

**ATOLL RESEARCH BULLETIN**

**NO. 475**

**EPIPHYTIC FORAMINIFERA OF THE PELICAN CAYS,  
BELIZE: DIVERSITY AND DISTRIBUTION**

**BY**

**SUSAN L. RICHARDSON**

**ISSUED BY  
NATIONAL MUSEUM OF NATURAL HISTORY  
SMITHSONIAN INSTITUTION  
WASHINGTON, D.C., U.S.A.  
MARCH 2000**

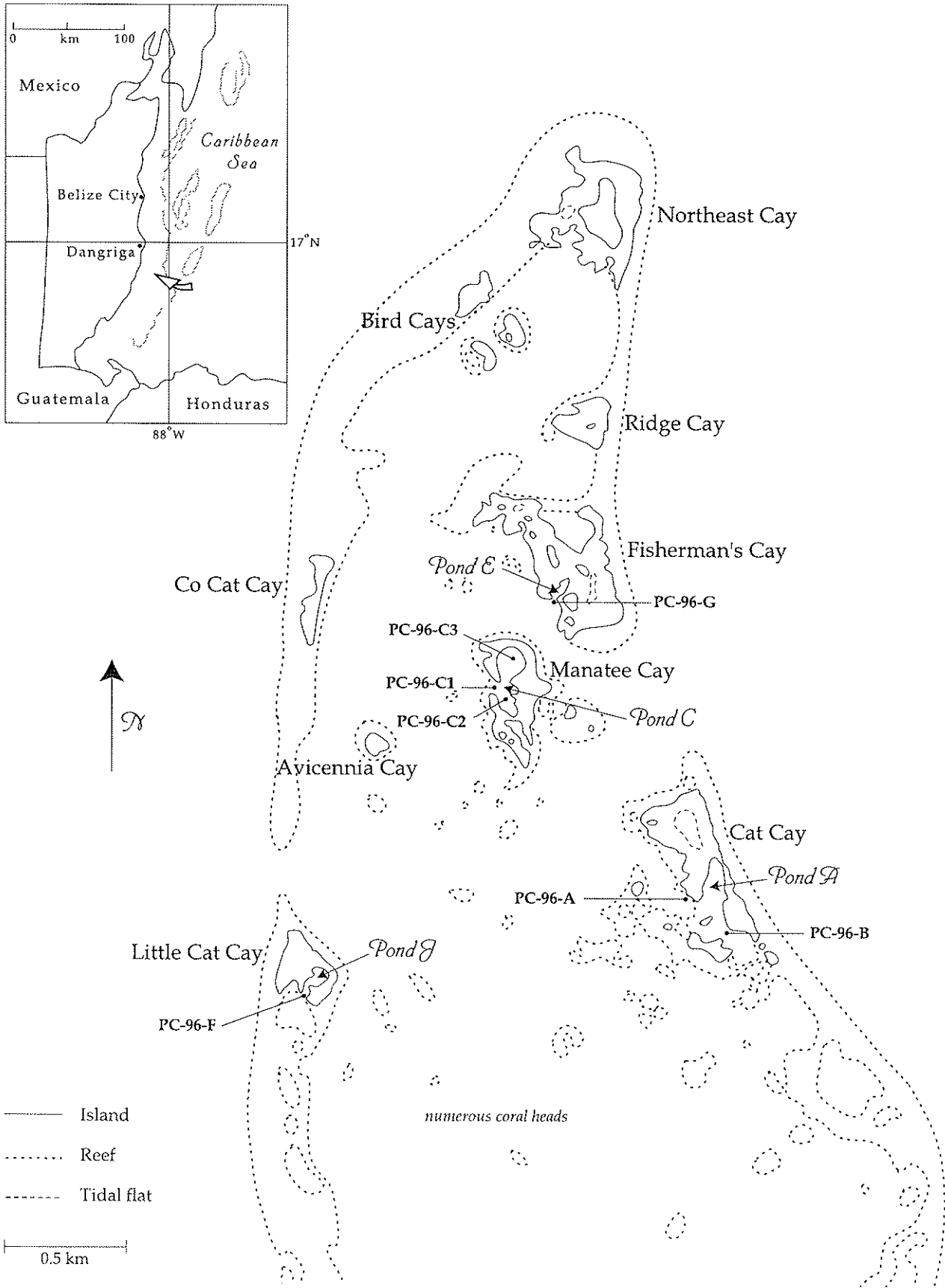


Figure 1. Map showing locations of sampling sites (August 1996) in the Pelican Cays, Belize.

# EPIPHYTIC FORAMINIFERA OF THE PELICAN CAYS, BELIZE; DIVERSITY AND DISTRIBUTION

BY

SUSAN L. RICHARDSON<sup>1</sup>

## ABSTRACT

The diversity and distribution of epiphytic foraminifera living on the seagrass *Thalassia testudinum* were surveyed at six localities in the Pelican Cays, Belize. A total of seven species, two of them new, were identified from these sites. Estimates of standing stock range from  $6.35 \times 10^3$  to  $6.90 \times 10^4$  individuals/m<sup>2</sup> of the seafloor, and population densities range from 13.60 to 80.81 individuals/100 cm<sup>2</sup> of leaf surface area. The faunal assemblages are characterized by low species richness (S = 3 to 6), high dominance (37.91 to 89.91%), and moderate evenness (E = 0.42 to 0.80). A SHE analysis (Buzas and Hayek, 1996) performed for the Pelican Cays data indicates that the distribution of epiphytic foraminifera on *Thalassia* most closely resembles a log-series pattern (Fisher et al., 1943).

## INTRODUCTION

As organisms, benthic foraminifera form an integral component of seagrass communities in the tropical Western Atlantic region, living both in the sediments (Bock, 1967, 1971; Buzas et al., 1977) and as epiphytes on blades of seagrass (Brasier, 1975 a, 1975b; Steinker and Steinker, 1976; Steinker and Rayner, 1981; Martin, 1986; Waszczak and Steinker, 1987; Martin and Wright, 1988). Previous studies of Belizean foraminiferal faunas have focused exclusively on the sediment-dwelling assemblages (Cebulski, 1969; Wantland, 1975). Wantland (1975, p. 358) observed the highest diversities and abundances in monospecific stands of the seagrass *Thalassia testudinum* and therefore speculated that most benthic foraminiferal inhabitants of "shallow back-reef environments live attached to plants and other floral and faunal elements above the sediment surface."

The objective of this study was to survey the diversity and distribution of the foraminiferal species living on *Thalassia testudinum* in the Pelican Cays, Belize, Central America (Fig. 1). This paper presents the results of preliminary field collections and observations that took place in August 1996.

---

<sup>1</sup>Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA.  
Present Address: Department of Geology and Geophysics, MS-08, Woods Hole Oceanographic Institution, Woods Hole, MA 02540, USA.

## MATERIAL AND METHODS

Samples of the seagrass *Thalassia testudinum* Banks ex König (Fig.2) were collected by snorkeling from seven localities in the Pelican Cays: off Cat Cay, Pond A of Cat Cay, three locations in Pond C of Manatee Cay, Pond J of Little Cat Cay, and Pond E of Fisherman's Cay (Fig. 1, Appendix 1). Samples were collected by removing all shoot bundles and attached seagrass blades from a 10-by-20 cm quadrat. They were then transported to the lab in a cooler, fixed in 4–5% formaldehyde in seawater, and transferred to 70% EtOH for storage. Live individuals still attached to their seagrass substrate were examined in the wet lab on Carrie Bow Cay using a binocular microscope (Wild M3).

At Pond A, J, and C sites, shoot densities of *Thalassia* were estimated by counting all shoots in two 25-by-25 cm quadrats, and the mean value was used to calculate the shoot densities per m<sup>2</sup> of seafloor. At the Pond E site, shoot densities were estimated by counting all shoots in a single 10-by-20 cm quadrat. Leaf area indices (LAIs) were calculated for each site by measuring all *Thalassia* blades collected from two 10-by-20 cm quadrats and using the mean value as an estimate of the leaf surface area available for settlement by epiphytic organisms per m<sup>2</sup> of seafloor. Epiphyte load was determined from the average dry weights of leaves and epiphytes removed from all *Thalassia* blades collected from two 10-by-20 cm quadrats. Epiphytes were scraped from both sides of each leaf with a razor blade, and leaves and epiphyte scrapings were dried for 8 hrs. at 105°C prior to weighing.

