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PALEOENVIRONMENTAL AND PALEOECOLOGIC IMPLICATIONS OF RECENT FORAMINIFERAN DISTRIBUTIONAL PATTERNS IN THE LOWER FLORIDA KEYS

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ABSTRACT

Phytal samples and associated bottom sediments containing foraminifera were collected from lagoonal, tidal channel, patch reef, and outer reef environments in the vicinity of Big Pine Key in the lower Florida Keys. The marine plants *Thalassia testudinum, Penicillus capitatus, Halimeda* spp., and *Dasycladus vermicularis* were identified as important habitats of foraminifera in this area. Most individuals on the plants were alive and most individuals among the sediments were determined to be dead when collected. Sanders' similarity index indicates that the biocoenoses on different plants within the same environment are similar and that the biocoenoses from different environments are dissimilar. The diversity and evenness of living species are related to environmental variability.

Additionally, biocoenoses from vegetation generally are dissimilar to thanatocoenoses among the associated bottom sediments from the same area, although the degree of similarity between the two increases in environments with more restricted circulation. Postmortem processes, such as size sorting and differential destruction of tests, affect the general character of species diversity and evenness indigenous to living faunas. The data suggest that the thanatocoenosis preserved in the sediments may not be an accurate reflection of the nature of the living fauna, thus hindering paleoecologic analysis. In the area studied, the sediment assemblages from various environmnets are sufficiently distinct so as to permit their use in paleoenvironmental reconstruction based on degree of sorting, species diversity, suborder percentages, characteristic species, and diagnostic associations.

INTRODUCTION

Foraminifera are important both as biotic elements of marine communities and as skeletal constituents of sediments in shallow-water carbonate depositional provinces such as south Florida. Most studies of foraminifera in such modern environmnets have concentrated upon the distribution of total (living and dead) populations found among sediments. Some recent studies, however, suggest that in nearshore carbonate environments foraminifera live primarily on or among benthic marine vegetation and that the foraminiferal assemblage among the sediments is primarily a thanatocoenosis that may not accurately reflect the biocoenosis of the local area.

The purposes of this study were: 1) to determine major habitats of benthic foraminifera from a variety of environments in the vicinity of Big Pine Key, Florida; 2) to correlate changes in living populations with environmental gradients and environmental variability; 3) to compare living populations (biocoenoses) with death assemblages (thanatocoenoses) in different environments; and 4) to evaluate the significance of the results in relation to paleoenvironmental reconstruction and paleoecological analysis. A more detailed analysis of the fauna and discussion of diagnostic assemblages from the different environments will appear in a publication now in preparation.

PREVIOUS WORK

Distributional patterns of foraminifera in modern seas are well known (Brady, 1884; Cushman, 1910-17, 1918-31). In addition, more detailed patterns of faunal distribution have been established for local areas. Bock (1971) described the foraminiferal fauna of south Florida and recognized five major faunal groups correlated with changes in the physical environment, and Rose and Lidz (1977) described diagnostic assemblages of foraminifera from the shallow waters of south Florida and the Bahamas. Further studies on shallow-water benthic foraminifera from south Florida and the Bahamas were summarized by Steinker (1977). Other significant contributions to the subject are those of Weiss and Steinker (1977) who compared foraminiferal assemblages from patch reef and outer reef sediments in the lower Florida Keys, Poag (1981), who published an ecologic atlas of foraminifers from the Gulf of Mexico, and Steinker (1982), who reported on late Pleistocene foraminifera from the Florida Keys.

Most distributional studies of modern shallow-water foraminifera have been based upon assemblages from sediment samples, with living individuals determined by staining techniques. Whereas the geologist is concerned mainly with skeletal materials that get incorporated into the sedimentary record, the ecologist is interested in interactions within communities, and the paleoecologist must consider both of these aspects. L. V. Illing (1954) summarized the previous work of M.A. Illing (1950, 1952) on the distribution of foraminifera on the Bahama Banks and concluded that the pattern of the indigenous fauna among the sediments is largely masked by the sorting action of waves and currents. Such postmortem processes result in a loss of information concerning the original community, and in paleoecology it is necessary to discriminate between factors that influence the distribution of living populations and those that determine the death assemblage among the sediments. It has been demonstrated in shallow-water carbonate environments that various types of marine vegetation constitute the major habitat of foraminifera (Grant and others, 1973; Steinker and Steinker, 1976; Steinker, 1980; Steinker and Rayner, 1981; Brasier, 1975a, 1975b), and few studies have made accurate comparisons between the living fauna and the assemblage preserved among the sediments.

LOCATION AND DESCRIPTION OF AREA

The south Florida shelf is a carbonate depositional province, dominated by biogenic calcareous sediments. Ginsburg (1956) described the marine environments and sediments of this area and recognized two major sedimentary environments: 1) the reef tract, extending from the Florida Keys southward to the outer edge of the shelf; and 2) Florida Bay, between the Keys and the southern tip of the mainland. The reef tract is characterized by open water circulation, whereas Florida Bay has semi-restricted circulation. Tidal channels between the Keys represent a transitional environment between the more variable waters of Florida Bay and the less variable waters of the reef tract. The reef tract lies on a shallow platform extending seaward of the Keys

