

ATOLL RESEARCH BULLETIN

NO. 517

SEASONAL VARIATION IN EPIPHYTIC FORAMINIFERAL BIOTAS FROM
THALASSIA SEAGRASS HABITATS, TWIN CAYS, BELIZE

BY

SUSAN L. RICHARDSON

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
SEPTEMBER 2004

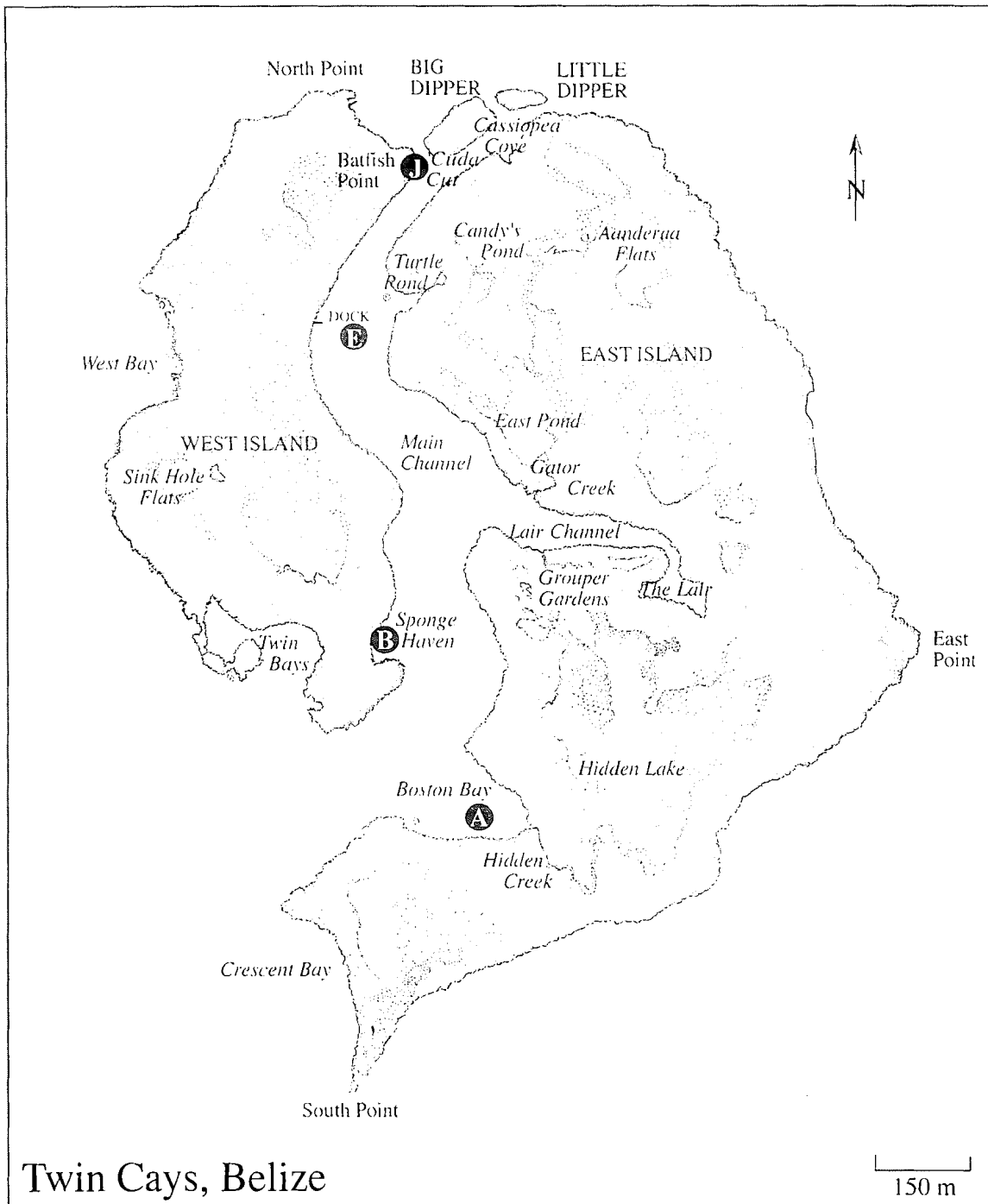


Figure 1. Map of Twin Cays showing location of sites sampled in June 2001 and February 2002. A. Boston Bay, B. Sponge Haven, E. Main Channel near Dock, J. 'Cuda Cut.

SEASONAL VARIATION IN EPIPHYTIC FORAMINIFERAL BIOTAS FROM *THALASSIA* SEAGRASS HABITATS, TWIN CAYS, BELIZE

BY

SUSAN L. RICHARDSON

ABSTRACT

The epiphytic foraminiferal biotas living on the seagrass *Thalassia testudinum* were surveyed at four sites in the Twin Cays, Belize (Boston Bay, Sponge Haven, the Main Channel near the dock, and 'Cuda Cut) during June 2001 and February 2002 in order to investigate seasonal variation in diversity, distribution, and abundance. Twelve blades were surveyed from each site and all live epiphytic foraminiferans were identified to species ($S=41$) and counted ($N=15,455$). The sites surveyed showed distinct seasonal differences in mean density of individuals per unit blade area (N/cm^2), species richness (S), and evenness (E), between June 2001 (the warmer, wet season) and February 2002 (the cooler, dry season). The mean density of individuals per unit blade area was higher at all sites in June 2001, compared with February 2002. Although mean species richness per blade did not show a significant seasonal signal, the total species richness recorded at each site was higher during June 2001, relative to February 2002, for all sites except Boston Bay. Likewise, values of evenness were higher in June 2001, relative to February 2002, except for the Boston Bay site. Both abiotic and biotic factors are considered to influence the seasonal differences in the population densities and species composition of the epiphytic foraminiferans living on *T. testudinum* in the vicinity of the Twin Cays mangrove island. It is suggested that seasonal differences at this locality may result from an influx of nutrients from the adjacent mangrove fringe during the wet season, an incursion of open-water species into the mangrove habitats during the dry season, and the thermal tolerances of individual species. The high dominance of the encrusting, milioline species *Rhizonubecula* sp. observed at all sites in the Main Channel in June 2001, and again at the Dock site in February 2002, highlights the potential utility of this species as a bioindicator of increased nutrients in mangrove habitats.

INTRODUCTION

Foraminifera is a monophyletic clade of single-celled eukaryotes that has recently been found to be most closely related to chlorarachniophytes, cercozoans, euglyphiid amoebans, and other cercozoans (Archibald et al., 2003; Keeling, 2000; Pawlowski et al., 2003). The clade has a long geological history, reaching back to at least the Early Cambrian (Culver, 1991; Lipps and Rozanov, 1996; McIlroy et al., 2001), and the group

is considered by many to have one of the best fossil records of any organism (Culver and Buzas, 1998). Fossil foraminiferans are widely used in biostratigraphic, paleoecological, paleoenvironmental, and evolutionary studies (Culver and Buzas, 2000). Extant species are ubiquitous in the marine realm and occupy a diversity of habitats in near-shore tropical to subtropical waters. Foraminiferans can be found dwelling within the sediments of mangrove swamps and seagrass meadows as well as living attached to seagrass blades, macroalgae, coral rubble, and other firm substrates (Sen Gupta, 1999).

Traditionally, ecological studies of extant foraminiferans have focused primarily on the sediment-dwelling species and there exists an extensive literature documenting the diversity, distribution and abundance of living foraminiferal communities from an array of sediment types in different marine environments (Culver, 1990; Murray, 1973; 1991a, b). More recently, a number of studies have examined the ecology of foraminiferans living attached to phytal substrates, such as seagrasses and macroalgae, in nearshore marine ecosystems (Fujita and Hallock, 1999; Langer, 1993; Richardson 2000, Semeniuk, 2000, 2001). These studies indicate that the standing stock of epiphytic foraminiferal populations may be as high as those of the sediment-dwelling biota, suggesting that a considerable component of the overall foraminiferal biodiversity has been overlooked by surveys employing traditional sampling methods. In his study of the distribution of foraminiferans in the sediments of the Belize Shelf, Wantland (1975: 358) observed that the highest species diversity occurred in regions colonized by moderate-to-dense stands of turtle grass (*Thalassia testudinum*) and speculated that “many, if not most, of the benthonic foraminifera inhabiting shallow back-reef environments live attached to plants and other floral and faunal elements above the sediment surface.”

Thalassia testudinum is the dominant seagrass in the Caribbean and its broad, strap-like leaves provide a substantial amount of surface area (LAI = 4-12 m² blade surface area/m² seafloor) for the settlement of epiphytic organisms (Philips and Meñez, 1988; Zieman, 1975). The species richness of epiphytic foraminiferans from *Thalassia* habitats in the central province of the Belizean Barrier Reef Complex (i.e., Carrie Bow Cay, Twin Cays, Man O’ War Cay, and the Pelican Cays) totals 49 species to date (Richardson, 2000; S. Richardson, unpublished data). These foraminiferal species compete for space and resources with numerous multicellular organisms, such as encrusting calcareous algae, filamentous microalgae, hydroids, bryozoans, copepods, spirorbids, ascidians, sponges, barnacles, and oysters (Richardson 2000; S. Richardson, unpublished observations).

Estimates of the biomass of *T. testudinum* from this region are among the highest in the Caribbean, with above-ground biomass ranging from 883±254 g m⁻² dry weight (August) to 731±211 g m⁻² dry weight (December) (Koltes et al., 1998; Zieman and Zieman, 1989). Areal productivity shows minimal seasonal variation, with slightly higher values of productivity recorded during August (2.86±0.96 g dry weight m⁻² day⁻¹) relative to December (2.30±0.88 g dry weight m⁻² day⁻¹), and the turnover rate for *T. testudinum* leaves averages about 2.4% per plant per day (Koltes et al., 1998).

Since *T. testudinum* provides a relatively stable and predictable substratum for the settlement, growth and reproduction of epiphytic organisms throughout the year, one might ask whether or not the epiphytes colonizing the leaf blades also exhibit minimal seasonality? The objective of the present study was, therefore, to investigate the seasonal

changes in abundance, diversity, and species composition of the epiphytic foraminiferal biotas living on *T. testudinum* growing in the vicinity of the Twin Cays, Belize.

MATERIAL AND METHODS

Description of Study Sites

Seagrass samples for this study were collected from the vicinity of Twin Cays, Belize, a 91.5 ha-mangrove island that is located within the central province of the Belizean Barrier-Reef Complex, approximately 21 km SE of Dangriga and 2 km west of the reef crest (Koltes et al., 1998). Sampling sites were located along a north-south transect, in the Main Channel between East and West Islands as well as in the adjacent embayment of Boston Bay (Fig. 1). Blades of *T. testudinum* with their associated epiphytes were collected during field excursions in the summer (wet season) of 2001 (22 June-03 July) and again in the winter (dry season) of 2002 (31 January-11 February).

Site A was located in Boston Bay in approximately 1.5-m water depth in a monospecific stand of *T. testudinum*. The overlying water column at this site was reddish-brown in color due to the high tannin content and the sediment consisted of a thick accumulation of mangrove-derived, organic flocculent. Numerous individuals of the "upside-down" jellyfish, *Cassiopeia xamachana*, were present in sand patches interspersed throughout the seagrass stands. Site B was located in approximately 2-m water depth in a monospecific stand of *T. testudinum* at Sponge Haven. The overlying water was cloudy, presumably due to suspended sediment load in the channel, and the sediment surface consisted of a thick accumulation of mangrove-derived, organic flocculent (Calem and Pierce, 1993). Site E was located southeast of Turtle Cove, near the dock, in 1.5-m water depth in a dense, monospecific stand of *T. testudinum* growing in the middle of the channel (Fig. 1). The overlying water column was cloudy with suspended sediment, and the bottom sediments were comprised of a fine silty, calcareous mud (Calem and Pierce, 1993). Site J was located at Cuda Cut in 1.5-m water depth in a monospecific stand of *T. testudinum*. The overlying water column at this site was cloudy with suspended sediment and the bottom sediments were comprised of a silty, calcareous mud (Calem and Pierce, 1993).

Field and Laboratory Protocols

Twelve shoots of *T. testudinum* were collected haphazardly (*sensu* Hayek and Buzas, 1997) at each site from within an area of approximately nine m² of sea floor. Seagrass samples were stored in Ziploc bags immersed in seawater and kept in a cooler until return from the field. Collections from each sampling site were maintained temporarily in separate tanks with running seawater in the wet lab on Carrie Bow Cay until the leaf blades could be examined.

The longest blade from each shoot was selected and examined for live foraminiferans using a binocular, dissecting microscope (Leica M5). Living individuals were recognized by their cytoplasmic coloration and/or the presence of pseudopodial arrays and feeding cysts. Notes on the abundance, reproductive state of each specimen,

and the occurrence and distribution of other epiphytic organisms were also recorded. Several voucher specimens of each foraminiferal species identified were removed from the blades and stored on microslides for comparison with the type Foraminifera collections housed in the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Specimens illustrated by scanning electron microscopy (SEM) were cleaned with distilled water, air-dried, mounted on stubs, coated with a 400-Å layer of gold in a Technics Hummer II sputter coater, and examined in a JEOL JSM-6400V model SEM (Smithsonian Marine Station at Fort Pierce, FL).

RESULTS

Forty-one species of epiphytic foraminiferans were identified among 15,455 individuals identified from a total of 96 seagrass blades (Appendix I). The total leaf-surface area surveyed was 6568.58 cm² (0.66 m²)--3267.66 cm² blade surface was surveyed in June 2001 and 3300.92 cm² was surveyed in February 2002. The mean total blade area surveyed per site was slightly lower in June 2001 (816 cm², $\sigma=213.04$, $\sigma^2=45,386.95$) than in February 2002 (825.23 cm², $\sigma=107.21$, $\sigma^2=11,493.50$); however, the mean blade surface area surveyed at each sampling site was observed to be approximately the same in both seasons (Fig. 2, Tables 1, 2).

