never vice-versa. Most foraminiferal species occur in both habitats. These observations and the significance of the hypothesis

Table 4. Probability that F ratio is exceeded for foraminifera at Linkport (macrofaunal cage). $\alpha \leq .05$ is in bold type.

	Hypotheses		
Species	time	in vs out	interaction
Ammonia beccarii	**.0004**	.07	.69
Elphidium mexicanum	**.0001**	.49	.94
Miliolids	**.0000**	.08	.86
Total Foraminifera	**.0000**	.38	.63

for environmental variables for total bivalves suggest that abiotic variables are more important for bivalves than for foraminifera. At Linkport in the Indian River, Florida, patterns of periodicity for individual species of gastropods differ widely, but not for foraminifera. While there is a significant difference of densi-

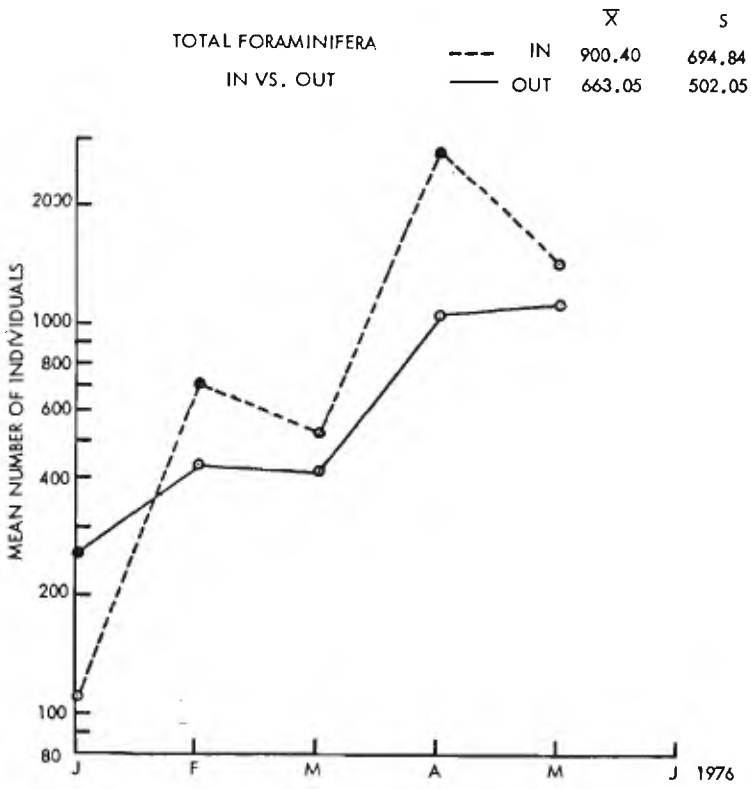

Figure 10. Variation in density of total foraminifera inside vs outside macrofaunal cage at Linkport, Florida.