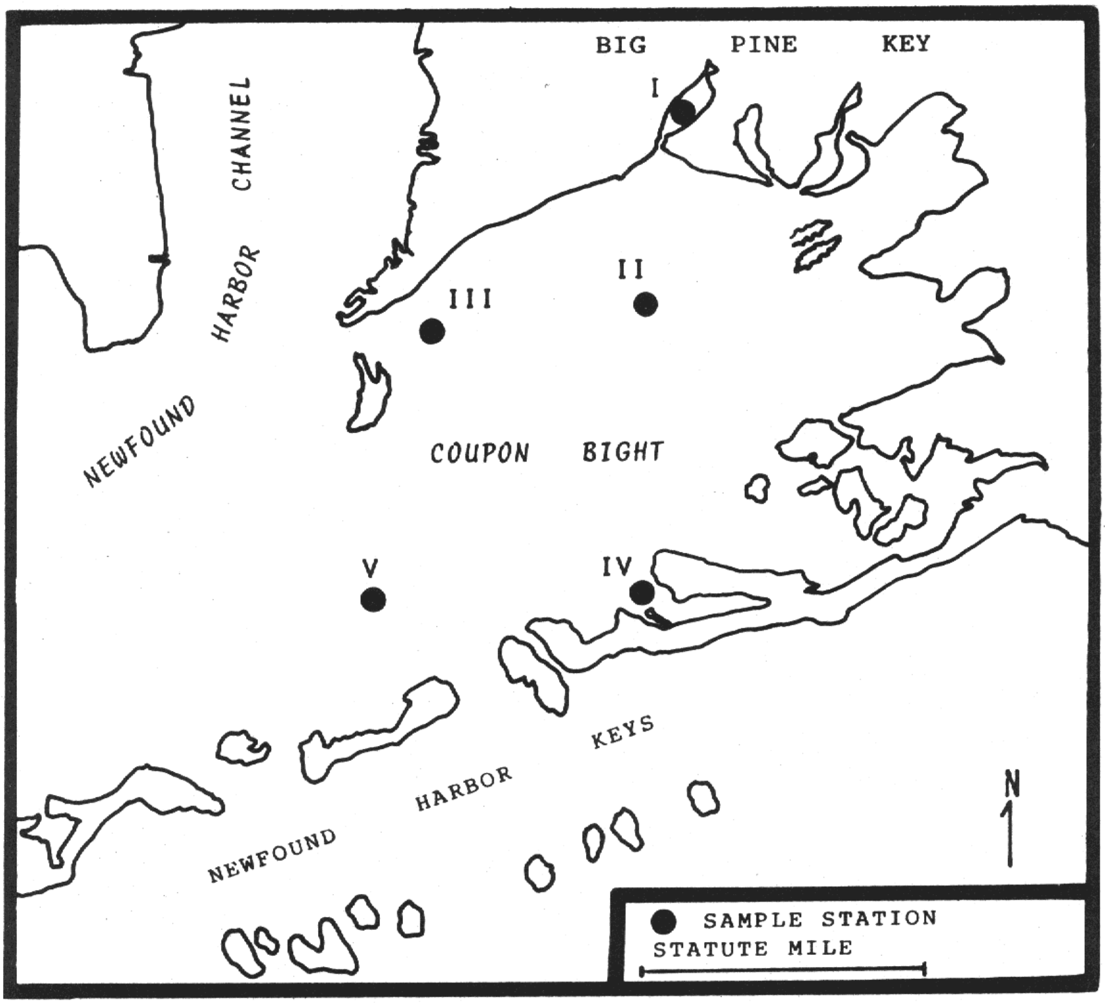

Figure 1. Coupon Bight Sample Stations. I, Restricted Bay; II Open Bay; III, Nearshore; IV, Nearshore-Restricted Bay; V, Baymouth Bank.

TABLE 1

Station	I	II	III	IV	V	VI	VII	VIII
I		74	72	69	65	38	26	17
II			78	69	72	41	36	20
III				80	79	52	34	24
IV					66	59	44	34
V						46	37	27
VI							53	56
VII								59
VIII								

Comparison of Foraminiferal Assemblages Found at Different Sample Stations Using the Similarity Index of Sanders. On average, values higher than 80 per cent indicate that the samples are nearly identical. Lower values indicate progressively greater differences. I, Restricted Bay; II, Open Bay; III, Nearshore; IV, Nearshore-Restricted Bay; V, Baymouth Bank; VI, Tidal Channel; VII, Patch Reef; VIII, Outer Reef.

for a distance of 5 to 10 km, and the Florida Current provides open tidal circulation across this platform.

Ginsburg (1956) further divided the reef tract into fore reef, outer reef, and back reef subenvironments. The outer reef tract at the edge of the shelf consists of a discontinuous series of reef and rocky shoals separated by deeper areas with rippled sand. Water depth is generally less than 12 m over the back reef, and patch reefs are scattered through this area. Swinchatt (1965) divided the back reef into two distinct sedimentary environments: 1) an outer back reef area dominated by rippled skeletal sand and generally lacking mud and marine grass, and 2) an inner back reef area with marine grass beds locally stabilizing sand and mud. Further information on the sediments, organisms, and physical factors of these various environments has been summarized by Ginsburg (1956), Bathurst (1975), Multer (1977), and Enos and Perkins (1977).

In addition to the large area of Florida Bay, much smaller semi-enclosed embayments with restricted tidal circulation are common along the Florida Keys. One such lagoon is Coupon Bight, between Big Pine Key and the Newfound Harbor Keys in the lower Florida Keys. Coupon Bight opens into the Newfound Harbor Channel to the west, and channels between the Newfound Harbor Keys to the south provide additional tidal exchange.

Samples for this investigation were collected from eight stations (Figs. 1 and 2) representing a variety of different environments ranging from lagoonal areas of Coupon Bight out to the reef flat at Looe Key reef off Big Pine Key. This area was selected for study because of the easy accessibility of a variety of environments and because of the availability of information on these environments.

Stations I through V were in Coupon Bight (Fig. 1). The general environment, sedimentary facies, and biota of the Bight have been described by Howard, Kissling, and Lineback (1970). They found that salinities average 3 parts per thousand higher than the average for the reef tract, with considerable variation following long periods of evaporation or rainfall. Diurnal summer water temperatures were found to range from 28° to 33° C. The water is turbid, and wave activity is less than that of the inner portion of the back reef. The sediments range from sand to mud in size, with an appreciable mud fraction in all samples. They reported that the chief sediment constituents greater than 1/16mm in order of decreasing abundance are: calcareous algae, foraminifera, rock fragments, and mollusk fragments. The more restricted portions of the Bight experience the greatest fluctuations in temperature and salinity and exhibit a larger mud fraction among the sediments because of reduced tidal exchange. As a result of the more rigorous conditions in Coupon Bight than in the reef tract environments, the biota is less diverse. Also, the more pronounced environmental gradients within the Bight produce more biotic variation than occurs in the more homogeneous reef tract environment.

Howard, Kissling, and Lineback (1970) recognized five major environments within Coupon Bight: open bay, nearshore, restricted bay, mangrove bay, and baymouth bank. Our sample stations generally correspond to these environments. With regard to the phytal varieties we sampled, *Thalassia testudinum, Penicillus capitatus*, and *Halimeda* spp. are present particularly where mud banks are developed, whereas *Dasycladus vermicularis* is locally abundant on rocky substrates.

Station I is from the restricted bay environment, approximately 15 m from shore in water 0.3 m in depth at low tide. This represents the most variable environment in the Bight with regard to temperature and salinity fluctuations. Water temperature was 32° C and salinity was 35.5 parts per thousand (ppt.) at the time of collection. Samples included *Thalassia, Dasycladus*, and associated bottom sediments.