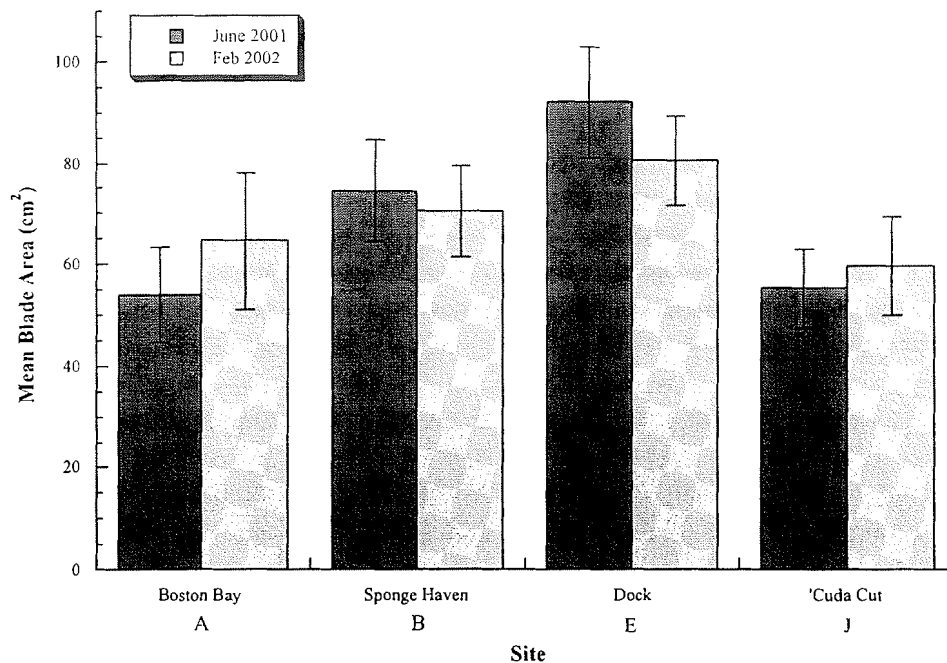


Figure 2. Mean seagrass blade surface area surveyed at each sampling site, Twin Cays, Belize (June 2001 and February 2002). 95% confidence limits were calculated following Hayek and Buzas (1997).

Table 1. Summary data table for sites sampled within Twin Cays, Belize, in June 2001.

	Boston Bay	Sponge Haven	Dock	'Cuda Cut
Field ID #	BZE01A	BZE01B	BZE01E	BZE01J
Collecting date	22 June 2001	24 June 2001	28 June 2001	03 July 2001
Total species richness (S)	19	25	27	31
Mean species richness	10.08 ($\sigma=2.23$, $\sigma^2=4.99$)	15.67 ($\sigma=2.02$, $\sigma^2=4.06$)	13.17 ($\sigma=5.18$, $\sigma^2=26.88$)	14.17 ($\sigma=3.69$, $\sigma^2=13.61$)
Shannon's H	1.6557 ($\sigma=0.0325$, $\sigma^2=0.0011$)	2.1965 ($\sigma=0.0207$, $\sigma^2=0.0406$)	1.4699 ($\sigma=0.0204$, $\sigma^2=0.0399$)	1.9324 ($\sigma=0.0204$, $\sigma^2=0.0399$)
Evenness (E)	0.2756	0.6824	0.4460	0.5627
Total blades surveyed	12	12	12	12
Total individuals (N)	1332	2617	4302	1862
Mean density (N/blade)	111.00 ($\sigma=48.77$, $\sigma^2=2378.18$)	218.08 ($\sigma=74.95$, $\sigma^2=5616.99$)	358.50 ($\sigma=208.57$, $\sigma^2=43,500.82$)	155.17 ($\sigma=96.10$, $\sigma^2=9234.33$)
Total blade area (cm ²)	646.26	854.54	1103.40	663.46
Mean blade area (cm ²)	99.42 ($\sigma=164.90$, $\sigma^2=27192.14$)	71.21 ($\sigma=15.46$, $\sigma^2=238.96$)	91.95 ($\sigma=17.14$, $\sigma^2=293.84$)	55.29 ($\sigma=12.05$, $\sigma^2=145.26$)
Mean density per unit blade area (N/cm ²)	2.26 ($\sigma=1.20$, $\sigma^2=1.45$)	3.10 ($\sigma=0.96$, $\sigma^2=0.92$)	4.27 ($\sigma=2.26$, $\sigma^2=5.09$)	2.92 ($\sigma=1.39$, $\sigma^2=1.92$)

The site with the lowest total blade surface area surveyed was the Boston Bay site in June 2001 (646.26 cm²) and the site with the highest total blade surface area was the Dock site in June 2001 (1103.40 cm²) (Tables 1, 2). A higher number of individuals was counted in June 2001 (10,113 individuals), relative to February 2002 (5,342 individuals), with the highest populations observed at the Dock site in June 2001 (4,320 individuals) (Fig. 3). The lowest population numbers were recorded at the Boston Bay site in February 2002 (626 individuals). Mean densities per blade (N/blade) were higher at all sites in June 2001 relative to February 2002 (Tables 1, 2). Higher mean densities per unit-blade area (mean N/ cm²) were recorded during June 2001, compared to February 2002, at all sites

except for 'Cuda Cut which had approximately the same density per unit blade area (cm^2) during both seasons (Fig. 4). The highest mean densities were recorded at the Dock site

Table 2. Summary data table for sites sampled within Twin Cays, Belize, in February 2002.

	Boston Bay	Sponge Haven	Dock	'Cuda Cut
Field ID #	BZE02A	BZE02B	BZE02E	BZE02J
Collecting date	31 Jan. 2002	06 Feb. 2002	11 Feb. 2002	11 Feb. 2002
Total species richness (S)	21	24	19	23
Mean species richness	10.08 ($\sigma=3.00$, $\sigma^2=8.99$)	10.83 ($\sigma=3.79$, $\sigma^2=14.33$)	9.58 ($\sigma=2.07$, $\sigma^2=4.27$)	9.00 ($\sigma=2.09$, $\sigma^2=4.36$)
Shannon's H	2.1989 ($\sigma=0.0389$, $\sigma^2=0.0015$)	2.3493 ($\sigma=0.0349$, $\sigma^2=0.0012$)	1.1521 ($\sigma=0.0280$, $\sigma^2=0.0008$)	1.8030 ($\sigma=0.0283$, $\sigma^2=0.0008$)
Evenness (E)	0.4293	0.4366	0.1666	0.2638
Total blades surveyed	12	12	12	12
Total individuals (N)	626	786	2220	1710
Mean density (N/blade)	52.17 ($\sigma=31.68$, $\sigma^2=1003.79$)	65.50 ($\sigma=49.33$, $\sigma^2=2433.91$)	185.00 ($\sigma=78.64$, $\sigma^2=6184.91$)	142.50 ($\sigma=62.51$, $\sigma^2=3907.73$)
Total blade Area (cm^2)	775.62	845.76	964.62	714.92
Mean blade area (cm^2)	64.64 ($\sigma=21.01$, $\sigma^2=441.31$)	70.48 ($\sigma=13.79$, $\sigma^2=190.23$)	80.39 ($\sigma=13.55$, $\sigma^2=183.67$)	59.58 ($\sigma=15.25$, $\sigma^2=232.63$)
Mean density per unit blade area (N/cm^2)	0.84 ($\sigma=0.43$, $\sigma^2=0.18$)	0.91 ($\sigma=0.65$, $\sigma^2=0.42$)	2.35 ($\sigma=0.1.07$, $\sigma^2=1.15$)	2.50 ($\sigma=1.18$, $\sigma^2=1.40$)

in June 2001 ($4.27 \text{ individuals}/\text{cm}^2$) while the lowest densities were recorded at the Boston Bay and Sponge Haven sites in February 2002 (0.84 and $0.91 \text{ individuals}/\text{cm}^2$, respectively). Table 3. Relative abundance of epiphytic species at sites sampled within Twin Cays, Belize, in June 2001. 95% confidence intervals were calculated from

standard error for species proportions for cluster sampling (Hayek and Buzas 1997).

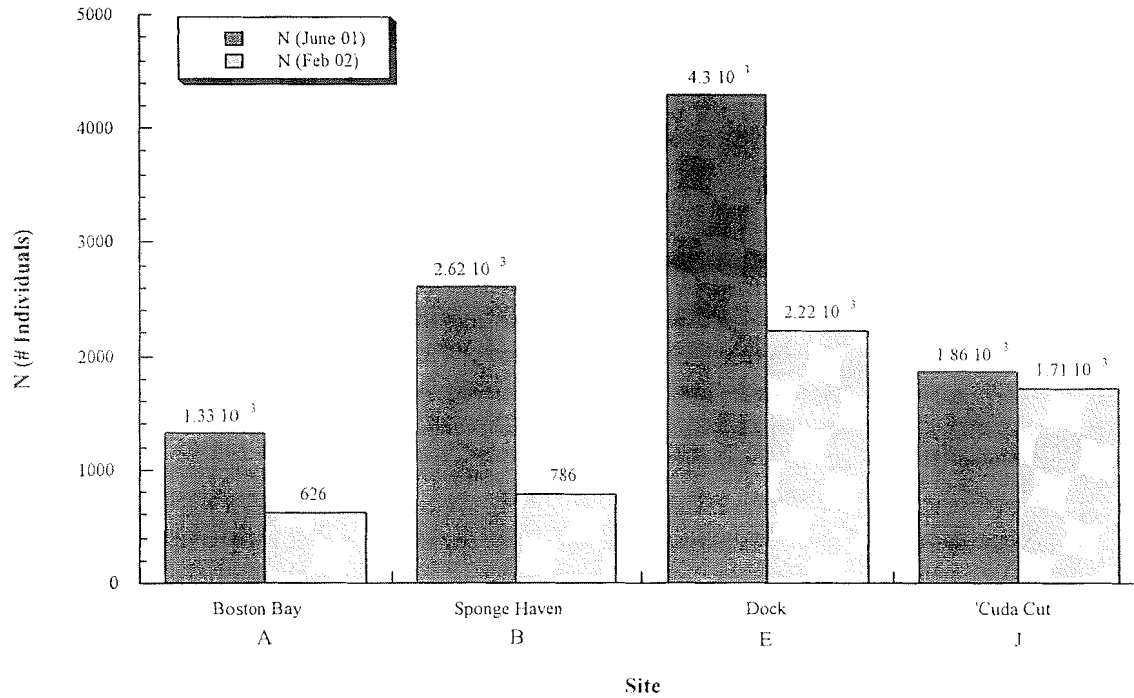


Figure 3. Total number of foraminiferal individuals counted at each site, Twin Cays, Belize (June 2001 and February 2002).

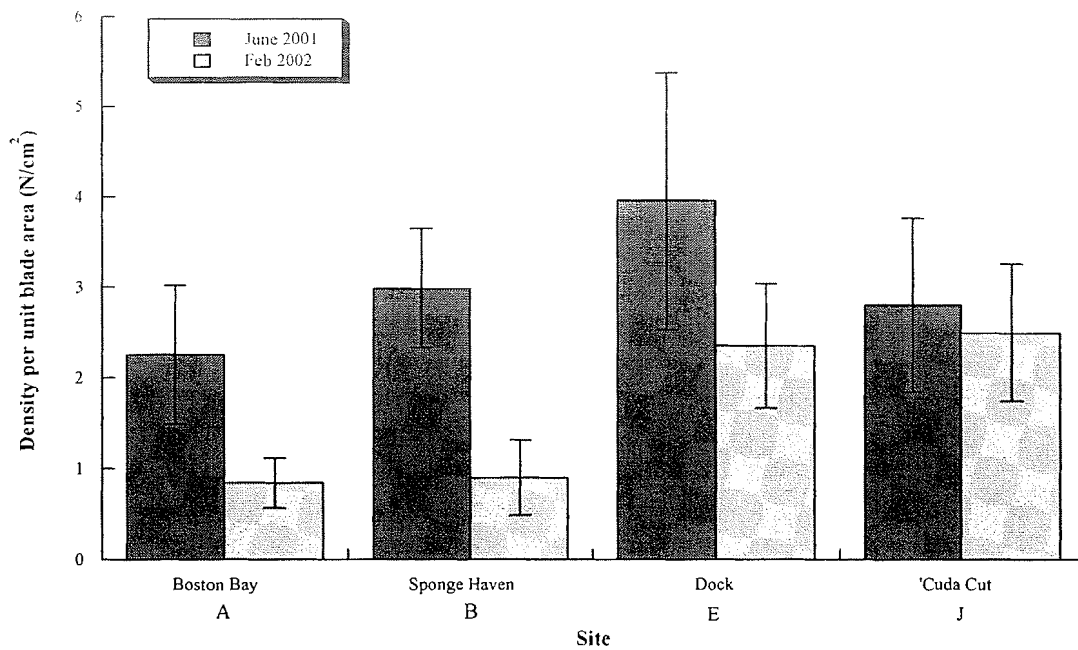


Figure 4. Density of epiphytic foraminiferans per unit blade area (N/cm²) on *Thalassia testudinum* at each site, Twin Cays, Belize (June 2001 and February 2002). 95% confidence limits were calculated following Hayek and Buzas (1997).

Diversity indices calculated for each site include: S (species richness), H (Shannon's H), and E (evenness) (Hayek and Buzas, 1997) (Tables 1, 2). Except for Boston Bay, the total species richness recorded at each site was higher in June 2001 than in February 2002 (Fig. 5). The highest values of S were recorded at the 'Cuda Cut site in

Table 3. Relative abundance of epiphytic species at sites sampled within Twin Cays, Belize, in June 2001. 95% confidence intervals were calculated from standard error for species proportions for cluster sampling (Hayek and Buzas, 1997).