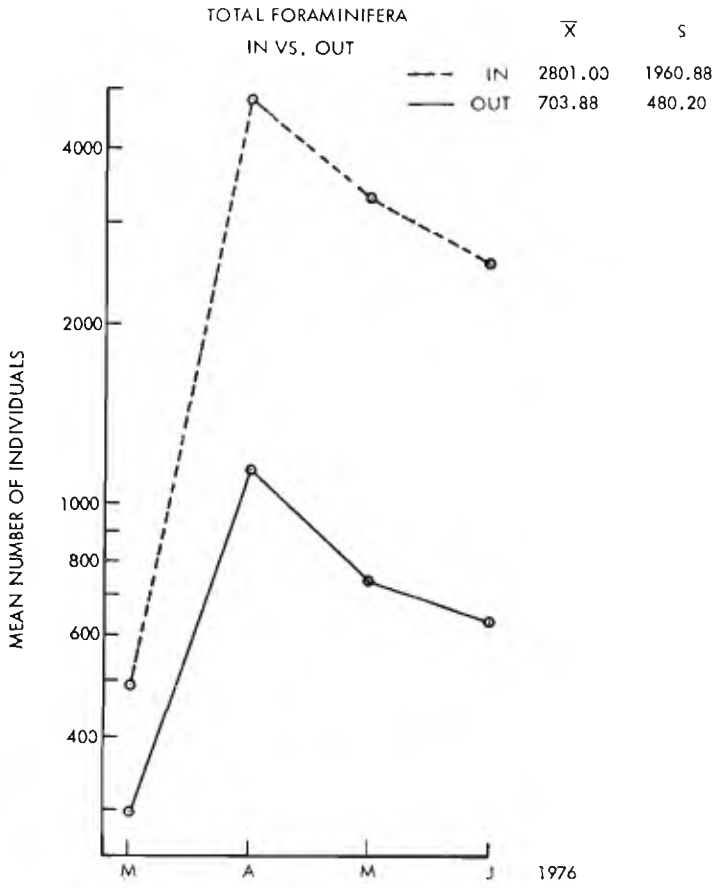

Figure 11. Variation in density of total foraminifera inside vs outside meiofaunal cage at Linkport, Florida.

Table 5. Probability that F ratio is exceeded for foraminifera at Linkport (meiofaunal cage). $\alpha \leq .05$ is in bold type.

	Hypotheses		
Species	time	in vs out	interaction
Ammonia beccarii	**.0000**	**.0000**	**.02**
Elphidium mexicanum	**.0000**	**.0000**	.23
Miliolids	**.0001**	**.0000**	.22
Total Foraminifera	**.0000**	**.0000**	.15

ties between inside and outside of a cage for bivalves, the differences are not nearly as large as for the foraminifera. Clearly, foraminifera and molluscs do not "see" the environment in the same way.

The results of this paper are not in agreement with Warme *et al.* (1976) who regarded as minor the differences between mollusc and foraminiferal biofacies identified through cluster analysis. They believed foraminifera and molluscs cluster into similar areally-distributed communities that reflect major habitats in Southern California and the eastern Yucatan. They suggested that foraminifera and molluscs are regulated by similar physical-chemical factors. There are, however, some difficulties with their comparisons. The mollusc data were clustered from correlation coefficients based on relative abundance and the foraminifera data were clustered from a simple matching coefficient using presence or absence. To further complicate matters, several other coefficients were used, and the one giving the best fit with the physical environment was chosen, a poor statistical procedure. Even so, there are many samples among the two groups that do not cluster in the same biofacies, and goodness of fit is a matter of opinion. In such analysis, much depends on whether you are looking for similarities or differences. Foraminifera and molluscs can probably be used to delimit the same biofacies on a relatively gross scale, but the data presented here, and I believe the data of Warme *et al.* (1976), indicate these organisms do not act as a simple unit.

Some ecologists and paleoecologists, e.g. Kauffman and Scott (1976), have suggested that all species should be included in community studies. With great difficulty a team of researchers could possibly survey and catalogue the fauna and flora of an estuary or similarly bounded area. This resulting community matrix containing abundances of all organisms could be stored in a large computer, but I have no idea what could be done with it. The wide discrepancies between patterns of density of molluscs and foraminifera as demonstrated here indicate that little can be learned by subjecting them jointly to sophisticated mathematical manipulation.

This study does not demonstrate that interactions between foraminifera and molluscs do not exist. Recently, K. Carle (personal communication) discovered two species of a small gastropod belonging to the genus *Acteocina* and a small fish *Gobionellus boleosoma* which eat foraminifera at Linkport, but most snails and fish do not. Consequently, we should not analyze all gastropods and foraminifera, but only those species whose life histories are sufficiently known so that specific hypotheses can be tested. Such an approach is in keeping with Young *et al.* (1976) who analyzed feeding types rather than taxonomic groups. We are still ill-prepared to tackle an entire community and must instead be content with studying parts for which we can formulate and test specific hypotheses.

Acknowledgments

Special thanks to K. Carle who did most of the field and laboratory work at Linkport. Thanks also to R. Bronson, K. D. Cairns, L. B. Ishman, M. A. Capone,

L. A. Hayek, J. E. Miller, D. H. Mook, R. W. Virstein, R. T. Wolcott, D. K. Young, and M. W. Young, who all helped in various ways.

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