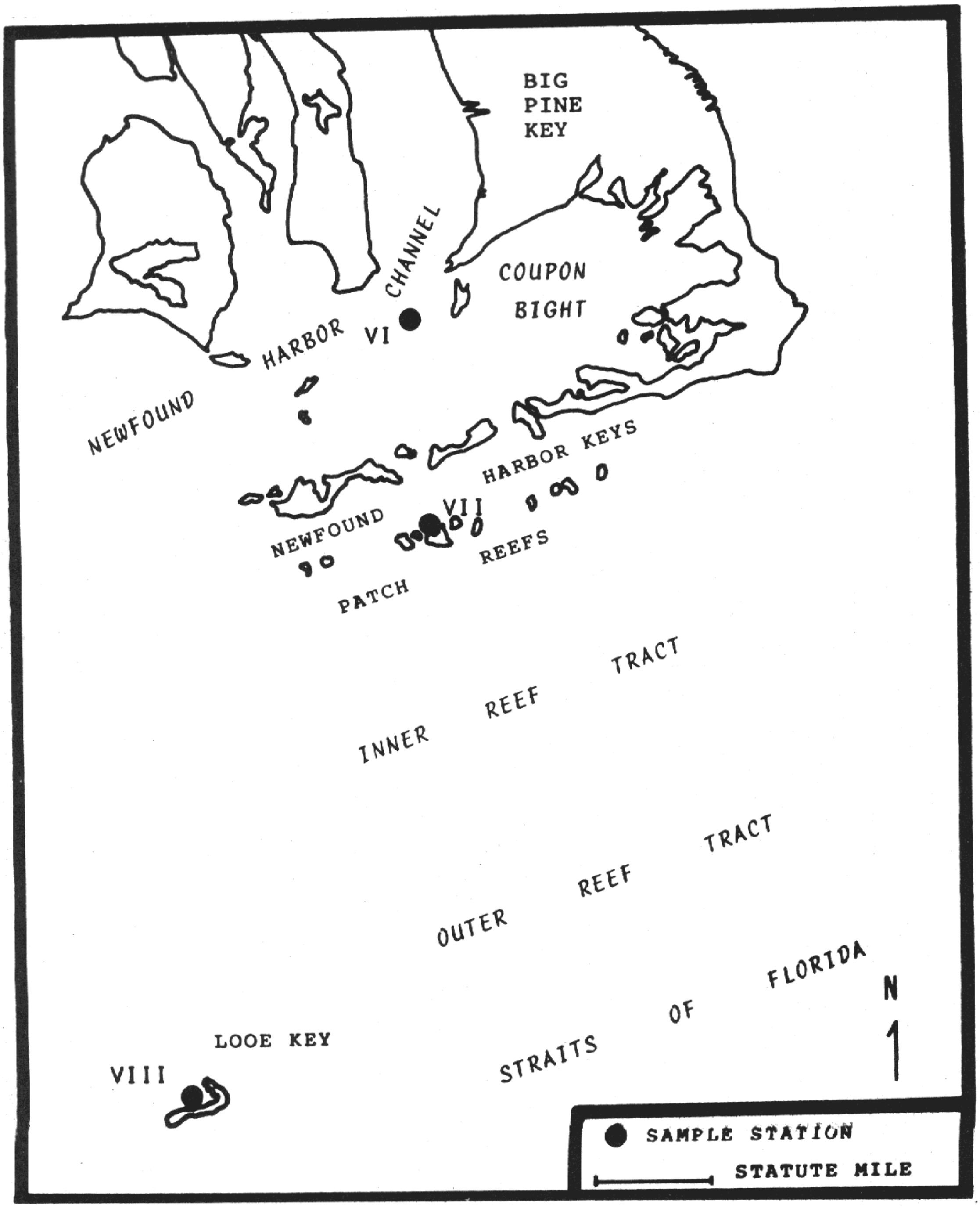

Figure 2. Reef Tract and Tidal Channel Sample Stations. VI, Tidal Channel; VII, Patch Reef, VIII, Outer Reef.

TABLE 2

	M	R	I
Outer Reef	21	77	2
Patch Reef	41	59	0
Tidal Channel	49	51	0
Baymouth Bank	80	18	2
Nearshore-Restricted Bay	67	30	3
Nearshore	79	18	3
Open Bay	74	19	7
Restricted Bay	86	13	1

Percent Occurrence of Suborders in Total Phytal Assemblage from each Station.

M = Miliolina
R = Rotaliina
T = Textulariina

Station II is in the open bay, about 150 m out from the north shore in water 1.2 m deep. Water temperature was 33°C and salinity was 36.0 ppt. *Thalassia, Dasycladus, Penicillus,* and sediments were collected.

Station III is in the nearshore environment on the western side of the Bight in water 0.5 m deep. Water temperature was 35°C and salinity was 36.0 ppt. Samples included *Thalassia, Dasycladus, Penicillus, Halimeda,* and sediments.

Station IV is from a nearshore-restricted bay environment along the south shore in water 0.3 m in depth. Water temperature was 33°C and salinity was 35.0 ppt *Thalassia, Penicillus, Dasycladus*, and associated sediments were sampled.

Station V is at a baymouth-bank near the western entrance to the Newfound Harbor Channel in water 0.3 to 0.6 m deep. Water temperature was 37°C and salinity was 36.0 parts per thousand. Samples of *Thalassia, Penicillus, Halimeda*, and bottom sediments were collected. Because of the proximity to the Newfound Harbor Channel and the resultant tidal exchange, this is assumed to be the least variable environment sampled within the Bight.

Station VI (Fig. 2) is on the east side of the Newfound Harbor Channel, just off the southwest corner of Big Pine Key. Water depth was 2.5 m, temperature was 32°C, and salinity was 36.0 ppt. Samples included *Thalassia, Penicillus,* and sediments. Because of tidal currents flowing through the channel, this is a more turbulent environment than at Stations I-V in Coupon Bight, and the biota is more closely allied to that of the inner back reef.

Station VII and VIII (Fig. 2) are from the reef tract south of Coupon Bight. Station VII is in the vicinity of a series of patch reefs in the inner portion of the back reef environment, approximately 0.8 km south of the Newfound Harbor Keys. Water depth was 1.8 m, temperature was 29°C, and salinity was 35.5 ppt. *Thalassia, Halimeda*, and bottom sediments were collected.