For the purposes of this study, an epiphyte is defined as "any organism that lives upon a plant and completes its production while it is still attached to that plant. This definition includes the coralline red algae but excludes mobile gastropods and benthic foraminifera which are able to move between leaves and thus are likely to produce for larger periods of time " (Frankovich and Ziemann, 1994, p. 682). This definition corresponds to Langer's (1993) category of "permanently attached" epiphytic foraminifera, but excludes species he categorized as "temporarily attached" and "motile."

All epiphytic foraminifera were within a single 10-by-20 cm quadrat of *Thalassia* blades for each locality. Examination of fresh material in the laboratory on Carrie Bow Cay showed that all specimens still attached to the leaf blades contained cytoplasm and were alive. Live specimens were recognized by evidence of pseudopodial activity, feeding cysts and cytoplasmic coloration. The original cytoplasmic coloration was also preserved in samples that had been initially fixed in 5% formaldehyde, then transferred to 70% EtOH.

## RESULTS

The estimated number of *Thalassia* shoots per m<sup>2</sup> of seafloor varied from site to site in the Pelican Cays (Table 1). The highest shoot densities were seen in Pond A (928 ± 32 shoots/m<sup>2</sup> seafloor), while the lowest densities were recorded just outside this pond, off the western side of Cat Cay (424 ± 56 shoots/m<sup>2</sup> seafloor). Ponds C and E yielded similar estimates of shoot density, 616 ± 56 and 600 shoots/m<sup>2</sup> seafloor, respectively. Leaf area indices calculated for each site appear to correlate with shoot densities in general, ranging from a low value of 1.99 at Cat Cay to a high value of 4.01 at Pond J. Observed values of epiphyte and seagrass dry weights appear to be positively correlated with shoot densities for each site. Seagrass dry weights range from 37.18 ± 17.13 gdw/m<sup>2</sup> seafloor at the Cat Cay site to 77.36 ± 17.18 gdw/m<sup>2</sup> seafloor at the Pond J site,

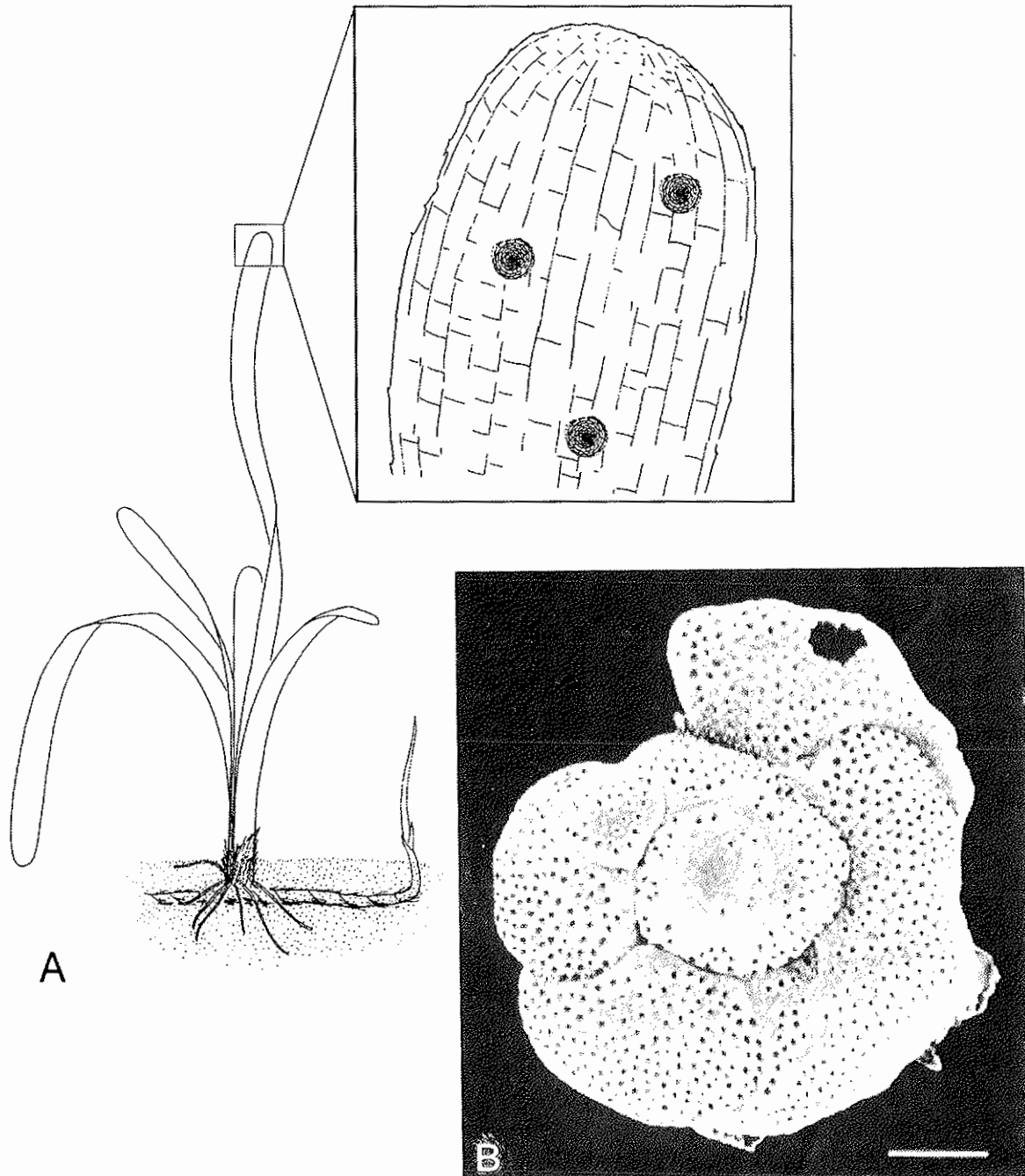


Figure 2. Examples of epiphytic foraminifera. A) Schematic illustration of seagrass *Thalassia testudinum* with detail of a blade showing attached epiphytic foraminifera (M.E. Parish after I.C. Feller). B) Scanning electron photomicrograph of *Belizeanella candeiana* (scale = 100  $\mu\text{m}$ ).

while epiphyte dry weights range from  $3.48 \pm 0.48$  gdw/m<sup>2</sup> seafloor to  $7.20 \pm 2.05$  gdw/m<sup>2</sup> seafloor at these same sites, respectively. Values of epiphyte load were calculated from the measured dry weights of the epiphytes and seagrass at each site in accordance with the method of Tomasko and Lapointe (1991). The lowest value of epiphyte load was observed at Pond A ( $7.56 \pm 6.06\%$ ), the highest value at Pond A ( $10.85 \pm 5.61\%$ ). Intermediate values of epiphyte load were calculated for the sites at the entrance to Pond C ( $8.08 \pm 3.40\%$ ) and Pond J ( $8.41 \pm 0.52\%$ ).

Table 1. Seagrass and epiphyte data from Pelican Cays sample locations.

Parameter <sup>a</sup>	Pond C				
	Cat Cay	Pond A	(entrance)	Pond J	Pond E
Mean shoot density (# shoots/ m <sup>2</sup> seafloor) <sup>b</sup>	424 ± 56	928 ± 32	616 ± 56	808 ± 152	600
Mean leaf area index (LAI) (m <sup>2</sup> leaf surface area/m <sup>2</sup> seafloor)	1.99 ± 0.78	3.26 ± 0.70	3.13 ± 0.26	4.01 ± 0.90	2.59
Mean epiphyte biomass (gdw/m <sup>2</sup> seafloor)	3.48 ± 0.48	5.00 ± 3.7	5.15 ± 2.58	7.20 ± 2.05	—
Mean seagrass biomass (gdw/m <sup>2</sup> seafloor)	37.18 ± 17.13	70.15 ± 14.95	56.40 ± 3.41	77.36 ± 17.18	—
Epiphyte load (%) <sup>a</sup>	10.85 ± 5.61	7.56 ± 6.06	8.08 ± 3.40	8.41 ± 0.52	—

<sup>a</sup>Mean values calculated from two quadrats ± deviation from mean.

<sup>b</sup>Shoot density calculated from a single 20-by-20-cm quadrat; LAI value calculated from a single 10-by-20-cm quadrat collected for epiphytic foraminiferal census.