Species	Boston Bay	Sponge Haven	Dock	'Cuda Cut
<i>A. cf. parkinsoniana</i>	0.00	0.00	0.00	0.16±0.82%
<i>A. gibbosa</i>	0.00	0.00	0.00	0.00
<i>A. cf. lucasi</i>	0.08±2.01%	0.61±0.85%	0.26±0.77%	0.16±1.46%
<i>A. antillarum</i>	0.00	0.00	0.07±1.16%	0.00
<i>A. mucronata</i>	0.15±1.89%	0.23±1.08%	0.05±1.27%	0.27±0.97%
<i>B. rhomboidalis</i>	0.00	0.04±1.99%	0.02±1.83%	0.00
<i>C. planorbis</i>	0.83±0.95%	0.65±0.59%	0.02±2.05%	0.38±0.55%
<i>Cor. antillarum</i>	0.53±0.53%	2.41±0.23%	0.40±0.71%	0.43±0.82%
<i>Cos. antillarum</i>	0.23±1.02%	0.42±0.70%	0.00	0.11±1.31%
<i>C. cushmani</i>	0.38±1.11%	0.11±1.43%	0.05±1.43%	0.05±2.05%
<i>Crithionina</i> sp.	0.00	0.00	0.09±0.96%	0.05±1.95%
<i>C. squamosa</i>	0.15±1.92%	0.00	0.00	0.00
<i>C. tobagoensis</i>	2.85±0.40%	5.31±0.22%	0.46±0.34%	0.64±0.43%
<i>C. poeyanum</i>	0.00	0.04±1.96%	0.00	0.00
<i>F. labiosa</i>	3.83±0.41%	1.41±0.59%	0.44±0.44%	1.34±0.48%
<i>H. palabunda</i>	1.95±0.49%	0.53±0.56%	1.79±0.28%	3.11±0.51%
<i>H. cf. cribrostoma</i>	0.30±0.70%	0.38±1.15%	9.34±0.69%	0.59±0.56%
<i>I. cf. diaphana</i>	39.26±0.20%	12.99±0.29%	17.76±0.17%	23.85±0.24%
<i>L. cf. karreri</i>	0.45±0.68%	3.02±0.36%	1.44±0.43%	0.70±0.67%
<i>M. fusca</i>	0.00	0.00	0.00	0.00
<i>N. cf. terquemi</i>	0.15±1.92%	0.80±1.39%	0.14±0.79%	0.27±0.94%
<i>P. corrugata</i>	0.00	0.04±1.85%	0.00	0.00
<i>P. acervalis</i>	7.21±0.31%	5.96±0.30%	3.51±0.28%	12.89±0.30%
<i>P. mediterraneensis</i>	0.00	0.00	0.16±0.60%	0.16±0.96%
<i>P. cf. squamiformis</i>	0.00	0.04±1.96%	0.02±1.83%	0.00
<i>P. occidentalis</i>	0.00	0.00	0.00	0.11±1.19%
<i>P. goesi</i>	2.03±0.43%	5.20±0.39%	0.21±0.58%	1.77±0.57%
<i>Quinqueloculina</i> sp.	0.00	0.31±0.67%	0.00	0.43±0.96%
<i>Q. bicostata</i>	0.00	0.00	0.00	0.00
<i>R. adherens</i>	0.15±1.86%	10.51±0.39%	0.19±0.74%	0.21±1.29%
<i>Rhizonubecula</i> sp.	5.63±0.44%	29.61±0.30%	57.37±0.11%	33.24±0.26%
<i>R. candeiana</i>	0.00	0.96±0.45%	0.93±0.97%	2.15±0.52%
<i>Rosalina</i> sp.	0.00	0.00	0.00	0.00
<i>R. auberii</i>	0.00	0.00	0.00	0.21±1.99%
<i>Sagenina</i> sp.	0.00	0.00	0.00	0.05±2.07%

Table 3 (cont'd.)

<i>S. atlantica</i>	0.00	0.38±0.81%	0.05±1.07%	0.21±0.78%
<i>S. dominicensis</i>	33.86±0.20%	18.04±0.32%	4.88±0.49%	15.41±0.52%
<i>T. agglutinans</i>	0.00	0.00	0.02±1.96%	0.05±1.99%
<i>Tretomphalus</i> sp.	0.00	0.00	0.21±0.73%	0.27±1.12%
<i>T. bicarinata</i>	0.00	0.00	0.00	0.11±1.22%
<i>T. cf. trigonula</i>	0.00	0.00	0.12±1.02%	0.59±0.75%

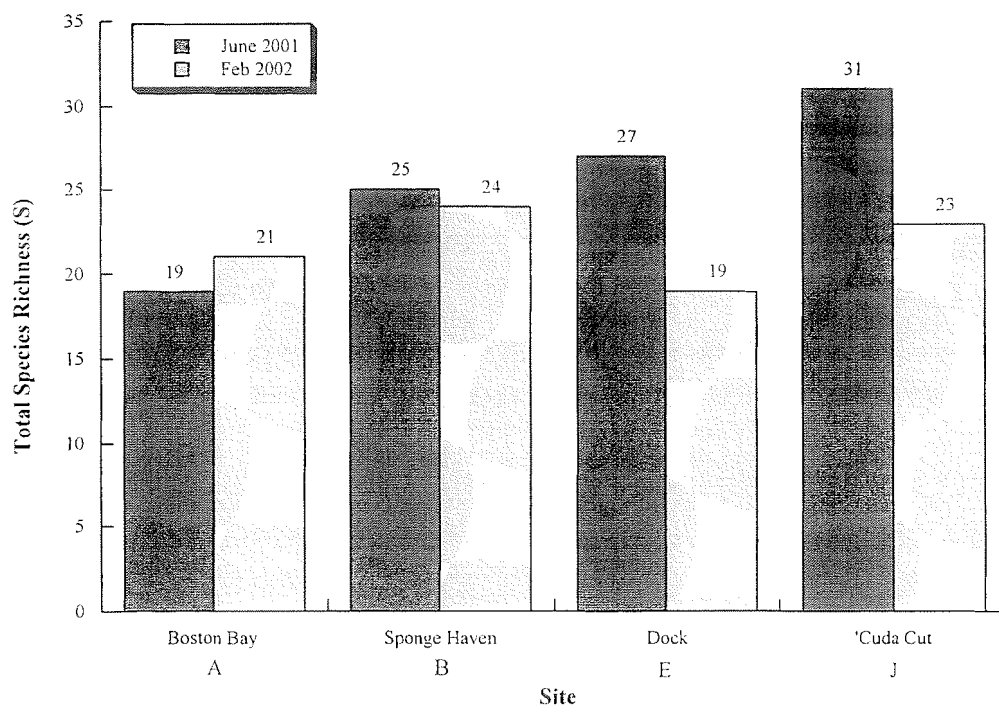


Figure 5. Total species richness of epiphytic foraminiferans identified at each site, Twin Cays, Belize (June 2001 and February 2002).

Table 4. Relative abundance of epiphytic species at sites sampled within Twin Cays, Belize, in February 2002. 95% confidence intervals were calculated from standard error for species proportions for cluster sampling (Hayek and Buzas, 1997).

SPECIES	Boston Bay	Sponge Haven	Dock	'Cuda Cut
<i>A. cf. parkinsoniana</i>	0.00	0.00	0.00	0.00
<i>A. gibbosa</i>	0.00	0.13±1.91%	0.00	0.00
<i>A. cf. lucasi</i>	0.00	0.00	0.00	0.00
<i>A. antillarum</i>	0.00	0.00	0.00	0.00
<i>A. mucronata</i>	0.00	0.25±1.86%	0.36±0.93%	0.18±1.46%
<i>B. rhomboidalis</i>	0.00	0.00	0.00	0.00
<i>C. planorbis</i>	0.80±1.33%	1.40±0.37%	0.14±1.04%	0.12±1.98%
<i>Cor. antillarum</i>	17.41±0.36%	5.34±0.96%	0.36±1.08%	0.88±1.05%
<i>Cos. antillarum</i>	0.00	0.00	0.00	1.17±1.14%

Table 4 (cont'd)

<i>C. cushmani</i>	8.95±0.49%	12.72±0.43%	0.00	0.00
<i>Crithionina</i> sp.	0.96±1.07%	0.64±1.67%	0.00	0.00
<i>C. squamosa</i>	0.00	0.38±1.34%	0.09±1.21%	0.12±1.42%
<i>C. tobagoensis</i>	0.96±0.75%	2.16±1.06%	0.00	0.06±1.98%
<i>C. poeyanum</i>	0.00	0.00	0.00	0.00
<i>F. labiosa</i>	7.67±0.32%	5.47±0.83%	0.86±0.44%	0.12±1.98%
<i>H. palabunda</i>	1.44±0.76%	0.89±0.84%	0.99±0.44%	6.37±0.86%
<i>H. cf. cribrostoma</i>	0.16±2.08%	0.00	0.05±1.93%	0.00
<i>I. cf. diaphana</i>	24.76±0.35%	16.67±0.32%	10.68±0.17%	18.36±0.37%
<i>L. cf. karreri</i>	0.00	0.25±1.44%	0.14±1.00%	0.00
<i>M. fusca</i>	0.00	0.13±2.05%	0.00	0.00
<i>N. cf. terquemi</i>	0.00	0.76±0.62%	0.18±1.03%	0.18±1.07%
<i>P. corrugata</i>	0.00	0.00	0.00	0.06±1.91%
<i>P. acervalis</i>	16.77±0.38%	19.72±0.32%	12.79±0.14%	28.07±0.32%
<i>P. mediterraneensis</i>	0.00	0.00	0.00	0.12±1.32%
<i>P. cf. squamiformis</i>	0.80±0.89%	1.15±0.74%	0.36±0.77%	0.64±0.50%
<i>P. occidentalis</i>	0.00	0.00	0.00	0.00
<i>P. goesi</i>	1.12±0.79%	0.76±0.91%	1.13±0.74%	0.18±1.50%
<i>Quinqueloculina</i> sp.	0.16±1.92%	0.25±1.94%	0.00	0.06±1.98%
<i>Q. bicostata</i>	0.16±1.92%	0.00	0.00	0.00
<i>R. adherens</i>	3.04±0.46%	2.29±0.46%	0.05±1.92%	0.06±1.94%
<i>Rhizonubecula</i> sp.	1.92±0.70%	14.63±0.82%	68.24±0.04%	26.55±0.25%
<i>R. candeiana</i>	0.16±2.08%	0.51±0.92%	1.26±0.59%	3.51±0.34%
<i>Rosalina</i> sp.	0.48±0.95%	0.00	0.00	0.00
<i>R. auberii</i>	0.00	0.00	0.00	0.06±2.01%
<i>Sagenina</i> sp.	0.00	0.00	0.00	0.00
<i>S. atlantica</i>	0.00	0.00	0.00	0.06±2.01%
<i>S. dominicensis</i>	10.70±0.60%	11.83±0.30%	2.21±0.51%	12.98±1.02%
<i>T. agglutinans</i>	0.00	0.00	0.00	0.00
<i>Tretomphalus</i> sp.	0.16±1.92%	0.89±0.55%	0.19±1.37%	0.12±1.32%
<i>T. bicarinata</i>	0.00	0.00	0.00	0.00
<i>T. cf. trigonula</i>	1.44±0.45%	0.76±1.05%	0.05±1.90%	0.00

June 2001 (S=31); the lowest values of S were recorded at Boston Bay (S=19) in June 2001 and the Dock (S=19) in February 2002. Mean species richness per blade varied from 9.02 at 'Cuda Cut in February 2002, to 15.67 at Sponge Haven in June 2001 (Tables 1, 2). Although the mean species richness was higher at all sites located in the Main Channel in June 2001 than February 2002 the width of the confidence intervals calculated from these values indicates that these differences are not significant (Fig. 6). There was not a clear cut temporal difference in values of Shannon's H calculated for each site (Tables 1, 2). Values of H were higher for the Dock and 'Cuda Cut samples collected in June 2001 relative to those collected in February 2002, and lower for the Boston Bay and Sponge Haven samples collected in June 2001 relative to those collected in February 2002 (Fig. 7). The lowest value of Shannon's H (H=1.4699) was observed at the Dock

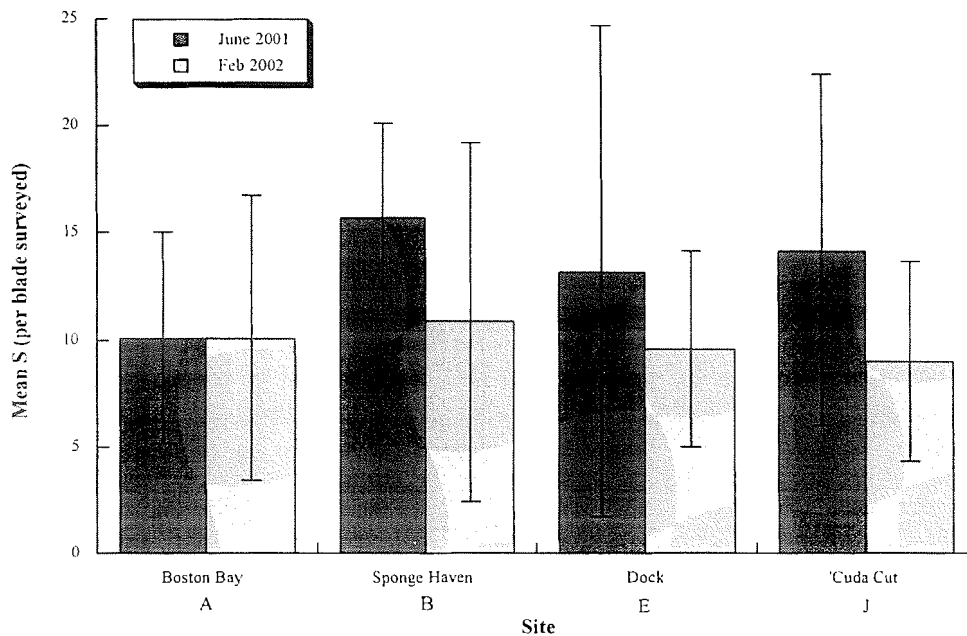


Figure 6. Mean species richness per blade surveyed at each site, Twin Cays, Belize (June 2001 and February 2002). 95% confidence limits were calculated following Hayek and Buzas (1997).

site in June 2001; the highest value of Shannon's H ($H=2.3493$) was calculated for the sample collected from Sponge Haven in February 2002. Evenness was highest at the Sponge Haven site in June 2001 ($E=0.6824$) and lowest at the Dock site in February 2002 ($E=0.1666$), reflecting the high dominance of the species *Rhizonubecula* sp. (68.24%) at the latter site (Fig. 8, Tables 3, 4).