Station VIII is at the outer reef at Looe Key, approximately 2.8 km south of the Newfound Harbor Keys. *Thalassia, Penicillus, Halimeda*, and sediments were collected from the reef flat, just behind the actively growing reef front dominated by *Acropora palmata*. Water depth was 3.6 m, temperature was 28°C, and salinity was 35.0 ppt.

As discussed by Enos (in Enos and Perkins, 1977, p. 23-29), wave energy is greatest at the edge of the shelf where waves break over the outer reefs and decreases considerably into the inner portion of the back reef environment. Water temperatures and salinities are quite stable at the outer reef because of wave mixing and the proximity of the Gulf Stream, but vary appreciably in the inner back reef because of somewhat restricted circulation. In general, the degree of environmental variability increases from the more open waters of the outer reef to the more restricted environments of Coupon Bight, resulting in environmental gradients that affect biotic distribution.

METHODS

Field work for this study was performed in June and July, 1976. Samples of marine vegetation and associated bottom sediments were obtained from stations representing eight different major environments, ranging from restricted waters of Coupon Bight to more open ocean conditions at the outer reef off Big Pine Key. Samples were collected by hand while wading or snorkeling. Water temperature, salinity, and depth were determined at each station, and the nature of the bottom was noted.

Preliminary sampling indicated that major habitats of foraminifera in the various environments covered in this study include the calcareous codiacean algae *Penicillus capitatus* and *Halimeda* spp., the dasycladacean alga *Dasycladus vermicularis*, and the marine grass *Thalassia testudinum*. Most other plants were found to be barren of live foraminifers or to harbor only small populations. As a result, we concentrated on the previously mentioned plants, which generally yielded large numbers of living foraminifera.

At each collecting station several patches of vegetation and numerous individual plants were sampled so as to average out the commonly spotty distribution of foraminifera over local areas. Generally, we collected plants from an area approximately 40 meters in diameter at each station, and sediment samples were taken from several places within the same area. Each macrophyte was carefully harvested by hand so as not to disturb the associated epifauna. Sediment samples were taken from the upper few centimeters of sediment in the vicinity of the vegetation. All samples were placed in sea water and transported to the laboratory for immediate examination (usually within an hour or so of the time of collection).

Prior to microscopic scrutiny, each sample was carefully washed in sea water and sieved using 2 mm and 0.062 mm mesh sieves. Most specimens with agglutinated or calcareous tests survived this process undamaged, although some of the allogromiids probably were destroyed. The 2mm fraction rarly contained any foraminifera, and very few passed through the 0.062 mm sieve. The 0.062 mm fraction commonly contained abundant foraminifers and associated microorganisms, as well as organic detritus. This fraction was transferred to shallow culture dishes with sea water for microscopic examination using a binocular dissecting microscope. Living and dead foraminifera were distinguished by the methods of direct observation described by Martin and Steinker (1973), LeCalvez and Cesana (1972), and Arnold (1974), rather than by means of the rose bengal stain technique of Walton (1952) or the sudan black B stain technique of Walker, Linton, and Schafer (1974), both of which had been determined to be of questionable reliability. Population counts were based upon approximately 300 individuals from each sample.

Sanders' (1960) similarity index was used to measure the similarity of foraminiferal assemblages between samples. This method is based upon the percentage of occurrence of species common to two samples. As indicated by Murray (1973, p. 12), values greater than 80 percent are taken to indicate that two assemblages are nearly identical, and lower values indicate progressively greater differences.

RESULTS

General

Approximately 90 percent of the foraminifers recovered from the phytal substrates were determined to be alive when collected, whereas almost all of those from the bottom sediments were dead. While both juveniles and adults were present on the plants, the sediment assemblages commonly were dominated by larger and more robust tests. All species present in the sediments generally were represented by living individuals on the plants at each station, but many of the species on the plants were not found among the sediments in the same local area. The few dead individuals found on the vegetation generally belong to species found living there. Therefore, the phytal assemblage is considered to mainly represent a biocoenosis (or living assemblage), whereas the sediment assemblage is considered to mainly represent a thanatocoenosis (or death assemblage).

A total of 6,738 foraminifers from 22 phytal samples and 3,098 foraminifers from 11 sediment samples representing eight different environments were identified (approximately 300 individuals from each sample). A total of 122 benthic species were recognized, including 106 from vegetation and 84 from sediments. Thirty-six species from the vegetation were not found among the sediments of this area, and 14 species from the sediments were not found on the vegetation. Of the three foraminiferan suborders represented in the population counts, the Miliolina comprise approximately 72 percent of the total assemblage examined, the Rotalina 23 percent, and the Textulariina 5 percent. The foraminiferan fauna from our study area is typical of the south Florida fauna described by Bock (1971). Most of the species are widely distributed through the tropical Western Atlantic region, including Bermuda, the Bahamas, and the West Indies.

Phytal Samples

We identified 106 species, representing 46 genera, from 22 phytal samples. Only 25 of these species occur in frequencies greater than 1 percent in the total assemblage from vegetation. The *Miliolina* comprise 62 percent, the *Rotaliina* 36 percent, and the *Textulariina* 2 percent of the total fauna. The foraminiferal assemblages on the vegetation sampled represent essentially a living fauna, or biocoenosis, and inlcude both juveniles and adults, species of small to large test size, and species with both robust and fragile tests.

The broad blades of *Thalassia* and the calcified segments of *Halimeda* provide firm substrates for foraminiferan habitation, and accumulations of organic detritus and microorganisms on the plants provide food and shelter for the foraminifera living there. Also, the Thalassia grass beds serve as current baffles, providing a somewhat sheltered habitat and allowing the accumulation of food materials. The capitular tuft of *Penicillus* also provides shelter and an accumulation of food particles for foraminifera. *Halimeda* and *Penicillus* plants were found both within the *Thalassia* beds and in bare sediment areas. Whereas *Thalassia* and *Penicillus* were found in both restricted and open water environments, *Halimeda* was absent in the more restricted environments and *Dasycladus* was absent from the more open water environments. *Dasycladus* was found attached to loose rock fragments in Coupon Bight. In quieter waters detritus accumulated among the whorls of branchlets of *Dasycladus*, and foraminifera commonly were present on the plants. In more current-swept areas, foraminifera generally were absent.