<sup>c</sup>Weight epiphytes/(weight epiphytes + weight seagrass) x 100.

Standing stock estimates of epiphytic foraminiferal populations were calculated from the total number of individuals counted in each quadrat (Tables 2 and 3). The highest standing stock was observed on the ridge at Pond C ( $6.90 \times 10^4$  individuals/m<sup>2</sup>seafloor); however, just inside the lagoon, the standing stock drops by an order of magnitude ( $7.85 \times 10^3$  individuals/m<sup>2</sup>seafloor). Relatively high estimates,  $1.29 \times 10^4$  and  $2.09 \times 10^4$  individuals/m<sup>2</sup> seafloor, respectively, were obtained from both the Pond A and Pond E sites. The lowest standing stock estimates were calculated for the Cat Cay ( $7.65 \times 10^3$  individuals/m<sup>2</sup> seafloor) and Pond J sites ( $6.35 \times 10^3$  individuals/m<sup>2</sup> seafloor).

Table 2. Number of individuals of epiphytic Foraminifera per sample from Pelican Cays locations.

Species	Cat Cay	Pond C		Pond J	Pond E	
		Pond A	(ridge)			(lagoon)
<i>Belizeanella candeiana</i>	1	0	0	0	0	
<i>Cornuspira planorbis</i>	0	0	2	0	0	
<i>Cornuspiramia antillarum</i>	58	194	549	0	31	48
<i>Hemidiscella palabunda</i>	0	1	2	10	0	0
<i>Iridia</i> n. sp.	36	21	471	141	14	62
<i>Planorbulina acervalis</i>	56	41	339	6	82	307
<i>Rhizonubecula</i> n. sp.	2	1	17	0	0	2
Total	153	258	1,80	157	127	419

Table 3. Standing stock of Foraminifera from Pelican Cays sample locations (# individuals/m<sup>2</sup> seafloor).

Species	Cat Cay	Pond C		Pond J	Pond E	
		Pond A	(ridge)			(lagoon)
<i>Belizeanella candeiana</i>	$5.00 \times 10^1$	0	0	0	0	
<i>Cornuspira planorbis</i>	0	0	$1.00 \times 10^2$	0	0	
<i>Cornuspiramia antillarum</i>	$2.90 \times 10^3$	$9.70 \times 10^3$	$2.75 \times 10^4$	0	$1.55 \times 10^3$	$2.40 \times 10^3$
<i>Hemidiscella palabunda</i>	0	$5.00 \times 10^1$	$1.00 \times 10^2$	$5.00 \times 10^2$	0	0
<i>Iridia</i> n. sp.	$1.80 \times 10^3$	$1.05 \times 10^3$	$2.36 \times 10^4$	$7.05 \times 10^3$	$7.00 \times 10^2$	$3.10 \times 10^3$
<i>Planorbulina acervalis</i>	$2.80 \times 10^3$	$2.05 \times 10^3$	$1.70 \times 10^4$	$3.00 \times 10^2$	$4.10 \times 10^3$	$1.53 \times 10^4$
<i>Rhizonubecula</i> n. sp.	$1.00 \times 10^2$	$5.00 \times 10^1$	$8.50 \times 10^2$	0	0	$1.00 \times 10^2$
Total	$7.65 \times 10^3$	$1.29 \times 10^4$	$6.90 \times 10^4$	$7.85 \times 10^3$	$6.35 \times 10^3$	$2.09 \times 10^4$

Population densities of epiphytic foraminifera on *Thalassia* blades were calculated from the measured leaf surface area per quadrat and the total number of individuals counted in each sample (Table 4). The highest densities were observed in the samples collected from Pond E (80.81 individuals/100 cm<sup>2</sup> of leaf surface area) and the ridge in Pond C, Manatee Cay (69.38 individuals/100 cm<sup>2</sup> of leaf surface area). Intermediate densities were seen at Cat Cay (40.87 individuals/100 cm<sup>2</sup> of leaf surface area) and Pond A (36.58 individuals/100 cm<sup>2</sup> of leaf surface area), while the lowest densities were observed in samples collected from Pond J (16.97 individuals/100 cm<sup>2</sup> of leaf surface area) and Pond C (13.60 individuals/100 cm<sup>2</sup> of leaf surface area).

Table 4. Relative density of Foraminifera at Pelican Cays sample locations (# individuals/100m<sup>2</sup> leaf surface area).

Species	Pond C		Pond C		Pond J	Pond E
	Cat Cay	Pond A	(ridge)	(lagoon)		
<i>Belizeanella candeiana</i>	0.27	0	0	0	0	0
<i>Cornuspira planorbis</i>	0	0	0.10	0	0	0
<i>Cornuspiramia antillarum</i>	15.49	27.51	27.60	0	4.14	9.26
<i>Hemidiscella palabunda</i>	0	0.14	0.10	0.86	0	0
<i>Iridia</i> n.sp.	9.62	2.98	23.68	12.22	1.87	11.96
<i>Planorbulina acervalis</i>	14.96	5.81	17.04	0.52	10.96	59.21
<i>Rhizonubecula</i> n.sp.	0.53	0.14	0.86	0	0	0.38
Total	40.87	36.58	69.38	13.60	16.97	80.81

*Thalassia* provides substrate for a variety of organisms, such as encrusting coralline algae, filamentous algae, spirorbid polychaetes, bryozoans, hydroids, anemones, sponges, and molluscan egg cases (Table 5). Encrusting coralline algae are among the most conspicuous members of the epiphytic community and heavily encrust the leaf margins and distal portion of *Thalassia* blades at both Pond A and Pond C ridge sites. The diversity of nonforaminiferal epiphytes, including extremely abundant spirorbids, was highest (N = 340) in the sample collected from the ridge in Pond C.

Table 5. Distribution of nonforaminiferal epiphytes at Pelican Cays sample locations.

Species	Pond C		Pond C		Pond J	Pond E
	Cat Cay	Pond A	(ridge)	(lagoon)		
Coralline algae <sup>a</sup>	Light-moderate	Moderate-heavy	Moderate-heavy	Absent	Light-moderate	Light-moderate
Filamentous algae <sup>b</sup>	0	0	+	0	‡	0
Sponges	0	0	1	2	0	0
Hydroids	+	0	0	0	0	0
Anemones	1	0	0	0	0	0
Bryozoans	0	1	2	0	0	0
Spirorbid worms	0	1	340	12	15	11
Egg masses	0	0	2	0	0	0

<sup>a</sup>Coralline algae not identified. However, Littler and Littler (1997) report the following taxa occurring as epiphytes on *Thalassia* in the Pelican Cays: *Fosliella farinosa* (Lamouroux), *Pneumophyllum fragile* Kützing, and *Titanoderma pustulatum* (Lamouroux).

<sup>b</sup>Filamentous algae not identified. However, Littler and Littler (1997) record the following taxa occurring as epiphytes on *Thalassia* in the Pelican Cays: *Champia parvula* (C. Agardh) var. *parvula*, *Ceramium flaccidum* (Kützing), *Wrangelia penicillata* (C. Agardh), *Polysiphonia flaccidissima* Hollenberg, *P. scopulorum* Harvey, *Feldmannia indica* (Sonder in Zollinger), *Rosenvigea sanctaerucis* Børgesen, and *Sphaelaria tribuloides* Meneghini.

‡Phaeophyte tentatively identified as *Dictyota* sp. attached to *Thalassia* blades at this locality.



A low-diversity assemblage composed of the following seven species comprised the total community of epiphytic foraminifera living on the seagrass *Thalassia testudinum* in the Pelican Cays: *Belizeanella candeiana* (d'Orbigny), *Cornuspira planorbis* Schultze, *Cornuspiramia antillarum* (Cushman), *Hemidiscella palabunda* (Bock), *Iridia* n. sp., *Planorbulina acervalis* Brady, and *Rhizonubecula* n. sp. The species *Cornuspiramia antillarum* has previously been reported from Belize, off Carrie Bow Cay (Richardson, 1996), and has been cited as a minor component of the shallow-water foraminiferal faunas in other regions of the tropical Western Atlantic (Cushman, 1922, 1929; B ermudez, 1935; Hofker, 1964, 1971, 1976; Brasier 1975a; Manning, 1985). The two species recognized as new, *Iridia* n. sp. and *Rhizonubecula* n. sp., also occur as seagrass epiphytes off Carrie Bow Cay and the Twin Cays (Richardson, 1996). The remaining four species—*B. candeiana*, *C. planorbis*, *H. palabunda*, and *P. acervalis*—have been recorded from sediments of the Belizean shelf by Cebulski (1969) and Wantland (1975) (see Appendix 2 for synonymies).