The proportions of all species recorded during the course of this study are presented in Table 3 (June 2001) and Table 4 (February 2002). Ninety-five percent confidence intervals were calculated from the standard error for species proportions for cluster sampling as outlined in Hayek and Buzas (1997:189). In most instances, when the proportion of a species is less than 1%, the width of the confidence limits for these rare species is approximately the same value (or wider) than the proportion. Figures 9 (June 2001) and 10 (February 2002) graphically depict the relative abundances at each site of those species for which the overall proportion (relative abundance) falls between the calculated 95% confidence limits. Likewise, Tables 5 and 6 list the rank abundance for these same species. Of the 41 total species identified in this study, only one species, *Iridia* cf. *I. diaphana*, a single-chambered agglutinated foraminiferan, was common in the samples surveyed at all sites during both seasons (Tables 3-6). In June 2001, *Rhizonubecula* sp., an encrusting milioline foraminiferan, was the dominant species at all collecting sites located within the Main Channel (Sponge Haven, Dock, and 'Cuda Cut) but ranked only fourth at the Boston Bay site (Tables 3, 5). *Sorites dominicensis*, a milioline species that possesses dinoflagellate endosymbionts, was found to be the second most common species at the Boston Bay, Sponge Haven, and 'Cuda Cut sites and the third most common species at the Dock site in June 2001. The patterns of relative

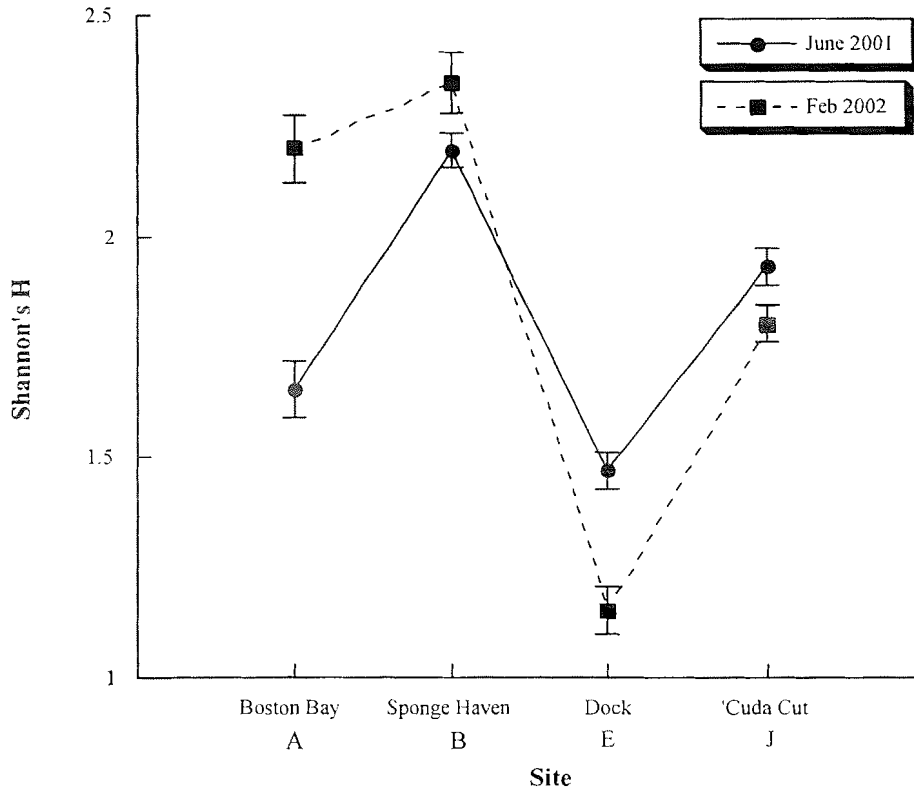


Figure 7. Values of H (Shannon Information Function) calculated for each site, Twin Cays, Belize (June 2001 and February 2002). $H = - \sum p_i \ln(p_i)$ (Hayek and Buzas 1997). Sponge Haven ($B=0.2239$) and the sites that were the most dissimilar were again Boston Bay and the Dock ($B=0.5601$).

abundance were more varied at each site in February 2002. In February 2002, *Iridia* cf. *I. diaphana* was again the most common species in Boston Bay, the second most common species at Sponge Haven, and the third most common species at both the Dock and 'Cuda Cut sites (Fig. 3, Tables 4, 6). *Rhizonubecula* sp. was observed to be the dominant species at the Dock site only, falling to the second most common species at 'Cuda Cut, the third most common species at Sponge Haven, and the eighth most common species in Boston Bay. *Planorbulina acervalis*, a multichambered, calcareous hyaline species, was observed to be the most common species at the Sponge Haven and 'Cuda Cut sites, the second most common species at the Dock site, and the third most common species in Boston Bay. *Cornuspiramia antillarum* was the second most common species at the Boston Bay site in February 2002 but ranked only seventh at Sponge Haven and was present, in proportions below 1% at both the Dock and 'Cuda Cut sites (Table 4).

The Bray-Curtis measure of dissimilarity (B) was calculated for each pair of sites in June 2001 (Table 7) and February 2002 (Table 8). The mean dissimilarity calculated for all sites was slightly lower in June 2001 ($B_{av}=0.3052$) than in February 2002 ($B_{av}=0.3852$). In June 2001, the sites with the lowest values of dissimilarity (or highest

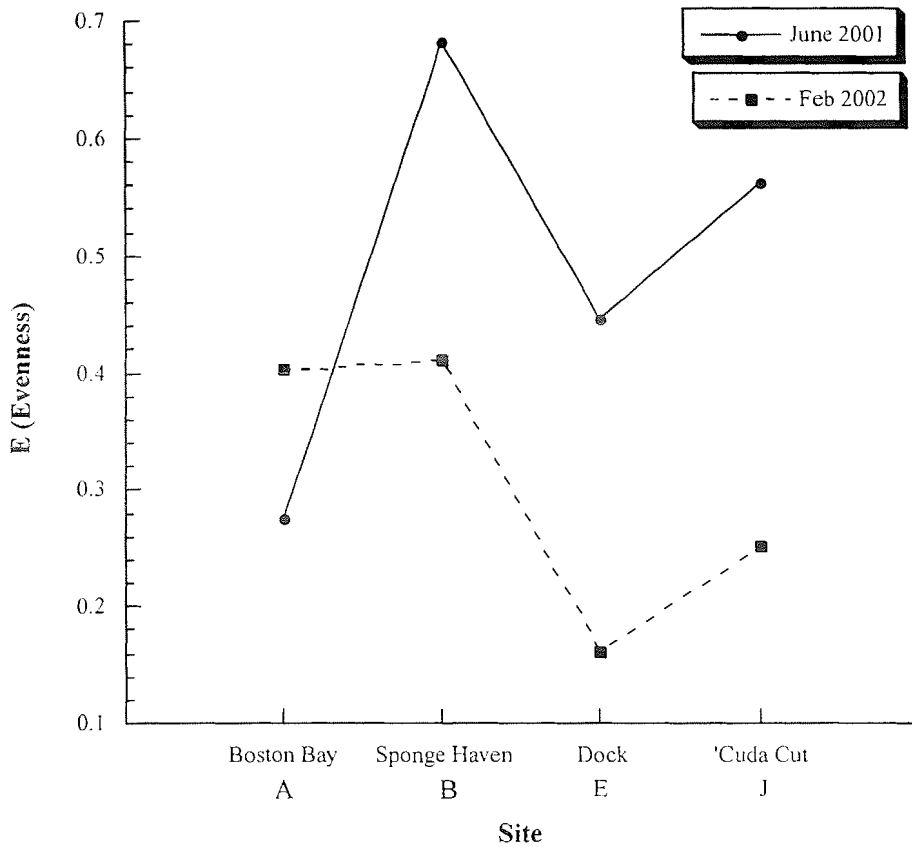


Figure 8. Values of E (Buzas-Gibson Evenness) calculated for each site, Twin Cays, Belize, during June 2001 and February 2002.

similarity) were Boston Bay and 'Cuda Cut ($B=0.1659$) and Sponge Haven and 'Cuda Cut ($B=0.1686$); the sites that were the most dissimilar were Boston Bay and the Dock ($B=0.5272$). In February 2002, the sites that were the most similar were Boston Bay and Sponge Haven ($B=0.2239$) and the sites that were the most dissimilar were again Boston Bay and the Dock ($B=0.5601$).

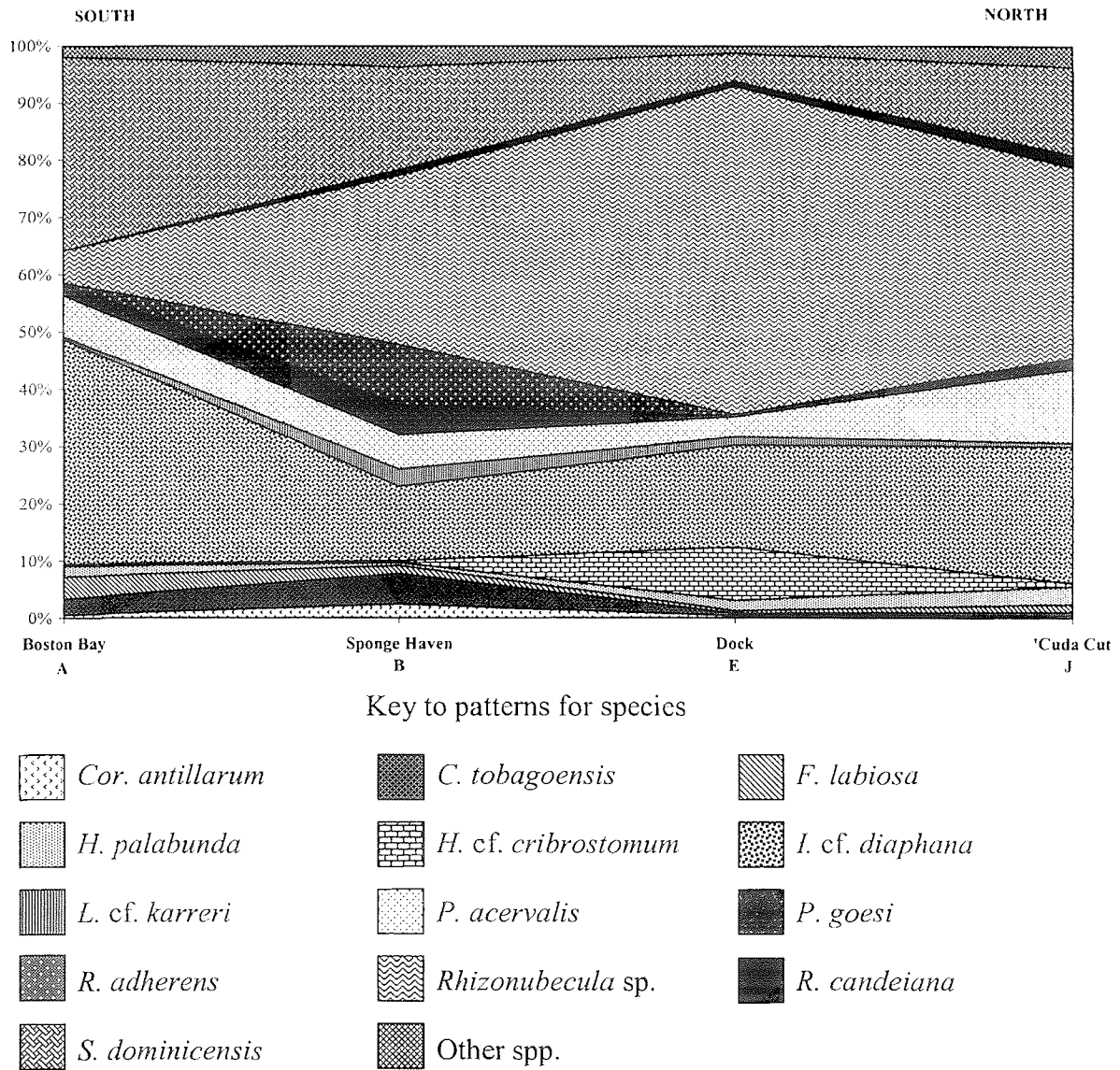
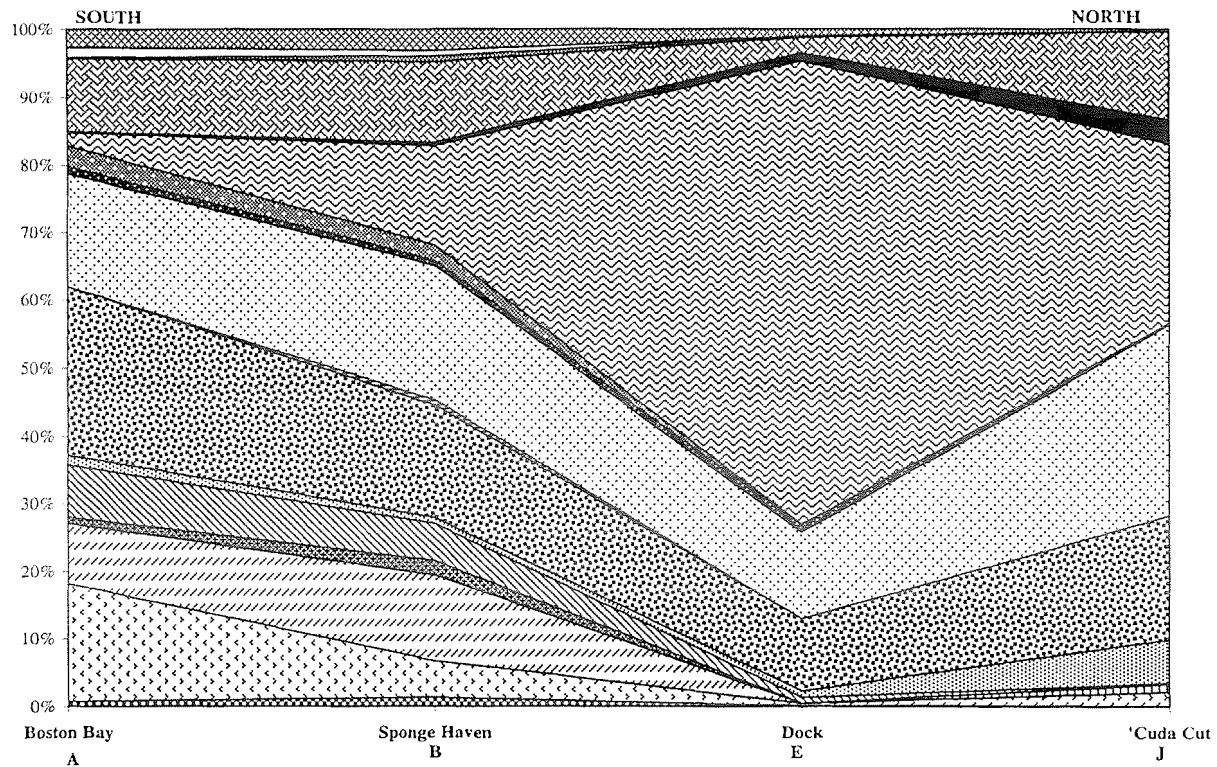


Figure 9. Relative abundance of the 13 most common epiphytic foraminiferal species at sites sampled within Twin Cays, Belize, in June 2001. Species arranged in alphabetical order from bottom to top of diagram. See key for species identification.