Based upon Sanders' (1960) similarity index, the living assemblages on the different plants sampled at each station showed a relatively high degree of similarity, generally ranging between 60 and 80 percent and averaging about 68 percent. Therefore, the phytal assemblages within each major environment tend to be rather similar and the foraminiferal species do not seem to be particularly plant specific for the major phytal habitats sampled.

Because the living foraminiferal assemblages from different plants are more similar than dissimilar within each major environment, the foraminiferal population from all plants sampled at a station can be totaled to produce a more accurate representation of the local assemblage. Table 1 indicates that the total assemblages from different environments within Coupon Bight are rather similar to one another, but are dissimilar to the assemblages from the tidal channel, the patch reef, and the outer reef. Furthermore, the assemblages from the tidal channel, the patch reef, and the outer reef, when mutually compared, show intermediate values. The greatest degree of similarity is between the nearshore assemblage and the nearshore-restricted bay assemblage (80%). The least degree of similarity, as expected, is between the restricted bay assemblage and the outer reef assemblage (17%). This dissimilarity is attributed to the fact that the restricted bay experiences the greatest amount of fluctuation in environmental variables, whereas the outer reef is the most uniform environment. The intermediate values attained for comparisons of the restricted bay or outer reef assemblages with all remaining assemblages then may illustrate contrasts of environmental variability along a stress gradient, suggesting ecological regulation of populations.

TABLE 3

Outer Reef:	
<u>Thalassia</u>	37
<u>Penicillus</u>	57
<u>Halimeda</u>	25
Patch Reef:	
<u>Thalassia</u>	39
<u>Halimeda</u>	42
Tidal Channel:	
<u>Thalassia</u>	26
<u>Penicillus</u>	33
Baymouth Bank:	
<u>Thalassia</u>	23
<u>Penicillus</u>	29
<u>Halimeda</u>	38
Nearshore-Restricted Bay:	
<u>Thalassia</u>	20
<u>Dasycladus</u>	22
<u>Penicillus</u>	20
Nearshore:	
<u>Thalassia</u>	25
<u>Dasycladus</u>	29
<u>Penicillus</u>	33
<u>Halimeda</u>	32
Open Bay:	
<u>Thalassia</u>	25
<u>Dasycladus</u>	24
<u>Penicillus</u>	28
Restricted Bay:	
<u>Thalassia</u>	24
<u>Dasycladus</u>	19

Species Diversity Among the Diffrent Phytal Samples from Each Station.

For example, when comparisons so described are made with the restricted bay assemblage, and the similarity indices are ranked ordinally, the following results are obtained:

Restricted Bay vs. Open Bay	74%
Restricted Bay vs. Nearshore	72%
Restricted Bay vs. Nearshore-Restricted Bay	69%
Restricted Bay vs. Baymouth Bank	65%
Restricted Bay vs. Tidal Channel	38%
Restricted Bay vs. Patch Reef	26%
Restricted Bay vs. Outer Reef	17%

Comparisons with the outer reef assemblages produce similar results; i.e., the outer reef assemblage is most similar to the patch reef assemblage and is least similar to the restricted bay assemblage. Hence, the general trend established suggests that the assemblages reflect environmental variability along a stress gradient, with the restricted bay and outer reef as endpoints of the gradient.

As illustrated in Table 2, in the total phytal assemblages for each environment the *Miliolina* increase and the *Rotaliina* decrease in abundance from the outer reef to the more restricted waters of Coupon Bight, and the *Textulariina* (although rare in all samples) reach their greatest abundance in Coupon Bight.

Species diversity for the phytal samples ranged from a low of 19 species on *Dasycladus* in the restricted bay to a high of 57 species on *Penicillus* at the outer reef (Table 3). In general, different plants within the same major environment yielded similar diversity figures. The greatest discrepancy occurs at the outer reef where *Penicillus* yielded 57 species, *Thalassia* 37 species, and *Halimeda* 25 species. At this locality the capitular tuft of Penicillus provides a more sheltered habitat against water movement than the surfaces of *Thalassia* and *Halimeda*, which are dominated by species with greater powers of adhesion, such as *Planorbulina acervalis, Rosalina floridana*, and *Porites marginalis*. *Thalassia* is the only plant collected from all eight stations, and it shows a general increase in species diversity from Coupon Bight to the patch reef and outer reef. In addition, species diversity for the total phytal assemblage at each station increases from a low of 25 species in the restricted bay environment to a high of 71 species at the outer reef.

It is generally known that faunas in highly variable environments contain a relatively few species with chiefly large populations, whereas more stable environments tend to support more species with chiefly smaller populations. Therefore, there should be a correlation between species diversity (total number of species in a fauna) and species equitability (degree of evenness of the proportional representation of species in a fauna) that may be related to environmental variability.

The outer reef is considered to be the most stable environment and, therefore, could be expected to yield an assemblage with high diversity and evenness. In fact, species diversity at the outer reef is highest for all stations and 89 percent of the species occur in abundances of 1 percent or less, indicating a high degree of evenness. The patch reef assemblage produced the second highest number of species, 80 percent of which occur in abundances of 1 percent or less, reflecting a rather stable environment. The restricted bay and baymouth bank assemblages, as expected, serve as accurate endpoints for the Coupon Bight assemblages plotted along the inferred environmental variability gradient. The baymouth bank assemblage shows the greatest diversity (46 species) and evenness (78 percent occur in abundances of 1 percent or less). The restricted bay assemblage yielded the lowest diversity (25 species) and evenness (64 percent occur in abundances of 1 percent or less), and only three species comprise 70 percent of the fauna, reflecting a rather variable environment. Thus, the living foraminiferal assemblages

TABLE 4

	M	R	I
Outer Reef	56	39	5
Patch Reef	69	28	3
Tidal Channel	69	30	1
Baymouth Bank	84	13	3
Nearshore-Restricted Bay	85	14	1
Nearshore	82	13	5
Open Bay	83	12	5
Restricted Bay	78	20	2

Percent Occurrence of Suborders in Total Assemblage from Each Station.

M = Miliolina
R = Rotaliina
T = Textulariina

examined do generally illustrate a correlation between species diversity and equitability as related to environmental variability, and the living populations seem to be reliable indicators of environment.