Epiphytic foraminifera are known to attach to a variety of substrates other than seagrasses (Brasier, 1975a, 1975b; Langer, 1988, 1993). Samples of *Turbinaria* sp. from Pond A contained a few juvenile specimens of *P. acervalis* attached to the blades and a relatively dense growth of epiphytes on the stalk (including filamentous algae, erect bryozoans, and molluscan egg masses), but few foraminifera (2-3 *Iridia* n. sp.). Examination of *Halimeda* sp. from Pond C revealed only minor epiphytes: filamentous algae and a few specimens of *Iridia* n. sp. At Pond J, examination of several individuals of *Penicillus* sp. yielded a few spirorbids and two foraminifera (1 *P. acervalis* and 1 *C. antillarum*); however, dense epiphytic growth was observed to cover *Halimeda* sp. collected from the same locality. A single individual of *Halimeda* sp. contained numerous specimens of adult *P. acervalis*, several *C. antillarum*, and a few *Iridia* n. sp., in addition to moderate to heavy encrustation by calcareous algae, spirorbid worms, *Dictyota* sp., and a few sponges and anemones.

The relative abundance of foraminiferal species living on *Thalassia* varies, with different species dominating in different proportions at each site (Tables 6 and 7). Species dominance is high, ranging from 37.91% in the Pond A sample to 89.81% in the Pond C sample. *Cornuspiramia antillarum* is the most abundant species at Cat Cay, Pond A, and Pond C ridge sites, and the second most abundant species at Pond J. *C. antillarum* was not found in the sample collected in Pond C because encrusting coralline algae are not present on seagrasses at this site. *Cornuspiramia antillarum* has been observed to preferentially encrust calcareous substrate such as coralline algae or shell fragments (S. Richardson, unpublished observations). *Planorbulina acervalis* is the most abundant species at the Pond J and Pond E sites, the second most abundant species at the Cat Cay and Pond A sites, and the third most abundant species in the Pond C ridge sample. *Iridia* sp. accounts for the most abundant species at the Pond C lagoon site, the second most abundant species at the Pond C ridge and Pond E sites, and the third most abundant species in Pond J, off Cat Cay, in Pond A. *Hemidiscella palabunda* was the second most abundant species in the sample from Pond C, but comprised less than 1% of assemblages from the Pond C ridge and Pond A samples. *Rhizonubecula* n. sp. was recorded in abundances of less than 2% at all sites, except Ponds J and C, where it was not found at all. *Belizeanella candeiana* and *Cornuspira planorbis* were recorded in abundances of less than 1% at only a single site each, Cat Cay and the ridge in Pond C, respectively.

Table 6. Relative abundance of foraminiferan species at Pelican Cays sample locations (percent).

Species	Cat Cay	Pond A	Pond C	Pond C	Pond J	Pond E
			(ridge)	(lagoon)		
<i>Belizeanella candeiana</i>	0.65	0	0	0	0	0
<i>Cornuspira planorbis</i>	0	0	0.15	0	0	0
<i>Cornuspiramia antillarum</i>	37.91	75.19	39.78	0	24.41	11.46
<i>Hemidiscella palabunda</i>	0	0.39	0.15	6.37	0	0
<i>Iridia</i> n. sp.	23.53	8.14	34.13	89.81	11.02	14.80
<i>Planorbulina acervalis</i>	36.60	15.89	24.56	3.82	64.57	73.26
<i>Rhizonubecula</i> n. sp.	1.31	0.39	1.23	0	0	0.48
Total	100	100	100	100	100	100

Table 7. Rank abundance of foraminiferan species at Pelican Cays sample locations making up more than 5% of assemblage.

Rank	Cat Cay	Pond A	Pond C	Pond C	Pond J	Pond E
			(ridge)	(lagoon)		
1	<i>Cornuspiramia antillarum</i>	<i>Cornuspiramia antillarum</i>	<i>Cornuspiramia antillarum</i>	<i>Iridia</i> n. sp.	<i>Planorbulina acervalis</i>	<i>Planorbulina acervalis</i>
2	<i>Planorbulina acervalis</i>	<i>Planorbulina acervalis</i>	<i>Iridia</i> n. sp.	<i>Hemidiscella palabunda</i>	<i>Cornuspiramia antillarum</i>	<i>Iridia</i> n. sp.
3	<i>Iridia</i> n. sp.	<i>Iridia</i> n. sp.	<i>Planorbulina acervalis</i>		<i>Iridia</i> n. sp.	<i>Cornuspiramia antillarum</i>

The highest species richness (S) was observed in the sample collected from the ridge in Pond C (S = 6), followed by the sites off Cat Cay (S=5) and in Pond A (S = 5). The least speciose sites were observed to be Pond E (S=4), Pond J (S = 3), and inside Pond C (S = 3). In addition to species richness (S), values of the Shannon information function (H), and the Buzas and Gibson (1969) evenness function (E) were calculated for each sample individually (Table 8). These indices together can be used as measures of species diversity (S) and species equitability or dominance (E) (Hayek and Buzas, 1997). In addition to H, the equitability measure J was also calculated for each sample, because this measure is considered to be less dependent on S when the species number is less than 10 (Sheldon, 1969; Gibson and Buzas, 1973). In the Pelican Cays samples, values of H range from 0.40 in Pond C to 1.17 off Cat Cay, and values of E range from 0.42 in Pond A, to 0.80 off Pond J. The values of J exhibit a range similar to E's, from 0.36 in Pond C to 0.79 off Cat Cay (Table 8).

A SHE analysis (Buzas and Hayek, 1996; Hayek and Buzas, 1997) was performed for the Pelican Cays data. This procedure consists of calculating the values of H and E for cumulative quadrats, and then determining how these values change as a function of the number of individuals (N) (Fig. 2, Table 9). Results from the SHE analysis indicate that the distribution of epiphytic foraminifera on *Thalassia* in the Pelican Cays most closely resembles a log-series pattern (Fisher et al., 1943). As discussed by Buzas and Hayek (1996) and Hayek and Buzas

(1997), this pattern is one in which values of  $H$  remain relatively constant with increasing  $N$ .

Table 8. Summary of data on distribution of Foraminifera at Pelican Cays sample locations.

Parameter	Pond C		Pond C		Pond J	Pond E
	Cat Cay	Pond A	(ridge)	(lagoon)		
S (# species/sample)	5	5	6	3	3	4
N (# specimens/sample)	153	258	1380	157	127	419
H (Information function) <sup>a</sup>	1.17	0.75	1.15	0.40	0.87	0.78
E (Evenness measure) <sup>b</sup>	0.64	0.42	0.53	0.50	0.80	0.54
J (Equitability measure) <sup>c</sup>	0.72	0.47	0.64	0.36	0.79	0.56
# leaves surveyed	34	50	47	25	44	33
Length: width (average for all leaves)	6.82	9.59	15.71	19.19	9.29	13.51
Total leaf surface area (cm <sup>2</sup> )	374.34	705.30	1988.96	1154.18	748.38	518.50
Density (# forams/100 cm <sup>2</sup> leaf)	40.87	36.58	69.38	13.60	16.97	80.81
Standing stock (# forams/m <sup>2</sup> seafloor)	$7.65 \times 10^3$	$1.29 \times 10^4$	$6.90 \times 10^4$	$7.85 \times 10^3$	$6.35 \times 10^3$	$2.09 \times 10^4$

<sup>a</sup>Shannon information function:  $H = -\sum p_i \ln(p_i)$  (Hayek and Buzas, 1997).

<sup>b</sup>Buzas and Gibson (1969) measure of equitability or evenness:  $E = e^{H/S}$  (Hayek and Buzas, 1997).

<sup>c</sup>Equitability measure:  $J = H/\ln S$  (Pielou, 1966).