Key to patterns for species depicted in Figure 10.

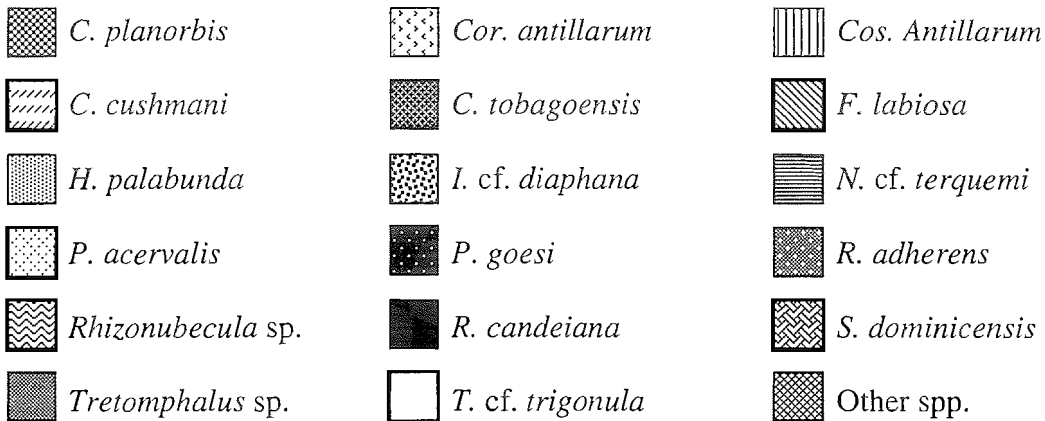


Figure 10. Relative abundance of the 17 most common epiphytic foraminiferal species at sites sampled within Twin Cays, Belize, in February 2002. Species arranged in alphabetical order from bottom to top of diagram. See key for species identification.

Table 5. Rank abundance of the most common species identified at each collecting site in June 2001.

Boston Bay	Sponge Haven	Dock	'Cuda Cut
1. <i>I. cf. diaphana</i>	1. <i>Rhizonubecula</i> sp.	1. <i>Rhizonubecula</i> sp.	1. <i>Rhizonubecula</i> sp.
2. <i>S. dominicensis</i>	2. <i>S. dominicensis</i>	2. <i>I. cf. diaphana</i>	2. <i>I. cf. diaphana</i>
3. <i>P. acervalis</i>	3. <i>I. cf. diaphana</i>	3. <i>H. cribrstoma</i>	3. <i>S. dominicensis</i>
4. <i>Rhizonubecula</i> sp.	4. <i>R. adherens</i>	4. <i>S. dominicensis</i>	4. <i>P. acervalis</i>
5. <i>F. labiosa</i>	5. <i>P. acervalis</i>	5. <i>P. acervalis</i>	5. <i>H. palabunda</i>
6. <i>C. tobagoensis</i>	6. <i>C. tobagoensis</i>	6. <i>H. palabunda</i>	6. <i>R. candeiana</i>
7. <i>P. goesi</i>	7. <i>P. goesi</i>	7. <i>L. cf. karreri</i>	7. <i>P. goesi</i>
8. <i>H. palabunda</i>	8. <i>L. cf. karreri</i>	8. <i>R. candeiana</i>	8. <i>F. labiosa</i>
	9. <i>Cor. antillarum</i>		9. <i>L. cf. karreri</i>
	10. <i>F. labiosa</i>		10. <i>C. tobagoensis</i>
	11. <i>R. candeiana</i>		11. <i>H. cribrstoma</i>

Table 6. Rank abundance of the most common species identified at each collecting site in February 2002.

Boston Bay	Sponge Haven	Dock	'Cuda Cut
1. <i>I. cf. diaphana</i>	1. <i>P. acervalis</i>	1. <i>Rhizonubecula</i> sp.	1. <i>P. acervalis</i>
2. <i>Cor. antillarum</i>	2. <i>I. cf. diaphana</i>	2. <i>P. acervalis</i>	2. <i>Rhizonubecula</i> sp.
3. <i>P. acervalis</i>	3. <i>Rhizonubecula</i> sp.	3. <i>I. cf. diaphana</i>	3. <i>I. cf. diaphana</i>
4. <i>S. dominicensis</i>	4. <i>C. cushmani</i>	4. <i>S. dominicensis</i>	4. <i>S. dominicensis</i>
5. <i>C. cf. cushmani</i>	5. <i>S. dominicensis</i>	5. <i>R. candeiana</i>	5. <i>H. palabunda</i>
6. <i>F. labiosa</i>	6. <i>F. labiosa</i>	6. <i>P. goesi</i>	6. <i>R. candeiana</i>
7. <i>R. cf. adherens</i>	7. <i>Cor. antillarum</i>	7. <i>H. palabunda</i>	7. <i>Cos. antillarum</i>
8. <i>Rhizonubecula</i> sp.	8. <i>R. cf. adherens</i>	8. <i>F. labiosa</i>	8. <i>P. cf.</i> <i>squamiformis</i>
9. <i>Triloculina</i> sp. <i>I. cf. diaphana</i>	9. <i>C. tobagoensis</i>		
10. <i>P. goesi</i>	10. <i>C. planorbis</i>		
	11. <i>P. cf.</i> <i>squamiformis</i>		
11. <i>C. tobagoensis</i>	12. <i>Tretromphalus</i> sp. <i>H. palabunda</i>		
	13. <i>N. cf. terquemi</i>		

Table 7. Bray-Curtis Measure of Dissimilarity for sites sampled within Twin Cays, Belize, in June 2001.

	Boston Bay	Sponge Haven	Dock	'Cuda Cut
Boston Bay	0	0.3300	0.5272	0.1659
Sponge Haven	-----	0	0.2435	0.1686
Dock	-----	-----	0	0.3958
'Cuda Cut	-----	-----	-----	0

Table 8. Bray-Curtis Measure of Dissimilarity for sites sampled within Twin Cays, Belize, in February 2002.

	Boston Bay	Sponge Haven	Dock	'Cuda Cut
Boston Bay	0	0.1139	0.5601	0.4640
Sponge Haven	-----	0	0.4740	0.5601
Dock	-----	-----	0	0.1298
'Cuda Cut	-----	-----	-----	0

DISCUSSION

Even though the seagrass *T. testudinum* exhibits minimal seasonal variation in the vicinity of Twin Cays, Belize, the epiphytic foraminiferal communities living attached to the leaf blades show distinct seasonal differences in mean density per unit blade area (N/cm^2), species richness (S), and evenness (E), between June 2001 (the warmer, wet season) and February 2002 (the cooler, dry season) (Tables 1, 2).

These differences are potentially attributable to any number of biotic and abiotic factors that affect both the foraminiferal populations and their phytal substratum. Biotic factors, such as the life-history characteristics of individual species, competition, and predation, The benthic foraminiferal response to organic carbon flux is well documented (Loubere and Fariduddin, 1999; Murray, 2001). Benthic foraminiferans have been shown to feed on bacteria, diatoms and other microalgae (Bernhard and Bowser, 1992, Lipps, 1983; Schwab and Hofer, 1979), all of which are components of the microbial biofilm that coats the seagrass blades (Pl. 1, figs. a-g). A few foraminiferal species are also known to utilize directly dissolved organic material (Delaca et al., 1981). In low-nutrient, are all known to influence the species composition of communities (Krebs, 1994).

Abiotic factors, such as temperature, salinity, light, nutrients, and the water-flow regime (currents and tides), have been observed to vary on a seasonal basis in Belize which has a subtropical climate and a pronounced wet and dry season (Koltes et al., 1998, Rützler and Ferraris, 1982). Some of the factors that potentially impact the epiphytic foraminiferal populations off Twin Cays include an influx of nutrients from the surrounding mangroves during the wet season, an incursion of open-water species into the main channel during the dry season, and the thermal tolerances of individual species.

The benthic foraminiferal response to organic carbon flux is well documented (Loubere and Fariduddin, 1999; Murray, 2001). Benthic foraminiferans have been shown to feed

on bacteria, diatoms and other microalgae (Bernhard and Bowser, 1992, Lipps, 1983; Schwab and Hofer, 1979), all of which are components of the microbial biofilm that coats the seagrass blades (Pl. 1, figs. a-g). A few foraminiferal species are also known to utilize directly dissolved organic material (Delaca et al., 1981). In low-nutrient, oligotrophic regimes, mangroves represent a source of organic carbon and nutrients for the surrounding nutrient-limited marine ecosystems (Robertson et al., 1992). Mangrove-derived nutrients are exported primarily in the form of leaf litter, detritus, particulate organic matter, and dissolved organic material, the interchange being facilitated by tidal rhythms (Hemminga et al., 1995; Marguillier et al., 1997; Mohammed et al., 1999). Although the influence of nutrient enrichment is most pronounced in the seagrass beds that are in closest proximity to the mangrove fringe, mangrove-derived nutrients may be exported for considerable distances from their source (Hemminga et al. 1995, Marguillier et al., 1997; Mohammed et al., 1999; Moran et al., 1991). Mangrove-derived nutrient enrichment may result in increased growth rates, shoot densities, and biomass of nearby seagrass beds, as well as increased epiphyte levels on the seagrass blades (Frankovich and Fourqurean, 1997; Koch and Madden, 2001; Koltjes et al., 1998; Tomasko and Lapointe, 1991; van Tussenbroek, 1995). For example, in the Bahamas Koch and Madden (2001) recorded epiphyte loads that were 5 to 36 times higher on seagrasses in close proximity to the mangrove fringe of Sweeting's Cay than those recorded on seagrasses growing in the central lagoon or channel.

February 2002 also saw the incursion of predominantly open-water species into the mangrove habitats. The relative abundance of *Planorbulina acervalis* more than doubled in February 2002 at all sites and the species *Planogypsina* cf. *P. squamiformis* and *Tretomphalus* sp. were found in slightly higher abundances at some of the sites sampled. In February 2002, *Cornuspiramia antillarum* was the second most common species in Boston Bay, comprising $17.41 \pm 1.36\%$ of the epiphytic population, a dramatic increase in the population compared to June 2001 when it comprised only $0.53 \pm 0.53\%$ of the population in Boston Bay. *Cornuspiramia antillarum* is a dendritic, encrusting milioline species that dominates epiphytic foraminiferal populations in open-water habitats subject to high nutrient influx. Off Man O'War Cay, a small mangrove island approximately 5 km to the north of Twin cays that hosts a breeding population of frigate birds, *C. antillarum* comprised $91.1 \pm 1.01\%$ and $89.79 \pm 0.03\%$ of the epiphytic foraminiferal populations in June 2001 and February 2002, respectively (S. Richardson, unpublished data).

Very little information is known about the thermal tolerances and/or growth optima of most species of benthic foraminiferans (Murray, 2001). In the Twin Cays region, water temperatures range from a monthly mean low of 23.6°C in January to a monthly mean high of 37.7°C in August (Koltjes et al., 1998). Several of the epiphytic foraminiferal species observed living on *T. testudinum* in Belize (*Cornuspiramia antillarum*, *Hemidiscella palabunda*, *Iridia* cf. *I. diaphana*, *Planogypsina squamiformis*, *Rhizomibecula* cf. *R. adherens*, *Rosalina candeiana*, and *Sorites dominicensis*) appear to have broader thermal tolerances than they experience in Belize as they have their northernmost distributional limits in the Indian River Lagoon, Florida (Buzas and Severin, 1977; Culver and Buzas, 1980, 1982; S. Richardson, unpublished data). *Thalassia testudinum* in the latter region exhibits pronounced seasonal variation in leaf production, leaf elongation, and biomass (Gacia, 1999), and the epiphytic foraminiferal

populations in this region exhibit pronounced seasonality as well (S. Richardson, unpublished data). On 02 February 2001, a total of nine foraminiferal species ($S=9$, $H=1.5267$, $E=0.5114$) were identified among the 386 individuals surveyed on 20 seagrass blades (44.13 cm^2 mean blade area, $\sigma=8.77$, $\sigma^2=76.93$) collected from Jupiter Sound, Florida; and, on 26 May 2001, a total of 12 foraminiferal species ($S=12$, $H=1.6348$, $E=0.4274$) were identified among the 2,945 individuals surveyed on 20 seagrass blades (50.16 cm^2 mean blade area, $\sigma=6.18$, $\sigma^2=38.15$) collected from the same site (S. Richardson, unpublished data). Buzas and Hayek (2000) also reported strong seasonality in the densities of the sediment-dwelling foraminiferal biota in the Indian River Lagoon with densities highest in the summer months (June-August) and lowest in the winter months (December-February).