Sediment Samples

We identified 84 species, representing 36 genera, from 11 sediment samples collected in the vicinities of the phytal samples at the eight stations. Only 21 of these species occur in frequencies greater than 1 percent in the total assemblage from the sediments. The *Miliolina* comprise 77 percent, the *Rotaliina* 17 percent, and the *Textulariina* 6 percent of the total fauna. The foraminiferal assemblage from the sediments represents essentially a thanatocoenosis, with very few living individuals. In the more turbulent environments of the outer reef and the patch reef most of the tests among the sediments are relatively large and robust and many are abraded. In the less dynamic environments of Coupon Bight there is an increase in the number of juveniles and of smaller and more fragile tests. Species diversity generally decreases from the outer reef to the restricted bay environment. The *Miliolina* increase in abundance and the *Rotaliina* decrease in abundance from the outer reef to Coupon Bight (Table 4). The *Textulariina* occur in low frequencies in all environments.

As with the phytal assemblages, Sanders' similarity index was used to compare the sediment assemblages from the different environments (Table 5). The sediment assemblages, even from adjacent environments, generally do not show a high degree of similarity to one another. The greatest degree of similarity is between the open bay assemblage and the nearshore assemblage within Coupon Bight. The least degree of similarity, as might be expected is between the restricted bay assemblage and the outer reef assemblage.

When the restricted bay assmeblage is compared with each of the other assemblages, as with the phytal samples, the following results are obtained:

Restricted Bay vs. Open Bay	24%
Restricted Bay vs. Nearshore	36%
Restricted Bay vs. Nearshore-Restricted Bay	56%
Restricted Bay vs, Baymouth Bank	19%
Restricted Bay vs. Tidal Channel	28%
Restricted Bay vs. Patch Reef	11%
Restricted Bay vs. Outer Reef	5%

No general trend can be discerned from these figures, except that the sediment assemblages within the Bight are somewhat more similar to one another than they are to the assemblages from the reef tract. Furthermore, the correlation between species diversity and equitability as related to environmental variability established for the phytal assemblages is less evident among the sediment assemblages. For example, the patch reef assemblage yielded the highest number of species, 66 percent of which occur in abundances of 1 percent or less, and the outer reef assemblage yielded the second highest number, 68 percent of which occur in abundances of 1 percent or less. Among the Coupon Bight samples, the nearshore-restricted bay produced the highest number of species, 41 percent of which occur in abundances of 1 percent or less, and the restricted bay produced the lowest number, 47 percent of which occur in abundances of 1 percent or less and three of which comprise 69 percent of the fauna.

It appears that postmortem processes result in a loss of information, so that the sediment assemblages do not accurately reflect changes in the character of the living faunas along the inferred gradient of environmental variability.

TABLE 5

STATION	I	II	III	IV	V	VI	VII	VIII
I		24	36	56	19	28	11	5
II			71	36	55	40	42	30
III				49	60	48	44	31
IV					36	41	20	13
V						44	42	30
VI							31	21
VII								52
VIII								

Comparison of Total Sediment Assemblages Found at Different Sample Stations Using the Similarity Index of Sanders. I, Restricted Bay; II, Open Bay; III, Nearshore; IV, Nearshore-Restricted Bay; V, Baymouth Bank; VI, Tidal Channel; VII, Patch Reef; VIII, Outer Reef.

Comparison of Phytal Samples and Sediment Samples

A greater total number of species was found living on the vegetation (106 species) than was found among the bottom sediments (84 species). Also, at each station species diversity was generally higher for the phytal samples than for the sediment samples. In both sets of samples diversity generally decreased from the outer reef to the restricted bay environment (Table 6).

Among the vegetation assemblages, there was a fairly consistent increase in the Miliolina and decrease in the Rotaliina from the more open waters of the outer reef to the more restricted environments of Coupon Bight, and the same is generally true for the sediment assemblages. However, whereas the ratios of *Miliolina* to *Rotaliina* are similar for both sets of samples in Coupon Bight, the *Miliolina* comprise a significantly higher percentage of the sediment assemblages and lower percentage of the phytal assemblages of the outer reef, the patch reef, and the tidal channel. In these more turbulent environments, many of the smaller and more fragile tests of the *Rotaliina* evidently are winnowed out or destroyed by wave and current action and larger and more robust tests of the *Miliolina* (particularly *Archaias angulatus*) are differentially preserved among the sediments. The generally slightly higher number of tests of the Textulariina among the sediments than on the vegetation suggests that some members of this suborder may regularly live upon the sediment substrate as well as upon plants.

As shown below, there is a general increase in the similarity between sediment and phytal assemblages from the outer reef to the restricted bay environment, suggesting that among the sediments the amount of size sorting of tests and differential destruction of fragile tests decreases in more sheltered environments.

Outer Reef	25%
Patch Reef	27%
Tidal Channel	41%
Baymouth Bank	31%
Nearshore-Restricted Bay	49%
Nearshore	60%
Open Bay	52%
Restricted Bay	59%

The average similarity index for total phytal and sediment assemblages from the same environments is 43 percent, indicating no great similarity between the two. The range for the similarity index is from 25 percent at the outer reef to 60 percent in the nearshore environment in Coupon Bight.

On the reef flat at Looe Key the dominant species living on the vegetation were *Rosalina floridana* (46%), *R. floridensis* (6%), *Sorites marginalis* (5%), and *Asterigerina carinata* (3%), whereas the dominant species among the sediments were *Archaias angulatus* (17%), *Asterigerina carinata Rotalia rosea* (10%), *Peneroplis proteus* (9%), *Textularia agglutinans* (5%), *Discorbis mira* (4%), *Peneroplis pertusus* (3%), and *Quinqueloculina agglutinans* (3%). Therefore, the two assemblages show little similarity with regard to the dominant species.

At the patch reef the dominant species living on the vegetation were *Rosalina floridana* (31%), *Planorbulina acervalis* (8%), *Rosalina floridensis* (6%), *Triloculina oblonga* (6%), *Discorbis mira* (5%). *Miliolinella circularis* (5%), *M. fichteliana* (3%), and *Sorites marginalis* (3%), whereas the dominant species among the sediments were *Archaias angulatus* (17%), *Discorbis mira* (9%), *Quinqueloculina lamarckiana* (7%), *Rotalia rosea* (6%), *Borelis pulchra* (4%), *Miliolinella labiosa* (4%), *Peneroplis pertusus* (4%), *Quinqueloculina bidentata* (4%), *Q. bradyana* (4%), *Q.tricarinata* (3%), *Rosalina floridana* (3%), and *Triloculina linneiana* (3%). Again, there is little similarity in proportional representation of species, and the sediment assemblage is dominated by larger and more robust forms.