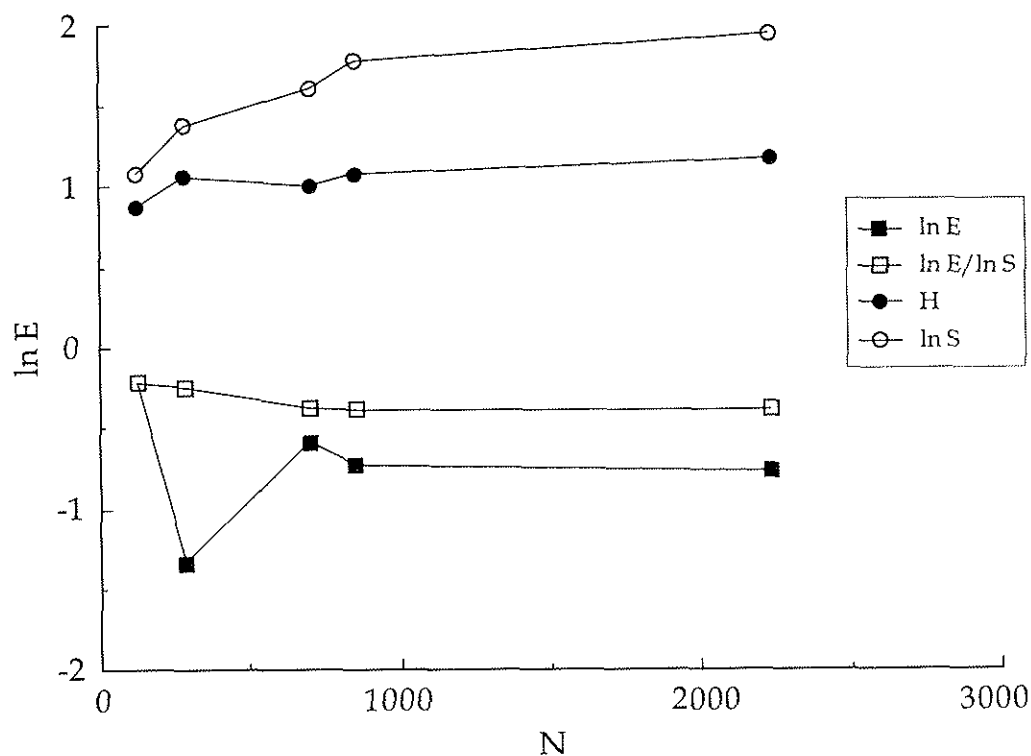


Figure 2. SHE analysis plot for Pelican Cays epiphytic Foraminifera data (refer to Table 9).

Table 9. SHE analysis for Pelican Cays data on distribution of Foraminifera at Pelican Cays sample locations (cf. Fig. 2).

Quadrat	N	S	H	E	ln E	ln S	ln E/ ln S
1	127	3	0.8698	0.7954	-0.2289	1.0986	-0.2084
2	284	4	1.0531	0.7167	-1.3331	1.3863	-0.2403
3	703	5	1.0095	0.5488	-0.6000	1.6094	-0.3728
4	856	6	1.0683	0.4851	-0.7234	1.7918	-0.4037
6	2236	7	1.1768	0.4634	-0.7692	1.9459	-0.3953

Note: N = cumulative number of individuals; S = cumulative number of species;  $H = -\sum p_i \ln(p_i)$  (Hayek and Buzas, 1997);  $E = e^{H/S}$  (Hayek and Buzas, 1997; Buzas and Gibson, 1969). Samples were added to SHE analysis in order of increasing species richness. Quadrat # 5 (Pond A) was dropped from the analysis because it resulted in an anomalously high value of E.

## DISCUSSION

*Thalassia testudinum* Banks ex König is the dominant seagrass in the Caribbean and grows in extensive meadows in shallow waters down to 20 m (den Hartog, 1970; Littler et al., 1989; Norris and Bucher, 1982; Phillips and Menez, 1988). The vegetative morphology of *Thalassia* consists of horizontal rhizomes (= long shoots) that grow beneath the sediment, and branching from them are lateral, erect leaf-bearing short shoots (Tomlinson and Vargo, 1966; Tomlinson, 1974). Leaves grow from the base, and new leaves are produced from the center of the leaf bundles (Tomlinson and Vargo, 1966; Tomlinson, 1974).

The shoot densities of *Thalassia* in the Pelican Cays are within the range of shoot densities measured by the author for *Thalassia* in 0.5-m water depths off Carrie Bow Cay (range = 552–1,160 shoots/m<sup>2</sup> seafloor) (S. Richardson, unpublished observations), but somewhat higher than previous estimates for several localities in Belize (117–404 shoots/m<sup>2</sup> seafloor) (Tomasko and Lapointe, 1991). Estimates of seagrass biomass in the Pelican Cays were observed to be slightly lower than off Carrie Bow Cay (range = 73.50–108.85 gdw/m<sup>2</sup> seafloor) (S. Richardson, unpublished observations), but higher than previously published estimates for other localities in Belize (range = 17.30–49.20 gdw/m<sup>2</sup> seafloor) (Tomasko and Lapointe, 1991). Estimates of epiphyte biomass (range = 12.70–41.25 gdw/m<sup>2</sup> seafloor) and epiphyte load (range = 10.73–31.26%) obtained for *Thalassia* off Carrie Bow Cay (S. Richardson, unpublished observations) were found to be considerably higher than the values obtained for *Thalassia* in the Pelican Cays (Table 1).

The most significant environmental factor known to influence the biomass of seagrass epiphytes is the nutrient content of the water column (Borowitzka and Lethbridge, 1989). High levels of dissolved nutrients in the water column (e.g., ammonium, nitrite plus nitrate, dissolved inorganic nitrogen, and soluble reactive phosphate) have been shown to be correlated with higher epiphyte loads (Tomasko and Lapointe, 1991; Frankovich and Fourqurean, 1997). For example, Tomasko and Lapointe (1991) report levels of dissolved nutrients that are 6 to 25 times higher in the water column off Big Pine Cay, Florida, than off Carrie Bow Cay, Belize. Likewise, epiphyte loads off Big Pine Cay, Florida, are three times higher than at Carrie Bow Cay, and 4 to 6 times

higher than the values calculated for the Pelican Cays (Tomasko and Lapointe, 1991). The oligotrophic waters of the Pelican Cays represent a pristine environment isolated from anthropogenic pollution (Littler and Littler, 1997) and, correspondingly, low values of epiphyte load have been recorded for these sites (Table 1).

The maximum standing stocks calculated for epiphytic foraminifera living on *Thalassia testudinum* in the Pelican Cays (Tables 3, 8) are comparable to the values obtained by the author for Carrie Bow Cay ( $6.82 \times 10^4$  individuals/m<sup>2</sup> seafloor) and are similar to published estimates from other regions in the Western Atlantic and world's oceans. According to Erskian's (1972) estimates, population densities of *Planorbulina* sp. and *Sorites* sp. on *Thalassia* in Discovery Bay, Jamaica, exceed  $6.0 \times 10^5$  individuals/m<sup>2</sup> seafloor and  $1.2 \times 10^5$  individuals/m<sup>2</sup> seafloor, respectively. In Barbuda, between  $1.24 \times 10^4$  and  $2.07 \times 10^5$  epiphytic foraminifera/m<sup>2</sup> seafloor live attached to various phytal substrates in depths less than 2 m (Brasier, 1975a). In the Gulf of Elat, Red Sea, an estimated  $1.54 \times 10^5$  epiphytic foraminifera/m<sup>2</sup> seafloor have been recorded living on the both the leaves and rhizomes of *Halophila stipulacea* collected from 20 m (Faber, 1991). In the Mediterranean, off Banyuls-sur-Mer, France, the standing stock of epiphytic foraminifera living on *Posidonia oceanica* increases with increasing water depth, with an estimated  $3.0 \times 10^4$  individuals/m<sup>2</sup> seafloor reported at 5 m and  $1.7 \times 10^5$  individuals/m<sup>2</sup> seafloor at 20 m (Véneç-Peyré and Le Calvez, 1988).

The densities of epiphytic foraminifera observed living on *Thalassia* blades in the Pelican Cays (Table 4) are similar to but somewhat higher than the densities reported by Wilson (1998) for epiphytic foraminifera living on *Thalassia* (19.05 individuals/100 cm<sup>2</sup> leaf surface area) and *Syringodium* (17.65 individuals/100 cm<sup>2</sup> leaf surface area) in Cockleshell Bay, St. Kitts. Brasier (1975a), however, has reported exceedingly high densities (4,000–8,333 individuals/100 cm<sup>2</sup> leaf surface area) of epiphytic foraminifera living on *Thalassia* collected off Barbuda. Lewis and Hollingworth (1982) recorded total densities ranging from 1.69 to 1757 individuals/100 cm<sup>2</sup> leaf surface area for all epiphytic organisms (excluding foraminifera) encrusting *Thalassia* blades collected from a variety of localities off Barbados.