Values of Shannon's H generally range between 1.5 and 3.5 (Magurran 1988) and can vary according to the evenness, or distribution, of individuals within each species used to calculate H (Hayek and Buzas, 1997). This effect was seen in the Twin Cays data in June 2001 when a higher value of H was obtained for the Sponge Haven site ($H=2.1965$) than the Dock site ($H=1.4699$) even though Sponge Haven had a lower value of species richness ($S=25$) than the Dock ($S=27$). Evenness was higher at Sponge Haven ($E=0.6824$) than the Dock ($E=0.4460$) due to the higher dominance of the species *Rhizonubecula* sp. at the latter site. The low value of H seen at the Dock site ($H=1.1521$) in February 2002 is due to the low evenness ($E=0.1666$), and corresponding high dominance, of the encrusting milioline species *Rhizonubecula* sp. (Tables 3, 4).

High dominance has been shown to be characteristic of marine communities that are subject to stress from eutrophication and pollution (Lambshhead et al., 1983; Tomascik and Sander, 1987). The dominance of *Rhizonubecula* sp. in June 2001 at the Sponge Haven, Dock, and 'Cuda Cut sites, where it was observed to be the most abundant species, and the continuing dominance of this species at the Dock site in February 2002 may indicate that *Rhizonubecula* sp. can be used as a marker for increased nutrients in the water column of mangrove habitats. Calem and Pierce (1993) measured moderately high concentrations of organic suspended material in the Main Channel of Twin Cays compared to the open lagoon during the dry season (February and March), although no published data is available for the wet season at these localities.

Iridia cf. *I. diaphana* is a single-chambered agglutinated foraminiferan that appears to be tolerant of fluctuating salinities in nearshore, tropical to subtropical marine ecosystems (S. Richardson, unpublished data). The dominance of this species in Boston Bay during June 2001 may reflect increased freshwater runoff from Hidden Lake into Boston Bay during the wet season (Calem and Pierce, 1993). *Sorites dominicensis*, the second most abundant species in Boston Bay in June 2001, has been observed to flourish in semiprotected embayments with low-water movement (Kloos and MacGillavry, 1984). *Crithionina* cf. *C. cushmani*, a single-chambered agglutinated foraminiferan that builds its dome-shaped test with sponge spicules and sediment grains, exhibited increased abundances at both Sponge Haven and Boston Bay in February 2002. This increase may reflect higher suspended sediment loads in the water column during the times that these sites were sampled (Calem and Pierce, 1993).

It is difficult to ascertain whether the differences observed in the relative abundance of the various species identified in this study truly reflect seasonal responses to changing environmental conditions without first conducting a long-term study that

extends over several years and involves more closely spaced sampling intervals. Buzas and Hayek (2000) analyzed data collected over a 20-year period from the Indian River Lagoon, Florida and found that both the population densities and the relative abundance of the five most common species of sediment-dwelling foraminiferans, varied considerably from season-to-season, as well as from year-to-year. Their results emphasize the importance of long-term monitoring programs for understanding regional trends in the population dynamics of specific taxa (Buzas and Hayek, 2000). Continued long-term monitoring of the epiphytic foraminiferal populations at Twin Cays will be important for establishing base-line data that can be used to assess any future changes that might result from both human-induced and climate-related environmental stresses.

Tilman et al. (2001) predict that expansion of agriculture over the next 50 years will result in 2.4-2.7-fold increases in the nitrogen- and phosphorus-driven eutrophication of near-shore marine ecosystems. In Belize, continued development is expected to result in increased erosion and sedimentation in coastal areas leading to the subsequent decline of nearshore mangrove, seagrass and coral reef habitats (Heyman and Kjerfve, 1999). It is hoped that the substantial body of knowledge on the Twin Cays mangrove ecosystem that has been assembled over the past 20 years will serve as a foundation for implementing a more comprehensive and coordinated multispecies monitoring effort that will better enable us detect and respond to these threats.

SUMMARY

In contrast to their phytal substrate, the epiphytic foraminiferal biotas living attached to the leaf blades of *Thalassia testudinum* in the vicinity of Twin Cays, Belize exhibit distinct seasonal differences in mean density per unit blade area (N/cm^2), species richness (S) and evenness (E). The most pronounced seasonal differences observed were in the mean densities per unit blade area (N/cm^2), which were higher at all sites in June 2001 (the warmer, wet season) relative to February 2002 (the cooler, dry season). The values of S recorded at Sponge Haven, the Main Channel near the Dock, and 'Cuda Cut, were higher in June 2001 than in February 2002. Likewise, values of E calculated for these sites were higher in June 2001 than in February 2002. The Boston Bay site had a lower values of S and E in June 2001 compared to February 2002. No significant differences were noted in the values of Shannon's H and the mean species richness per blade (N/cm^2) calculated for each site. These seasonal differences are suggested to result from a combination of biotic and abiotic factors, which may include the influx of nutrients from the adjacent mangrove fringe during the wet season, an incursion of open-water species into the mangrove habitats during the dry season, and the thermal and salinity tolerances of individual species.

Rhizomubecula sp. is identified as a potential indicator species of increased nutrients in mangrove habitats. This encrusting, milioline foraminiferan was observed to be the dominant species in June 2001 at the Sponge Haven, Dock, and 'Cuda Cut sites and again in February 2002 at the Dock site. Continued long-term monitoring of the epiphytic foraminiferal populations living in the vicinity of the Twin Cays mangrove island will be important for establishing baseline data that can be used to detect changes

due to increased anthropogenic activities, such as the eutrophication of coastal waters, and global climate change.

ACKNOWLEDGMENTS

This research was funded through a Smithsonian Institution Postdoctoral Fellowship, and grants from the Caribbean Coral Reef Ecosystems (CCRE) Program, National Museum of Natural History, Washington, DC. I would like to thank Janie and Colin Wulff, and Claudette DeCourley for their companionship in the field, and Julie Piraino for her assistance in taking the SEM photomicrographs. I would especially like to thank Marty Buzas, Klaus Rützler, and Mary Rice for their continued support. Steve Culver made helpful suggestions for the improvement of this manuscript. This is CCRE Contribution No. 687, and Smithsonian Marine Station at Fort Pierce Contribution No. 589.

REFERENCES

- Archibald, J.M., D. Longet, J. Pawlowski, and P.J. Keeling
2003. A novel polyubiquitin structure in Cercozoa and Foraminifera: Evidence for a new eukaryotic supergroup. *Molecular Biology and Evolution* 20 (1):62-66.
- Banner, F.T., C.P.G. Pereira, and D. Desai
1985. "Tretomphaloid" float chambers in the Discorbidae and Cymbaloporidae. *Journal of Foraminiferal Research* 15 (3):159-174.
- Bernhard, J.M., and S.S. Bowser
1992. Bacterial biofilms as a trophic resource for certain benthic foraminifera. *Marine Ecology Progress Series* 83 (2-3):263-272.
- Bock, W.D.
1968. Two new species of Foraminifera from the Florida Keys. *Contributions from the Cushman Foundation for Foraminiferal Research* 19:27-29.
1971. A handbook of the benthonic Foraminifera of Florida Bay and adjacent waters. In: Bock, W.D., Lynts, G.W., Smith, S., Wright, R., Hay, W.W., and Jones, J.I., eds. *A Symposium of Recent South Florida Foraminifera*. Miami Geological Society, Memoir 1:1-72.
- Brady, H.B.
1870. Part II. Analysis and description of Foraminifera. *Annals and Magazine of Natural History* 4:279-309.
- Brönnimann, P.
1949. Pflanzenbewohnende tropische Foraminiferen nebst Beschreibung von *Cymbalopora tobagoensis* n. sp. *Verhandlungen der Naturforschenden Gesellschaft in Basel* 60:179-185.
- Buzas, M.A., and L.-A. Hayek
2000. A case for long-term monitoring of the Indian River Lagoon, Florida: Foraminiferal densities, 1977-1996. *Bulletin of Marine Science* 67 (2):805-814.

- Buzas, M.A., and K.P. Severin
 1982. Distribution and systematics of foraminifera in the Indian River, Florida. *Smithsonian Contributions to Science* 36:1-38.
- Buzas, M.A., R.K. Smith, and K.A. Beem
 1977. Ecology and Systematics of Foraminifera in two *Thalassia* habitats, Jamaica, West Indies. *Smithsonian Contributions to Paleobiology* 31:1-139.
- Calder, D.R.
 1991. Abundance and distribution of hydroids in a mangrove ecosystem at Twin Cays, Belize, Central America. *Hydrologia* 216-217:221-228.
- Calem, J.A., and J.W. Pierce
 1993. Distributional control of seagrasses by light availability, Twin Cays, Belize, Central America. *Atoll Research Bulletin* 387:1-13.
- Culver, S.J.
 1990. Benthic Foraminifera of Puerto Rican mangrove-lagoon systems: potential for paleoenvironmental interpretations. *Palaios* 5:34-51.
 1991. Early Cambrian foraminifera from West Africa. *Science* 254:689-69.
- Culver, S.J., and M.A. Buzas
 1980. Distribution of Recent benthic Foraminifera off the North American Atlantic Coast. *Smithsonian Contributions to the Marine Sciences* 6:512 pp.
 1982. Distribution of Recent benthic Foraminifera in the Caribbean region. *Smithsonian Contributions to the Marine Sciences* 14:382 pp.
 1998. Patterns of occurrence of benthic Foraminifera in time and space. In: Donovan, S.K., and C.R.C. Paul, eds. *The Adequacy of the Fossil Record*. John Wiley and Sons, Chichester, UK.
 2000. Response of shallow water foraminiferal palaeocommunities to global and regional environmental change. In: Culver, S. J., and Rawson, P. F., eds. *Biotic Response to Global Change: The Last 45 Million Years*. Cambridge University Press, Cambridge, UK, pp. 122-134.
- Cushman, J.A.
 1922. Shallow-water Foraminifera of the Tortugas region. *Carnegie Institution of Washington, Marine Biology* 17 (311):1-85.
 1946. The genus *Hauerina* and its species. *Contributions from the Cushman Laboratory for Foraminiferal Research* 22:8-12.
- 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.
- Fujita, K., and P. Hallock
 1999. A comparison of phytal substrate preferences of *Archaias angulatus* and *Sorites orbiculus* in mixed macroalgal-seagrass beds in Florida Bay. *Journal of Foraminiferal Research* 29:143-151.
- Hallock, P., and M.W. Peebles
 1993. Foraminifera with chlorophyte endosymbionts: habitats of six species in the Florida Keys. *Micropaleontology* 20 (3/4):277-292.
- Hansen, H.J., and S.A. Revets
 1992. A revision and reclassification of the Discorbidae, Rosalinidae, and Rotaliidae. *Journal of Foraminiferal Research* 22(2):166-180.

- Hayek, L.-A., and M.A. Buzas
1997. *Surveying Natural Populations*. Columbia University Press, New York, 563 pp.
- Hemminga, M.A., and C.M. Duarte
2000. *Seagrass Ecology*. Cambridge University Press, Cambridge, England, 298 pp.
- Hemminga, M.A., P. Gwada, F.J. Slim, P. de Koeyer, and J. Kazungu
1995. Leaf production and nutrient contents of the seagrass *Thalassodendron ciliatum* in the proximity of a mangrove forest (Gazi Bay, Kenya). *Aquatic Botany* 50:159-170.
- Heyman, W.D.
1999. Hydrological and oceanographic considerations for integrated coastal zone management in Southern Belize. *Environmental Management* 24 (2):229-245.
- Hofker, J.
1972. *Primitive Agglutinated Foraminifera*. E. J. Brill, Leiden, The Netherlands, 95 pp., 27 pls.
- Høglund, H.
1947. Foraminifera in the Gullmar Fjord and the Skagerak. *Zoologiska Bidrag från Uppsala* 26:328 pp., 32 pls.
- Hottinger, L., E. Halicz, and Z. Reiss
1993. Recent Foraminifera from the Gulf of Aqaba, Red Sea. *Academia Scientiarum et Artium Slovenica, Ljubljana, Opera* 33:1-179
- Kloos, D.P., and H.J. MacGillivray
1985. Variability and population dynamics of *Sorites orbiculus* (Foraminifera, Soritidae). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series B: Palaeontology, Geology, Physics, Chemistry, Anthropology 88 (2):199-209.
- Keeling, P.J.
2001. Foraminifera and Cercozoa are related in actin phylogeny: two orphans find a home? *Molecular Biology and Evolution* 18:1551-1557.
- Koch, M.S., and C.J. Madden
2001. Patterns of primary production and nutrient availability in a Bahamas lagoon with fringing mangrove. *Marine Ecology Progress Series* 219:109-119.
- Koltes, K., J.J. Tschirky, and I.C. Feller
1998. Carrie Bow Cay, Belize. In: Kjerfve, B. (ed.), CARICOMP--Caribbean coral reef, seagrass and mangrove sites. *Coastal region and small island papers* 3:79-94, UNESCO, Paris.
- Krebs, C.J.
1994. *Ecology: The Experimental Analysis of Distribution and Abundance*. Harper Collins, New York, 800 pp.
- Langer, M.R.
1993. Epiphytic foraminifera. *Marine Micropaleontology* 20:235-265.
- Lamshead, P.J.D., and H.M. Platt
1983. Detection of differences among assemblages of benthic species based on an assessment of dominance and diversity. *Journal of Natural History, London* 17:859-874.
- Le Calvez, J.
1935. Sur quelques Foraminifères de Villefranche et de Banyuls. *Archives de Zoologie Expérimentale et Générale* 77 (2):79-98.