At the other end of the environmental gradient, in less turbulent but more variable environments, in the nearshore environment in Coupon Bight the phytal assemblage is dominated by *Archaias angulatus* (28%), *Rosalina floridana* (16%), *Miliolinella circularis* (11%), *M. labiosa* (5%), *Quinqueloculina bidentata* (4%), *Q. poeyana* (4%), *Androsina lucasi* (3%), *Triloculina bassensis* (3%), *T. bermudezi* (3%), and *T. rotunda* (3%), and the sediment assemblage is dominated by *Archaias angulatus* (23%), *Triloculina bassensis* (10%), *Miliolinella labiosa* (8%), *Quinqueloculina poeyana* (8%), *Androsina lucasi* (6%), *Elphidium discoidale* (5%), *Valvulina oviedoiana* (5%), *Quinqueloculina bidentata* (4%), *Q. bosciana* (4%), *Q. lamarckiana (3%), Q. seminulinum* (3%), *Rosalina floridana* (3%), and Triloculina bermudezi (3%). In the restricted bay the dominant phytal species are *Androsina lucasi* (45%), *Miliolinella circularis* (12%), *Rosalina floridana* (10%), *Miliolinella labiosa* (4%), *Quinqueloculina poeyana* (4%), and *Triloculina bassensis* (3%), and the dominant sediment species are *Androsina lucasi* (42%), *Quinqueloculina bosciana* (15%), *Elphidium discoidale* (12%), *Quinqueloculina poeyana* (8%), *Triloculina bassensis* (6%), *Elphidium excavatum* (3%), and *Miliolinella labiosa* (3%). Thus, in these environments there is a closer correspondence between the dominant species on the vegetation and among the sediments.

DISCUSSION

It has long been known that at least some foraminifera live on benthic marine vegetation in shallow-water environments. In the Caribbean region, for example, Cushman (1922) reported an association of living species on marine grasses around the Dry Tortugas. M.A. Illing (1950, 1952) noted that living assemblages occur on phytal surfaces in the Bahamas and observed that the foraminiferal content in sediments rises in areas where there are large amounts of marine vegetation. Howard (1965) found the same to be true in the vicinity of Big Pine Key, Florida. Bock (1967) determined that 64 percent of the foraminifera found upon Thalassia samples in the Florida Keys were living and that only 2 percent among the sediments were alive. Wright and Hay (1971) found more living foraminifers on vegetation than among sediments and fewer living foraminifers among the sediments in bare sediment areas than in vegetated areas in south Florida. Grant and others (1973) determined that most individuals encountered on plants were alive and most among the sediments were dead in the nearshore zone of Coupon Bight. Brasier (1975a, 1975b) found a larger standing crop of foraminifers on plants than on other substrates at Barbuda. Marshall (1976) found abundant foraminifera living upon dead, algal-encrusted corals and on benthic algae at Pedro Bank, south of Jamaica, but found few living among the sediments of this area. Steinker and Steinker (1976) confirmed these observations at Jewfish Cay in the Bahamas, as did Steinker (1980) in Bermuda and Steinker and Rayner (1981) at St. Croix. These studies tend to corroborate our observations that the living populations of foraminifera in the Florida Keys are concentrated upon phytal surfaces rather than among the sediments.

We found that approximately 90 percent of the foraminifera recovered from the major plant habitats sampled were alive when collected. The dead portion of the phytal assemblages may be accounted for as recently deceased individuals that had not yet become detached and as tests that may have settled on the plants after displacement from sediments or from other plants by water turbulence.

Few studies mention specific kinds of plants upon which foraminifera are found to be living. Several authors have recognized the marine grass Thalassia testudinum as an important foraminiferal habitat (Cushman, 1922; Bock, 1967; Grant and others, 1973; Brasier, 1975a; Steinker and Steinker, 1976; Steinker, 1980; Steinker and Rayner, 1981). Grant and others (1973) found *Thalassia*, *Dasycladus*, *Penicillus*, and *Halimeda* to be important habitats in the

TABLE 6

	Vegetation	Sediments	Total
Outer Reef	71	48	87
Patch Reef	50	50	73
Tidal Channel	36	28	45
Baymouth Bank	46	29	55
Nearshore-Restricted Bay	31	34	42
Nearshore	44	29	48
Open Bay	36	29	45
Restricted Bay	25	17	29

Special Diversity. Total number of species from phytal samples, from sediment samples, and total number of species identified at each station.

nearshore zone in Coupon Bight, with other plants yielding few live foraminifers. Steinker and Steinker (1976) reported foraminifera living on *Thalassia, Penicillus, Rhipocephalus, Halimeda,* and *Dasycladus* in the shallow waters around Jewfish Cay in the Bahamas, but found few individuals on *Diplanthera, Udotea, Dictyota, Caulerpa,* and mats of filamentous algae. Steinker (1980) observed living foraminifera associated with *Thalassia, Diplanthera, Halimeda, Penicillus, Padina, Amphiroa*, and *Centroceras* in the nearshore zone at Bermuda. And at St. Croix Steinker and Rayner (1981) reported foraminifera living on *Thalassia, Penicillus, Halimeda, Padina, Amphiroa*, and *Cladophoropsis*, whereas *Caulerpa, Dictyota*, and *Dilophus* yielded few individuals.

Brasier (1975a, 1975b) found that the faunal composition and standing crop of foraminiferal populations on phytal substrates are related to the structure of the host plant, the amount of detritus present, and the physical conditions of the environment, such as turbulence, as was also discussed by Grant and others (1973), Steinker (1977), and Steinker and Rayner (1981). This is in agreement with our observations. Some plants are structurally more suitable for habitation than others. Accumulations of organic detritus provide food and shelter for foraminifera, and the amount of detritus present depends upon the structure of the host plant, the amount of water turbulence, and the presence of a biotic source for the detritus. Brasier (1975a, p.53) further concluded that "locality rather than weed type affects the similarity of phytal faunas," which agrees with our observations concerning the basic similarity of phytal faunas from different suitably habitable plants within the same environment.