Seagrass epiphytes must settle, grow, and reproduce within the life span of an individual blade, and they exhibit the rapid growth and reproductive rates characteristic of opportunistic species (Keough, 1986; Borowitzka and Lethbridge, 1989; Dirnberger, 1990, 1993, 1994; Kaehler and Hughes, 1992). Few details are known, however, about the life history traits of most species of epiphytic foraminifera. Cushman (1922, p. 59) documented a rapid growth rate for the species *Cornuspiramia antillarum*, observing that it was "one of the first organisms to be attached to the leaf." Previous authors have assumed an annual life span for *Planorbulina acervalis* and other epiphytic species (Le Calvez, 1936, 1938; Lutze and Wefer, 1980; Zohary et al., 1980; Hallock et al., 1986; Langer, 1988, 1993; Véneç-Peyré and Le Calvez, 1989; Hottinger, 1990). Recently, however, several specimens of *P. acervalis*, as well as *Iridia* n.sp., were found to reproduce by multiple fission and to still contain juveniles within the parental test (S. Richardson, unpublished observations), indicating that the generation time of these species falls within the life span of *Thalassia* blades.

The low total species richness of the epiphytic fauna in the Pelican Cays ( $S = 7$ ) contrasts sharply with the higher diversities that characterize epiphytic foraminiferal faunas described from other localities of the tropical Western Atlantic region. Brasier (1975a) identified a total of 49 species from various phytal substrates off Barbuda. Martin and Wright (1988) recorded 69 foraminiferal species living on *Thalassia* in the back-reef lagoon off Key Largo, Florida. Bock

(1969) reported 66 species epiphytic on *Thalassia* off Big Pine Key, Florida; 18 occurring in abundances >1% and 10 abundant throughout the year. Waszczak and Steinker (1987) recorded a total of 106 species of epiphytic foraminifera living on a variety of algal and seagrass substrates off Big Pine Key, Florida. These higher species diversities reflect, in part, the inclusion of mobile epiphytic species in the tallies of previous studies. Recently, Wilson (1998) described an assemblage of only 11 species of epiphytic foraminifera living on *Thalassia testudinum* and *Syringodium filiforme* in Cockleshell Bay, St. Kitts.

High-diversity epiphyte communities have been correlated with longer-lived phytal substrates (Borowitzka and Lethbridge, 1989; Langer, 1988, 1993; Hottinger, 1990). In Belize, the life span of individual leaves is short (35.3 to 42.7 days) and blade turnover rates are relatively high (2.34 to 2.83% a day) (Tomasko and Lapointe, 1991; Koltes et al., in press). As growth rates of *Thalassia testudinum* are relatively uniform throughout the Caribbean (Patriquin, 1973; Zieman, 1974; Zieman and Wetzel, 1980), the relatively low species diversity of the Pelican Cays fauna must be related to other factors.

Shallow-water tropical marine environments are generally characterized by high species richness, a trend that has been documented in benthic marine invertebrates, as well as benthic foraminifera (Fisher, 1960; Sanders, 1968, 1969; Buzas, 1972). Low species diversities are believed to characterize "physically controlled communities" in which the constituent organisms are subject to fluctuating environmental conditions and high physiological stress (Sanders, 1968, 1969). For example, Gibson and Buzas (1973) found lower species richness to characterize benthic foraminiferal faunas in areas subject to greater physical stress. And Gibson and Hill (1992) found low species richness (2–11 species), coupled with high dominance (30–95%), and low to moderate values of evenness (0.20–0.40), to characterize benthic foraminiferal faunas living in highly variable ecological habitats off the east coast of North America. The Pelican Cays fauna exhibit low species richness (3–6 species), high dominance (37.91–89.81%), and moderate species equitability (0.42–0.80) (Table 8); however, the overall environmental regime in this area is relatively constant (Koltes et al., in press). Wilson (1998) also records values of low species richness (5–11), high dominance (66.50–81.50%), and low to moderate equitability (0.30–0.40) for epiphytic foraminifera on *Thalassia* and *Syringodium* from Cockleshell Bay, St. Kitts, which suggests that this pattern may be representative of permanent, nonmotile epiphytic communities.

One environmental factor that has been shown to affect the species richness and abundance of epiphytic foraminifera is water turbulence (Bock, 1969; Ribes and Gracia, 1991). Martin and Wright (1988) observed a decrease in species richness and increase in species abundances with increasing distance from shore, which they attributed to increased wave, current, and storm activity. Waszczak and Steinker (1987) reported a general increase in species richness with increasing distance from shore but speculated that this trend resulted from the greater stability of the outer-reef environment. The coral-ridge system at the entrance to, and within, Pond C has been observed to affect circulation patterns within the lagoon (Macintyre et al., this volume; Littler and Littler, 1997). The contrast in species composition, relative abundance, and standing stock between epiphytic species living on seagrasses collected from the ridge and from within Pond C indicates that hydrodynamic conditions also play a role in the species composition and distribution of epiphytic faunas of this area.

The results from the SHE analysis indicate that the distributional pattern of foraminifera epiphytic on *Thalassia* in the Pelican Cays is most similar to a log-series pattern (Buzas and

Hayek, 1996; Hayek and Buzas, 1997). A log-series pattern is characteristic of communities with relatively few species that are subject to a single, dominant environmental factor (May, 1975). As the log-series model predicts that the greatest number of species will have minimal abundance, an increased sampling effort would be expected to yield a larger number of rare species (Fisher et al., 1943; May, 1975).

### SUMMARY

Estimates of epiphyte load (7.56–10.85%) obtained for *Thalassia* in the Pelican Cays are much lower than estimates calculated for the area off Carrie Bow Cay and previously published estimates obtained for *Thalassia* at other sites in Belize. These low values of epiphyte load can be considered an environmental indicator of the pristine water quality in the Pelican Cays, a region removed from the influence of anthropogenic pollution. Increased anthropogenic input to coastal regions has been implicated as the primary factor responsible for the recent worldwide decline in seagrasses.

The total epiphytic community of foraminifera living on the seagrass *Thalassia testudinum* in the Pelican Cays, Belize, is made up of seven species: *Belizeanella candeiana* (d'Orbigny), *Cornuspira planorbis* Schultze, *Cornuspiramia antillarum* (Cushman), *Hemidiscella palabunda* (Bock), *Iridia* n. sp., *Planorbulina acervalis* Brady, and *Rhizonubecula* n. sp. The two species recognized as new, *Iridia* n. sp. and *Rhizonubecula* n. sp., have also been observed as seagrass epiphytes off Carrie Bow Cay and the Twin Cays.

The overall pattern of species abundances and distribution in the quadrats sampled is one of low species richness ( $S = 3-6$ ), high dominance (37.91–89.91%), and moderate evenness ( $E = 0.42-0.80$ ). This pattern has been previously recognized as characteristic of foraminiferal communities living under stressful conditions (fluctuating salinities and temperatures) in temperate regions, but not of shallow-water tropical reef environments.

Results of a SHE analysis indicate that the distribution of foraminiferal species on *Thalassia* in the Pelican Cays most closely resembles a log-series pattern.

### ACKNOWLEDGMENTS

Fieldwork for this project was supported by a grant from the National Museum of Natural History's Caribbean Coral Reef Ecosystems Program (CCRE Contribution No. 585). I am grateful to Marty Buzas and Jon Moore for their valuable comments on this manuscript, and I would like to extend special thanks to Mike Carpenter and Robyn Spittle for their advice and assistance in the field.