- Le Calvez, Y.
1977. Révision des Foraminifères de la collection d'Orbigny. II. Foraminifères de l'île de Cuba—Tome I. *Cahiers de Micropaléontologie* 1, 127 pp.
- Lipps, J.H., and A.Y. Rozanov
1996. The Late Precambrian-Cambrian agglutinated fossil *Platysolenites*. *Paleontological Journal* 30 (6):679-687.
- Loeblich, A.R., Jr., and Tappan, H.
1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida. *Treatise on Invertebrate Paleontology, Part C, Protista 2, Volume 1*, 511 pp.
- Loubere, P., and M. Fariduddin
1999. Benthic Foraminifera and the flux of organic carbon to the seabed. In: Sen Gupta, B.K., ed. *Modern Foraminifera*. Kluwer Academic Publishers, Great Britain, pp. 181-199.
- Magurran, A.E.
1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, New Jersey, 179 pp.
- Marguillier, S., G. Van der Velde, Dehairs, F., Hemminga, M.A., and Rajagopal, S.
1997. Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. *Marine Ecology Progress Series* 151 (1-3):115-121.
- McIlroy, D., O. Green, and M. Brasier
2001. Palaeobiology and evolution of the earliest agglutinated Foraminifera: *Platysolenites*, *Spirosolenites* and related forms. *Lethaia* 34 (1):13-29.
- Mohammed, S.M., R.W. Johnstone, B. Widen, and E. Jordelius
2001. The role of mangroves in the nutrient cycling and productivity of adjacent seagrass communities, Chwaka Bay, Zanzibar. In: Richmond, M. D., and Francis, J., eds. *The 20th Anniversary Conference on Advances in Marine Science in Tanzania, Zanzibar (Tanzania), 28 June-1 July 1999*. Marine Science Development in Tanzania and Eastern Africa 1:205-226.
- Moran, M.A., R.J. Wicks, and R.E. Hodson
1991. Export of dissolved organic matter from a mangrove swamp ecosystem: evidence from natural fluorescence, dissolved lignin phenols, and bacterial secondary production. *Marine Ecology Progress Series* 76:175-184.
- Murray, J.W.
1973. *Distribution and Ecology of Living Benthic Foraminiferids*. Heinemann Educational Books, London.
1991a. *Ecology and Paleoecology of Benthic Foraminifera*. John Wiley, New York and Longman Scientific and Technical, Harlow, U.K.
1991b. Ecology and distribution of benthic foraminifera. In: Lee, J.J., and Anderson, O.R., eds. *Biology of Foraminifera*. Academic Press, London and San Diego, pp. 221-368.
2001. The niche of benthic foraminifera, critical thresholds and proxies. *Marine Micropaleontology* 41:1-7.
- Orbigny, A.D. d'
1839. Foraminifères. In: de la Sagra, M.R., *Histoire Physique, Politique et Naturelle de L'Île de Cuba*, 223 pp.

- Pawlowski, J., M. Holzmann, C. Berney, J. Fahrni, A.J. Gooday, and T. Cedhagen
2003. The evolution of early Foraminifera. *Proceedings of the National Academy of Sciences* 100 (20):11494-11498.
- Phillips, R.C., and E.G. Meñez
1988. *Seagrasses*. *Smithsonian Contributions to the Marine Sciences* 34:104 pp.
- Richardson, S.L.
2000. Epiphytic Foraminifera of the Pelican Cays, Belize: Diversity and Distribution. In: Macintyre, I. B., Rützler, K., eds. *The Natural History of the Pelican Cays*. Atoll Research Bulletin 475:208-228.
- Robertson, A.I., D.M. Alongi, and K.G. Boto
1992. Food chains and carbon fluxes. In: Robertson, A.I. and Alongi, D.M., eds. *Tropical Mangrove Ecosystems*. Coastal and Estuarine Studies 41:293-326. American Geophysical Union, Washington, DC.
- Rützler, K., and I.C. Feller
1996. Caribbean mangrove swamps. *Scientific American* 1996 (March):94-99.
- Rützler, K., and J.D. Ferraris
1982. Terrestrial environment and climate, Carrie Bow Cay, Belize. In: Rützler, K., and Macintyre, I.G., eds. *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize. I. Structure and communities*. *Smithsonian Contributions to the Marine Sciences* No. 12:77-91.
- Schwab, D., and H.W. Hofer
1979. Metabolism in the protozoan *Allogromia laticollaris* Arnold. *Zeitschrift für mikroskopisch-anatomische Forschung*, Leipzig 93:715-727.
- Semeniuk, T.A.
2000. Spatial variability in epiphytic Foraminifera from micro- to regional scale. *Journal of Foraminiferal Research* 30 (2):99-109.
2001. Epiphytic Foraminifera along a climatic gradient, Western Australia. *Journal of Foraminiferal Research* 31 (3):191-200.
- Sen Gupta, B.K.
1999. Foraminifera in marginal marine environments. In: Sen Gupta, B. K., ed. *Modern Foraminifera*. Kluwer Academic Publishers, Great Britain, pp. 141-159.
- Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer
2001. Forecasting agriculturally driven global environmental change. *Science* 292:281-284.
- Tomascik, T., and F. Sander
1987. Effects of eutrophication on reef building corals. II. Structure of scleractinian coral communities in fringing reefs, Barbados, West Indies. *Marine Biology* 94:53-75.
- 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.
- Tussenbroek, I.B. van
1995. *Thalassia testudinum* leaf dynamics in a Mexican Caribbean coral reef lagoon. *Marine Biology*, Berlin, 122 (1):33-40.

Wantland, K.F.

1975. Distribution of Holocene benthonic Foraminifera on the Belize Shelf. In: Wantland, K.F., and Pusey, W.C., eds. *Belize Shelf--Carbonate Sediments, Clastic Sediments, and Ecology*. American Association of Petroleum Geologists, Tulsa, Oklahoma, pp. 332-399.

Williams, S.L., and K.L. Heck, Jr.

2001. Seagrass community ecology. In: Bertness, M.D., Gaines, S.D., and Hay, M.E., eds. *Marine Community Ecology*. Sinauer Associates, Sunderland, MA, pp. 317-337.

Williamson, W.C.

1858. On the Recent Foraminifera of Great Britain. Ray Society, London, 107 pp.

Wilson, B.

1998. Epiphytal foraminiferal assemblages on the leaves of the seagrasses *Thalassia testudinum* and *Syringodium filiforme*. *Caribbean Journal of Science* 34 (1-2):132-136.

Zieman, J.C.

1975. Quantitative and dynamic aspects of the ecology of turtle grass, *Thalassia testudinum*. *Estuarine Research* 1:541-562.

Zieman, J.C., R.T. Zieman

1989. The Ecology of the Seagrass Meadows of the West Coast of Florida: A Community Profile. Biological Report 85(7.25), U.S. Fish and Wildlife Service, Washington DC, USA, 155 pp.

APPENDIX 1

List of species

1. *Ammonia* cf. *A. parkinsoniana* (d'Orbigny, 1839) (not figured). *Ammonia beccarii* (Linné, 1758): WANTLAND, 1975, p. 395, text-figs. 3 l, 4 a-d, 5 a.
2. *Amphistegina gibbosa* d'Orbigny, 1839 (not figured). *Amphistegina gibbosa* d'Orbigny, 1839: LE CALVEZ, 1977b, p. 6, text-figs. 4, 5.
3. *Androsina* cf. *A. lucasi* Lévy, 1977 (Pl. 1, fig. f). *Archaias angulatus* (Fichtel and Moll, 1803): WANTLAND, 1975, p. 392, text-figs. 9 o-r, 12 b, 16 j, k, m-0); *Androsina lucasi* Lévy, 1977. HALLOCK AND PEEBLES, 1993, p. 278, pl. 1, fig. 1-4.
4. *Articulina antillarum* Cushman, 1922 (Pl. 2, fig. e). *Articulina antillarum* CUSHMAN, 1922, p. 71, pl. 12, fig. 5. *Articulina sagra* d'Orbigny, 1839: BRADY, 1884, p. 184, pl. 12, figs. 17, 18; BOCK, 1971, p. 33, pl. 13, fig. 7. *Articulina lineata* Brady, 1884: WANTLAND, 1975, p. 391, text-fig. 9 j.
5. *Articulina mucronata* (d'Orbigny, 1839) (Pl. 2, fig. b). *Vertebralina cassis* var. *mucronata* d'Orbigny, 1839: CUSHMAN, 1922, p. 63; CUSHMAN, 1929, p. 96, pl. 22, fig. 5. *Vertebralina cassis* d'Orbigny, 1839: WANTLAND, 1975, p. 389, text-fig. 9 i.
6. *Bolivinita rhomboidalis* (Millet, 1899) (Pl. 2, fig. h). ?*Bolivina compacta* (Sidebotton, 1905): CUSHMAN, 1922, p. 26, pl. 1, fig. 10. ?*Bolivina lowmani* Phleger and Parker, 1951: BOCK, 1971, p. 46, pl. 16, fig. 14. *Bolivinita rhomboidalis* (Millet, 1899): WANTLAND, 1975, p. 393, text-fig. 10 s. BUZAS, SMITH AND BEEM, 1977, p. 74, pl. 2, figs. 3, 4.
7. *Cornuspira planorbis* Schultze, 1854 (Pl. 2, fig. a). *Cornuspira planorbis* Schultze, 1854: WANTLAND, 1975, p. 387.
8. *Cornuspiramia antillarum* (Cushman, 1922) (Not figured). *Nubecularia antillarum* CUSHMAN, 1922, p. 58, text-figs. 7, 8.
9. *Coscinospira antillarum* (d'Orbigny, 1839) (Pl. 3, fig. h). *Dendritina antillarum* d'Orbigny, 1839: LE CALVEZ, 1977, p. 39, pl. 3, figs. 1-7. *Peneroplis pertusus* (Forskål, 1775): WANTLAND, 1975, p. 391.
10. *Criboelphidium poeyanum* (d'Orbigny, 1839) (Pl. 4, fig. g). *Criboelphidium poeyanum* (d'Orbigny, 1839): WANTLAND, 1977, p. 396, text-figs. 3m, 4i, 5b, c, 6g, h, 7h, 13a, 16i.
11. *Crithionina cushmani* Hofker, 1972 (Not figured). *Crithionina cushmani* HOFKER, 1972, p. 69, pl. 20, figs. 15, 16; pl. 21, figs. 1-3.
12. *Crithionina* sp. (Pl. 3, fig. c).
13. *Cymbaloporetta squamosa* (d'Orbigny, 1839) (Not figured). *Cymbaloporetta squamosa* (d'Orbigny, 1839): WANTLAND, 1975, p. 391, text-fig. 9 l. *Rosalina squamosa* d'Orbigny, 1839: LE CALVEZ, 1977b, p. 100, text-figs. 1-14 (p. 101).
14. *Cymbaloporetta tobagoensis* (Brönnimann, 1949) (Pl. 2, fig. i). *Cymbaloporetta bradyi* Cushman, 1915: WANTLAND, 1975, p. 398. *Cymbaloporetta tobagoensis* BRÖNNIMAN, 1949, p. 183, text-fig. 1a, b.

15. *Flintinoides labiosa* (d'Orbigny, 1839) (Pl. 4, fig. c). *Triloculina labiosa* d'Orbigny, 1839: CUSHMAN, 1922, p. 77, pl. 12, fig. 1. *Miliolinella labiosa* (d'Orbigny, 1839): WANTLAND, 1975, p. 390, text-figs. 9 a-g.
16. *Hemidiscella palabunda* Bock, 1968 (Pl. 3, fig. e). *Hemidiscella palabunda* BOCK, 1968, p. 27, pl. 4, figs. 3-9; WANTLAND, 1975, p. 385, text-figs. 10 i, j.
17. *Heterillina* cf. *H. cribrostoma* (Heron-Allen & Earland, 1915) (Not figured).
Heterillina cribrostoma (Heron-Allen & Earland, 1915: WANTLAND, 1975, p. 391, text-figs. 8 r, 14 a-m).
18. *Iridia* cf. *I. diaphana* Heron-Allen & Earland, 1914 (Pl. 1, figs. f, g; Pl. 3, fig. a).
Iridia diaphana Heron-Allen & Earland, 1914: CUSHMAN, 1922, p. 18.
19. *Laevipeneroplis* cf. *L. karreri* Wiesner, 1923 (Pl. 1, fig. a; Pl. 2, fig. d). *Peneroplis bradyi* Cushman, 1930: WANTLAND, 1975, p. 391, text-fig. 9 m.
20. *Miliammina fusca* (Brady, 1870) (Not figured). *Quinqueloculina fusca* BRADY, 1870, p. 286, pl. 11, figs. 2, 3.
21. *Neoconorbina* cf. *N. terquemi* (Rzehak, 1888) (Pl. 2, fig. g). *Neoconorbina terquemi* (Rzehak, 1888): WANTLAND, 1975, p. 394, text-figs. 6 k, 12 k.
22. *Patellina corrugata* Williamson, 1858 (Not figured). *Patellina corrugata* Williamson, 1858: CUSHMAN, 1931, p. 11, pl. 2, fig. 7.
23. *Planorbulina acervalis* Brady, 1884 (Pl. 3, fig. d). *Planorbulina acervalis* Brady, 1884: WANTLAND, 1975, p. 397, text-fig. 11 d.
24. *Planorbulina mediterranensis* d'Orbigny, 1826 (Not figured). *Planorbulina mediterranensis* d'Orbigny, 1826: WANTLAND, 1975, p. 397, text-fig. 11 b.
25. *Planogypsina* cf. *P. squamiformis* (Chapman, 1901) (Pl. 3, fig. f). *Planogypsina* cf. *P. squamiformis* (Chapman, 1901): HOTTINGER, HALICZ, AND REISS, 1993, p. 126, pl. 171, figs. 1-9.
26. *Pseudohauerina occidentalis* (Cushman, 1946) (Pl. 4, fig. e). *Hauerina occidentalis* Cushman, 1946: WANTLAND, 1975, p. 391, text-fig. 8 q.
27. *Pseudowebbinella goësi* (Höglund, 1947) (Pl. 3, fig. b). *Webbinella hemispherica* (Jones, Parker and Brady, 1865): LE CALVEZ, 1935, p. 88, text-fig. 7a, b.
Crithionina goësi HÖGLUND, 1947, p. 36, pl. 3, figs. 1-6; text-fig. 8.
Pseudowebbinella goësi (Höglund, 1947): HOFKER, 1972, p. 70, pl. 21, figs. 7-15.
28. *Quinqueloculina bicostata* d'Orbigny, 1839 (Not figured). WANTLAND, 1975, p. 387, text-fig. 3a, b. 13n.
29. *Quinqueloculina* sp. (Not figured). *Quinqueloculina seminulum* (Linné, 1758): WANTLAND, 1975, p. 389, text-fig. 3f, g.
30. *Rhizonubecula adherens* Le Calvez, 1935 (Not figured). *Rhizonubecula adherens* LE CALVEZ, 1935, p. 96, text-fig. 11 a, b.
31. *Rhizonubecula* sp. (Not figured).
32. *Rosalina candeiana* d'Orbigny, 1839 (Pl. 3, fig. i). *Rosalina candeiana* d'Orbigny, 1839: WANTLAND, 1975, p. 394, text-figs. 10 c, d, 12 n; LE CALVEZ, 1977b, p. 83, text-figs. 1-8 (p. 85).
33. *Rosalina* sp. (Not figured). *Rosalina* sp. WANTLAND, 1975, p. 395, text-figs. 10 f, g.
34. *Rotorbis auberii* (d'Orbigny, 1839) (Pl. 4, figs. a, b). *Rosalina auberii* D'ORBIGNY, 1839, p. 94, pl. 4, figs. 5-8. *Discorbis mira* CUSHMAN, 1922, p. 39, pl. 6, figs. 10, 11: WANTLAND, 1975, p. 394, text-figs. 10 a, b. *Discorbis auberii* (d'Orbigny,