Murray (1970), working in Abu Dhabi Lagoon in the Persian Gulf, concluded that in carbonate depositional environments living populations of foraminifera largely are found on seaweeds because of the low organic content of the sediments. But Brasier (1975a, 1975b), working on the foraminifera from lagoons, shoals, and reefs around Barbuda in the Lesser Antilles, recognized a sediment-dwelling fauna, a primary weed fauna, and a secondary weed fauna derived from the substrate, using rose bengal stain to distinguish living from dead individuals. He found living foraminifers to be scarce among coarser sediments in the shore zone, in sand blankets, and in interreef areas. On the other hand, he reported high standing crops among finer sediments in backreef and bay environments and in seagrass beds. Brasier attributed this association of living foraminifers with finer sediments to the higher organic content and consequently a greater food supply.

However, using direct methods of observation to determine living individuals, we were unable to recognize a primarily sediment-dwelling fauna from our samples, although it is possible that at least some of the agglutinated species do live regularly among the sediments. This general scarcity of sediment-dwellers applied not only to the coarser sediments of the reef areas, but also to the finer sediments of the grass beds and Coupon Bight where the organic content is higher. It was noted that in less turbulent environments where the organic content of the sediments is high the material immediately below the substrate surface usually was dark in color, indicating reducing conditions that may inhibit foraminiferan habitation. It might be noted that in culture many of the species we encountered tend to move up onto the sides of the container, suggesting that they might also tend to move up onto plants in their natural environment.

Brasier (1975a, 1975b) found a greater diversity of species and greater relative abundance of rotaliids in open waters than in the lagoonal environment at Barbuda, which is consistent with our findings. The greater species diversity in open waters where there is greater stability of physical conditions is attributed to the addition of more stenopic species to the fauna, whereas the lagoonal fauna is dominated by fewer, more euryopic species, occurring in large numbers. Past experience with some of these species in laboratory cultures suggests that many of the miliolids (such as *Miliolinella circularis, M. labiosa, Triloculina bermudezi, T. bassensis*, and *T. rotunda*) are more euryopic than the majority of rotaliids (except for a few species, such as

Rosalina floridana and *Discorinopsis aguayoi*), so that the relative abundance of miliolids increases in more variable environments.

Numerous studies have suggested that seasonal fluctuations regularly occur in nearshore foraminiferal populations. For example, Scott and Medioli (1980) reported highly variable living populations and assemblages in a Nova Scotia salt marsh over a three-year period, which they attributed to climatic or micro-environmental changes; however, the total assemblage did not change significantly during this time. Most such studies have been carried out in temperate waters, especially in marginal marine environments, and most have dealt with sediment assemblages; few have concentrated upon phytal assemblages from warm waters.

Bock (1967) monitored foraminiferal populations on *Thalassia* in south Florida for one year. He found that the population size of *Rosalina florida*na increased with a rise in temperature and at the same time the numbers of *Miliolinella* circularis decreased. Bock's findings are in accord with those of Buzas, Smith, and Beem (1977), who monitored for a year the effect of temperature on foraminifera from two *Thalassia* habitats in Jamaica. They found an increase in the population size of *Rosalina floridana* and other species during the summer months. These observations suggest that population size of at least some species may be correlated to the periodicity of seasonal temperature fluctuations.

The present study lacks the dimension of seasonality. It might be noted, however, in contrast to the findings of Bock (1967), that where *Rosalina floridana* is dominant on vegetation at the reef tract and tidal channel stations, *Miliolinella circularis* does occur in low abundance, but in Coupon Bight these two species occur in nearly equal numbers.

SUMMARY

Foraminifera are common both among the bottom sediments and on certain types of vegetation in reef tract and lagoonal environments in south Florida, and the foraminiferan fauna of this region is diverse. A total of 122 species were identified from phytal and sediment samples at eight stations representing a variety of environments. The large majority of individuals found upon selected marine algae and grass blades were alive, whereas almost all in the sediment samples were dead. Plants which provide a firm substrate for attachment or provide shelter for foraminifers and which are sites of organic detrital accumulation are favored habitats for foraminifera in the area studied.

The living fauna on the vegetation is more diverse than the dead assemblage among the sediments, with 106 species identified from phytal surfaces and only 84 species identified from sediment samples. Many species with small or fragile tests are only rarely represented among the sediments, especially in more turbulent environments. Also, both juveniles and adults are present on the plants, whereas the sediment assemblages are dominated by adult tests which frequently are worn and abraded.

Within each major environment the foraminiferal assemblages from the different plant habitats tend to be similar, so that most species are not particularly plant specific with regard to habitat. However, species with large, flattened tests, such as *Planorbulina acervalis* and *Sorites marginalis*, are more common on plants like *Thalassia* and *Halimeda* which provide a relatively firm and wide surface area for attachment, and some of the smaller species are more common on *Penicillus* where the density clumped filaments of the capitular tuft provide protection against water turbulence. Sanders' similarity index indicates that the phytal faunas from the various environments within Coupon Bight are all rather similar to one another, but are dissimilar to those from the tidal channel and reef tract. A major distinction between phytal assemblages from the different environments of Coupon Bight is that *Archaias angulatus* is common in the more open-water environments but is replaced by *Androsina lucasi* in more restricted environments. The phytal faunas of the tidal channel, patch reef, and outer reef are somewhat less similar to one another than are the faunas from the Bight.

The composition and distribution of the phytal fauna appear to largely be regulated by environmental variability, with the outer reef as the least variable and the restricted bay as the most variable environment. This conclusion is supported by the correlation between species diversity and evenness as related to environmental variability. The most variable environment supports a low diversity fauna, apparently composed of euryopic species, and the least variable environment supports a high diversity fauna, consisting of more stenopic species.

The sediment assemblages differ from the phytal faunas for each station, but the degree of similarity between the two generally increases from the more turbulent waters of the outer reef to the quieter environments of Coupon Bight. This is explained by the more intense differential destruction and sorting of tests among the coarser sediments of the more dynamic environments. In more turbulent environments the sediment assemblage bears little resemblance to the living fauna in terms of the proportional representation of species. In the fossil record this might preclude the accurate reconstruction of the original community, thus impeding paleoecologic analysis based on Community structure. However, in less turbulent environments the sediment assemblage more accurately reflects the original living fauna.

Even though the thanatocoenosis among the sediments may not closely correspond to the biocoenosis of the local area, the final death assemblage among the sediments can be used for paleoenvironmental reconstruction in the sedimentary record. For example, species diversity decreases as environmental variability increases. The number of small, fragile, and juvenile tests increases in less turbulent waters. The *Miliolina* generally increase and the *Rotaliina* decrease from the outer reef into lagoonal areas. And the general proportional representation of species and the presence of characteristic species can be used as indicators of environment.

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