### REFERENCES

- Bermudéz, P. J.  
1935. Foraminiferos de la costa norte de Cuba. *Memorias de la Sociedad Cubana de Historia Natural* 19(3):129–224, pls. 10–17.
- Bock, W. D.  
1967. Monthly variation in the foraminiferal biofacies on *Thalassia* and sediment in the Big

- Pine Key area. Unpublished Ph.D. thesis, University of Miami, Coral Gables, Florida, 243 p.
1968. Two new species of foraminifera from the Florida Keys. *Contributions from the Cushman Foundation for Foraminiferal Research* 29 (pt. 1):27-29, pl. 4.
1969. *Thalassia testudinum*, a habitat and means of dispersal for shallow water benthonic foraminifera. *Transactions of the Gulf Coast Association of Geological Societies* 19:337-340.
1971. A handbook of the benthonic foraminifera of Florida Bay and adjacent waters. In *A Symposium of Recent South Florida Foraminifera*, edited by J. I. Jones and W. D. Bock, 1-71, pls. 1-24. Miami Geological Society, Memoir 1.
- Borowitzka, M. A., and R. C. Lethbridge
1989. Seagrass epiphytes. In *Biology of Seagrasses: A treatise on the biology of seagrasses with special reference to the Australian region*, edited by A. W. D. Larkum, A. J. McComb, and S. A. Shepherd, 2:458-499. Amsterdam and New York: Elsevier, Aquatic Plant Studies.
- Brady, H. B.
1884. Report on the Foraminifera dredged by H.M.S. Challenger during the years 1873-1876: Reports of the Scientific Results of the Voyage of the H.M.S. Challenger during the years 1873-1876. *Zoology* 9 (pt. 1) (text):814, pt. 2 (plates), 115 p.
- Brasier, M. D.
- 1975a. Ecology of Recent sediment-dwelling and phytal foraminifera from the lagoons of Barbuda, West Indies. *Journal of Foraminiferal Research* 5(1):42-62.
- 1975b. The ecology and distribution of Recent foraminifera from the reefs and shoals around Barbuda, West Indies. *Journal of Foraminiferal Research* 5(3):193-210.
- Buzas, M. A.
1972. Patterns of species diversity and their explanation. *Taxon* 21(2/3):275-286.
- Buzas, M. A., and T. G. Gibson
1969. Species diversity: benthonic foraminifera in western North Atlantic. *Science* 163:72-75.
- Buzas, M. A., and L.-A. C. Hayek
1996. Biodiversity resolution: an integrated approach. *Biodiversity Research* 3:40-43.
- Buzas, M. A., R. K. Smith, R. K., and K. A. Beem
1977. *Ecology and Systematics of Foraminifera in Two Thalassia Habitats, Jamaica, West Indies*. Smithsonian Contributions to Paleobiology, v. 31, 139 p.
- Cebulski, D. E.
1969. Foraminiferal populations and faunas in barrier reef tract and lagoon, British Honduras. *American Association of Petroleum Geologists Memoir* 11:311-328.
- Cushman, J. A.
1922. *Shallow-water Foraminifera of the Tortugas Region*. Department of Marine Biology, Carnegie Institute of Washington, v. 17, no. 311, 85 p., 14 pls.
1929. *The Foraminifera of the Atlantic Ocean. Part 6. Miliolidae, Ophthalmitidae and Fischerinidae*. U. S. National Museum Bulletin 104 (pt. 6), 129 p.
- Dirnberger, J. M.
1990. Benthic determinants of settlement for planktonic larvae: availability of settlement sites for the tube-building polychaete *Spirorbis spirillum* (Linnaeus) settling onto



- seagrass blades. *Journal of Experimental Marine Biology and Ecology* 140:89–105.
1993. Dispersal of larvae with a short planktonic phase in the polychaete *Spirorbis spirillum* (Linnaeus). *Bulletin of Marine Science* 52(3):898–910.
1994. Influences of larval settlement location and rate on later growth in a sessile marine invertebrate population (*Spirorbis spirillum*). *Northeast Gulf Science* 13(2):65–78.
- Ehrenberg, C. G.  
1839. *Ueber die Bildung der Kreidefelsen und des Kreidemergels durch unsichtbar Organismen*. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin, 59–147, pls. 1–4.
- Erskian, M.  
1972. Patterns of distribution of foraminifera on *Thalassia testudinum*. In *Marine Studies on the North Coast of Jamaica*, edited by G. J. Backus. Atoll Research Bulletin, 152:3.
- Faber, W. W., Jr.  
1991. Distribution and substrate preference of *Peneroplis planatus* and *P. arietinus* from the *Halophila* meadow near Wadi Taba, Eilat, Israel. *Journal of Foraminiferal Research* 21(3):218–221.
- Fisher, A. G.  
1960. Latitudinal variations in organic diversity. *Evolution* 14:64–81.
- Fisher, R. A., A. S. Corbet, and C. B. Williams  
1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* 12:42–58.
- Frankovich, T. A., and J. W. Fourqurean  
1997. Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Marine Ecology Progress Series* 159:37–50.
- Frankovich, T. A., and J. C. Zieman  
1994. Total epiphyte and epiphytic carbonate production on *Thalassia testudinum* across Florida Bay. *Bulletin of Marine Science* 54(3):679–695.
- Gibson, T. G., and M. A. Buzas  
1973. Species diversity: Patterns in modern and Miocene foraminifera of the eastern margin of North America. *Geological Society of America Bulletin* 84:217–238.
- Gibson, T. G., and E. E. Hill  
1992. Species dominance and equitability: Patterns in Cenozoic foraminifera of eastern North America. *Journal of Foraminiferal Research* 22(1):34–51.
- Hallock, P., T. L. Cottey, L. B. Forward, and J. Halas  
1986. Population biology and sediment production of *Archaias angulatus* (Foraminiferida) in Largo Sound, Florida. *Journal of Foraminiferal Research* 16(1):1–8.
- Hartog, C. den  
1970. *The Sea-Grasses of the World*. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, afd. Natuurkunde, v. 59, no. 1.
- Hayek, L.-A. C., and M. A. Buzas  
1997. *Surveying Natural Populations*. New York: Columbia University Press, 563 p.
- Hofker, J.  
1964. Foraminifera from the tidal zone in the Netherlands Antilles and other West Indian Islands. *Studies on the Fauna of Curaçao and Other Caribbean Islands* 21(83):1–119.  
1971. The foraminifera of Piscadera Bay, Curaçao. *Studies on the Fauna of Curaçao and*

- Other Caribbean Islands* 35(127):1-62.
1976. Further studies on Caribbean foraminifera. *Studies on the Fauna of Curaçao and Other Caribbean Islands* 49(162):256 p.
- Hottinger, L.
1990. Significance of diversity in shallow benthic foraminifera. *Atti del Quarto simposio di Ecologia e paleoecologia delle Comunità Bentoniche*. Museo Regionale de Scienze Naturali, Torino, 35-51.
- Kaehler, S., and R. G. Hughes
1992. The distributions and growth patterns of three epiphytic hydroids on the Caribbean seagrass *Thalassia testudinum*. *Bulletin of Marine Science* 51(3):329-336.
- Keough, M. J.
1986. The distribution of a bryozoan on seagrass blades: Settlement, growth, and mortality. *Ecology* 67(4):846-857.
- Koltés, K. H., J. J. Tschirky, and I. C. Feller
- In press. CARICOMP site characterization: Carrie Bow Cay, Belize, Central America. UNESCO.
- Langer, M. R.
1988. Recent epiphytic Foraminifera from Vulcano (Mediterranean Sea). *Revue de Paleobiologie*, Special Volume 2, 827-832.
1993. Epiphytic foraminifera. *Marine Micropaleontology* 20:235-265.
- Le Calvez, J.
1936. Observations sur le genre *Iridia*. *Archives de Zoologie Expérimentale et Générale* 78:115-131.
1938. Recherches sur les Foraminifères. 1. Développement et reproduction. *Archives de Zoologie Expérimentale et Générale* 80(3):163-333.
- Lewis, J. B., and C. E. Hollingworth
1982. Leaf epifauna of the seagrass *Thalassia testudinum*. *Marine Biology* 71:41-49.
- Littler, D. S., and M. M. Littler
1997. An illustrated marine flora of the Pelican Cays, Belize. *Bulletin of the Biological Society of Washington* (9):1-149.
- Littler, D. S., M. M. Littler, K. E. Bucher, and J. N. Norris
1989. *Marine Plants of the Caribbean: A Field Guide from Florida to Brazil*. Washington, D.C.: Smithsonian Institution Press, 263 p.
- Lutze, G. F., and G. Wefer
1980. Habitat and asexual reproduction of *Cyclorbiculina compressa* (Orbigny), Soritidae. *Journal of Foraminiferal Research* 10(4):252-260.
- Manning, E. M.
1985. Ecology of Recent Foraminifera and ostracods of the continental shelf of southeastern Nicaragua. Unpublished Master's Thesis, Department of Geology, Louisiana State University.
- Martin, R. E.
1986. Habitat and distribution of the foraminifer *Archaias angulatus* (Fichtel and Moll) (Miliolina, Soritidae), northern Florida Keys. *Journal of Foraminiferal Research* 16(3):201-206.

- Martin, R. E., and R. C. Wright  
 1988. Information loss in the transition from life to death assemblages of foraminifera in back reef environments, Key Largo, Florida. *Journal of Paleontology* 62(3):399-410.
- May, R. M.  
 1975. Patterns of species abundance and diversity. In *Ecology and Evolution of Communities*, edited by M. L. Cody and J. M. Diamond, 81-120. Cambridge, Mass.: Belknap Press of Harvard University.
- Norris, J. N. and K. E. Bucher  
 1982. Marine algae and seagrasses from Carrie Bow Cay, Belize. In *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I: Structure and Communities*, edited by K. Rützler and I.G. Macintyre, 167-223. Smithsonian Contributions to the Marine Sciences No. 12.
- Orbigny, A. D. d'.  
 1839. Foraminifères. In *Histoire physique, politique et naturelle de L'île de Cuba*, edited by M. R. de la Sagra, 223 p.
- Patriquin, D. G.  
 1973. Estimation of growth rate, production and age of the marine angiosperm *Thalassia testudinum* König. *Caribbean Journal of Science* 13(1-2):111-123.
- Phillips, R. C., and E. G. Meñez  
 1988. *Seagrasses*. Smithsonian Contributions to the Marine Sciences No. 34, 104 p.
- Pielou, E. C.  
 1966. The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* 13:131-144.
- Ribes, T., and M. P. Gracia  
 1991. Foraminifères des herbiers de Posidonies de la Méditerranée occidentale. *Vie Milieu* 41(2/3):117-126.
- Richardson, S. L.  
 1996. Epiphytic foraminiferans from *Thalassia* habitats, Belize, C. A. *The Geological Society of America 1996 Annual Meeting, Abstracts with Programs*, A-38.
- Sanders, H. L.  
 1968. Marine benthic diversity: A comparative study. *American Naturalist* 102(925):1-40.  
 1969. Benthic marine diversity and the stability-time hypothesis. In *Diversity and Stability in Ecological Systems*, Report of Symposium held May 26-28 1969, 71-81. Brookhaven Symposia in Biology No. 22.
- Schultze, M. S.  
 1854. *Über den Organismus der Polythalmien (Foraminiferen) nebst Bemerkungen über die Rhizopoden im Allgemeinen*. Leipzig: Wilhelm Englemann, 1-68.
- Sheldon, A. L.  
 1969. Equitability indices: Dependence on the species count. *Ecology* 50(3):466-467.
- Short, F. T., and S. Wyllie-Escheverria  
 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23(1):17-27.
- Steinker, D. C., and A. L. Rayner  
 1981. Some habitats of nearshore foraminifera, St. Croix, U.S. Virgin Islands. *Compass of Sigma Gamma Epsilon* 59(11):15-26.

Steinker, P. J., and D. C. Steinker

1976. Shallow-water foraminifera, Jewfish Cay, Bahamas. In *First International Symposium on Benthonic Foraminifer of Continental Margins, Part A: Ecology and Biology*, edited by C. T. Schafer and B. R. Pelletier, 171-180. Maritime Sediments Special Publication No. 1.

Tomasko, D. A., and B. E. Lapointe

1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: Field observations and experimental studies. *Marine Ecology Progress Series* 75:9-17.

Tomlinson, P. B.

1974. Vegetative morphology and meristem dependence--the foundation of productivity in seagrasses. *Aquaculture* 4:107-130.

Tomlinson, P. B., and G. A. Vargo

1966. On the morphology and anatomy of turtle grass, *Thalassia testudinum* (Hydrocharitaceae) I. Vegetative morphology. *Bulletin of Marine Science* 161(4):748-761.

Véneç-Peyré, M.-T., and Y. Le Calvez

1988. Les foraminifères épiphytes de l'herbier de Posidonies de Banyuls-sur-Mer (Méditerranée occidentale): Etude des variations spatiotemporelles du peuplement. *Cahiers de Micropaléontologie*, n.s., 3(2):21-40, pl. 1.

Wantland, K. F.

1975. Distribution of Holocene benthonic foraminifera on the Belize Shelf. In *Belize Shelf—Carbonate Sediments, Clastic Sediments, and Ecology*, edited by K. F. Wantland and W. C. Pusey III, 332-399. American Association of Petroleum Geologists, Tulsa, Oklahoma, Studies in Geology No. 2.

Waszczak, R. F., and D. C. Steinker

1987. Paleoenvironmental and paleoecologic implications of Recent foraminiferan distribution patterns in the lower Florida Keys. In *Symposium on South Florida Geology*, edited by F. Maurrass, 203-225. Miami Geological Society Memoir 3.

Wilson, B.

1998. Epiphytal foraminiferal assemblages on the leaves of the seagrasses *Thalassia testudinum* and *Syringodium filiforme*. *Caribbean Journal of Science* 34(1-2): 131-132.

Zieman, J. C.

1974. Methods for the study of the growth and production of turtle grass, *Thalassia testudinum* König. *Aquaculture* 4:139-143.

Zieman, J. C., and R. G. Wetzel

1980. Productivity in seagrasses: methods and rates. In *Handbook of Seagrass Biology: An Ecosystem Perspective*, edited by R. C. Phillips and C. P. McRoy, 87-116. New York: Garland STPM Press.

Zohary, T., Z. Reiss, and L. Hottinger

1980. Population dynamics of *Amphisorus hemprichii* (Foraminifera) in the Gulf of Elat (Aqaba), Red Sea. *Eclogae geologicae Helvetiae* 73(3):1071-1094.

## APPENDIX I

List of sample localities and species collected from Pelican Cays (see also Fig. 1).

Field #	Date collected	Water depth (m)	Locality	Type of data collected
PC-96-A	23 August 1996	≤1	Cat Cay: samples collected from off western side of the island	Census of epiphytic foraminiferans, shoot density, seagrass biomass, epiphyte biomass, leaf surface area
PC-96-B	23 August 1996	0.5	Pond A: samples collected along flat projecting into bay from south, located just between Cat Cay and Cat Cay South Island	Census of epiphytic foraminiferans, shoot density, seagrass biomass, epiphyte biomass, leaf surface area
PC-96-C1	25 August 1996	0.5	Pond C (entrance): samples collected from entrance to pond	Shoot density, seagrass biomass, epiphyte biomass, leaf surface area
PC-96-C2	25 August 1996	0.5	Pond C (ridge): samples collected from ridge crossing middle of pond	Census of epiphytic foraminiferans, leaf surface area
PC-96-C3	25 August 1996	0.5	Pond C (lagoon): samples collected from within pond	Census of epiphytic foraminiferans, leaf surface area
PC-96-F	27 August 1996	0.5	Pond J: samples collected on ridge at entrance to pond	Shoot density, seagrass biomass, epiphyte biomass, leaf surface area, census of epiphytic foraminiferans
PC-96-G	28 August 1996	≤1	Pond E: samples collected at entrance to pond	Shoot density, leaf surface area, census of epiphytic foraminiferans

## APPENDIX II

## List of species

- Belizeanella candeiana* (d'Orbigny, 1839): *Rosalina candeiana* d'Orbigny, 1839, p. 97, pl. 8, figs. 2-4; Wantland, 1975, p. 394, figs. 10c, d, 12n; *Discorbis candeiana* d'Orbigny, Cebulski, 1969, p. 326, pl. 2, fig. 4.
- Cornuspira planorbis* Schultze, 1854, p.40, pl. 2, fig. 21; Cebulski, 1969, p. 326; Wantland, 1975, p. 387.
- Cornuspiramia antillarum* (Cushman, 1922): *Nubecularia antillarum* Cushman, 1922, p. 59, figs. 7, 8.
- Hemidiscella palabunda* Bock, 1968, p. 27, pl. 4, figs. 3-9; Wantland, 1975, p. 385, figs. 10i, j.
- Iridia* n. sp.
- Planorbulina acervalis* H. B. Brady, 1884, v. 9, p. 657, p. 92, fig. 4; Cebulski, 1969, p. 326, pl. 2, fig.9; Wantland, 1975, p. 397, fig. 11d.
- Rhizonubecula* n. sp.