- 1839): LE CALVEZ, 1977, p. 77, pl. 9, figs. 1-8. *Rotorbis mira* (d'Orbigny, 1839): HANSEN AND REVETS, 1992, p. 175, pl. 3, figs. 1-3.
35. *Sagenina frondescens* (Brady, 1879) (Not figured). *Sagenina frondescens* (Brady, 1879): LOEBLICH & TAPPAN, 1964, p. C205, text-fig. 117-4.
36. *Sigmoihauerina atlantica* (Cushman, 1946) (Pl. 4, fig. h). *Hauerina bradyi* Cushman, 1917: CUSHMAN, 1922, p. 71; BOCK, 1971, p. 30, pl. 12, fig. 9; WANTLAND, 1975, p. 391. *Hauerina atlantica* CUSHMAN, 1946, p. 8, pl. 1, figs. 25-26.
37. *Sorites dominicensis* Ehrenberg, 1839 (Pl. 1, fig. c, d; Pl. 4, fig. i). *Amphisorus hemprichii* Ehrenberg, 1839: WANTLAND, 1975, p. 392, text-fig. 11 c.
38. *Textularia agglutinans* d'Orbigny, 1839 (Pl. 4, fig. d). *Textularia agglutinans* D'ORBIGNY, 1839, p. 144, pl. 1, figs. 17, 18, 32-34; WANTLAND, 1975, pl. 385, text-figs. 3 h, 11 g.
39. *Tretomphalus* sp. (Pl. 3, fig. g). *Tretomphalus bulloides* (d'Orbigny, 1839): WANTLAND, 1975, text-figs. 13 r, s. *Neoconorbina (Tretomphaloides) concinna* (Brady, 1884): BANNER, PEREIRA, AND DESAI, 1985, p. 166, pl. 1, figs. 6-10, pl. 2, figs. 1-3.
40. *Triloculina bicarinata* d'Orbigny, 1839 (Pl. 4, fig. f). *Triloculina bicarinata* d'Orbigny, 1839: WANTLAND, 1975, p. 389, text-fig. 8 l.
41. *Triloculina* cf. *T. trigonula* (Lamarck, 1804) (Pl. 2, fig. c). *Triloculina trigonula* (Lamarck, 1804): CUSHMAN, 1929, p. 56, pl. 12, figs. 10, 11; pl. 13, figs. 1, 2; BOCK, 1971, p. 28, pl. 12, figs. 3, 4.

PLATES

Plate 1. Scanning electron micrographs of *Thalassia testudinum* blade from Twin Cays, Belize. Scale bar=100 μm (Figs. a, f); 10 μm (Figs. b, g); 5 μm (Figs. c-e). **a** Specimen of *Laevipeneroplis* cf. *L. karreri* attached to seagrass blade. Note pseudopodia and feeding cyst along periphery of outermost chamber; **b** Close-up of pennate diatoms and dinoflagellate on blade surface; **c, d** View of pseudopodia emerging from apertures in test of *Sorites dominicensis*; **e** Close-up of microbial biofilm on blade surface; **f** Specimen of *Iridia* cf. *I. diaphana* attached to seagrass blade. Note network of reticulated pseudopodia emanating from test periphery; **g** Enlarged view of *I.* cf. *I. diaphana* pseudopodia. Note diatom frustule being engulfed by pseudopodia in upper center of image.

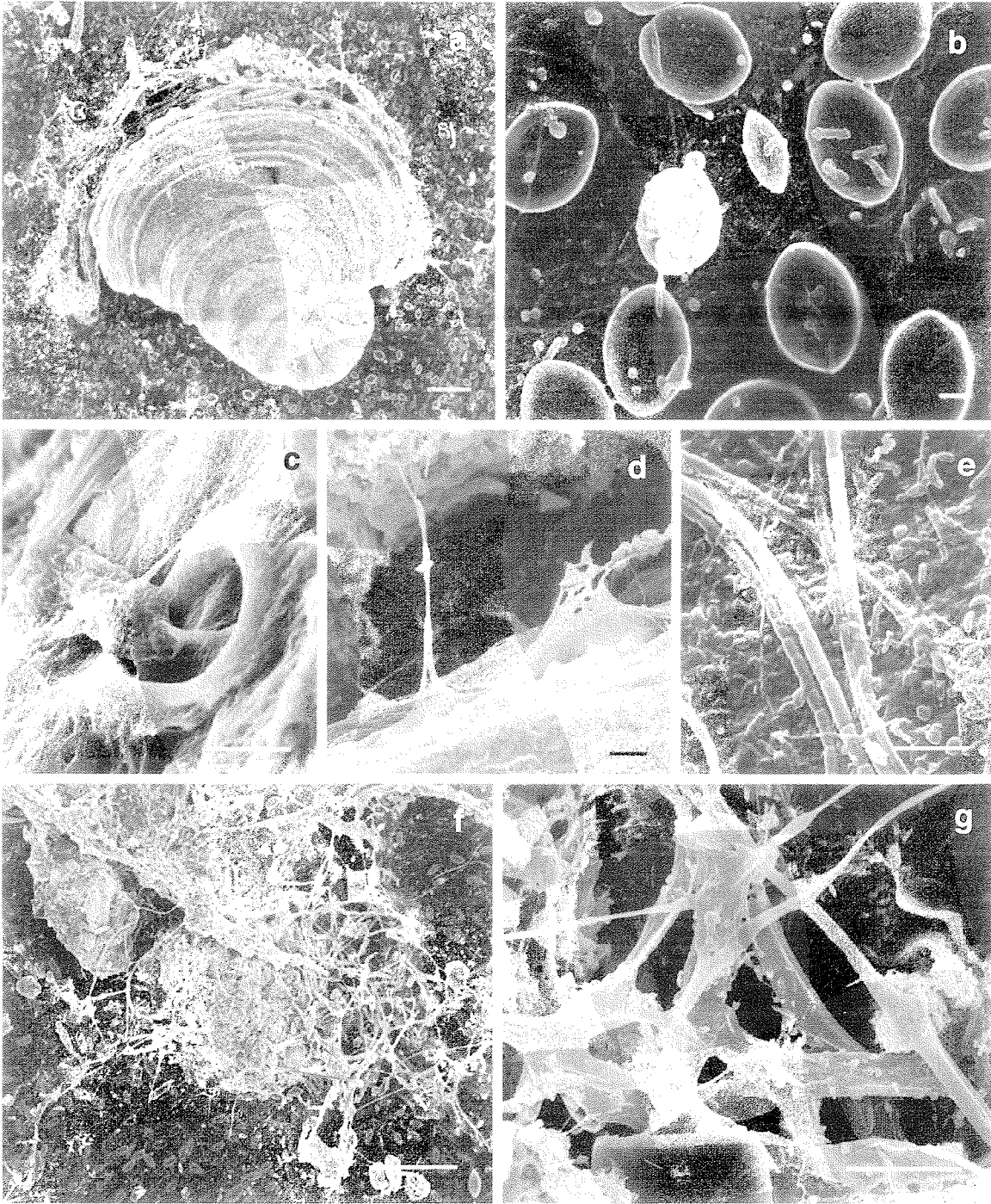


Plate 1

Plate 2. Scanning electron micrographs of epiphytic foraminiferans from Twin Cays, Belize. Scale bar=100 μm (Figs. a-g, i); 50 μm (Fig. h). **a** *Cornuspira planorbis*; **b** *Articulina mucronata*; **c** *Triloculina* cf. *T. trigonula*; **d** *Laevipeneroplis* cf. *L. karreri*; **e** *Articulina antillarum*; **f** *Androsina* cf. *A. lucasi*; **g** *Neoconorbina* cf. *N. terquemi*; **h** *Bolivinita rhomboidalis*; **i** *Cymbaloporetta tobagoensis*.

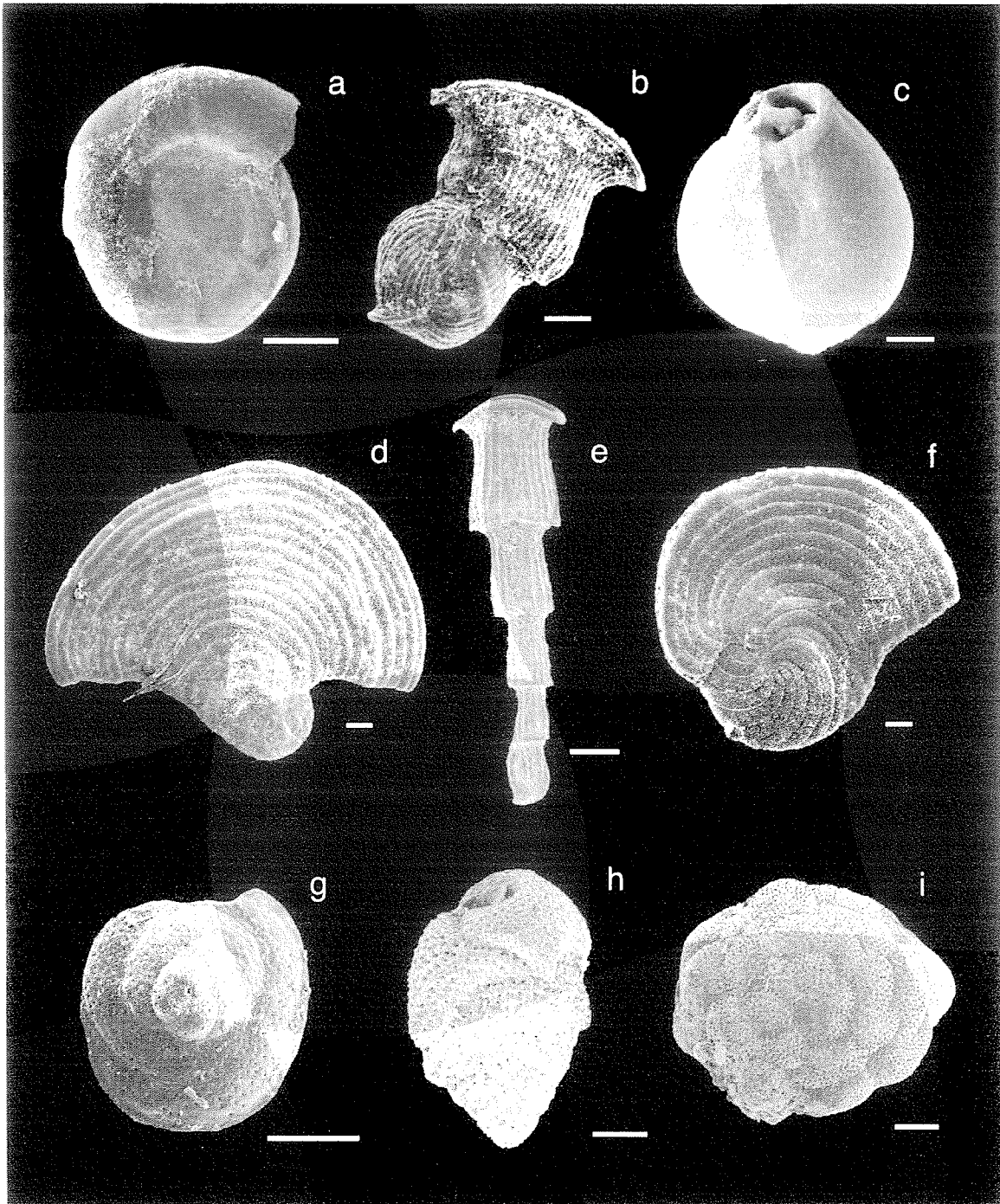


Plate 2

Downloaded from <https://pubs.cambridge.org/core>. Access provided by University of Cambridge on 01 Jun 2020 at 12:52:00, subject to the Cambridge Core terms of use, available at <https://www.cambridge.org/core/terms>. <https://doi.org/10.1017/S0007122620000000>

Plate 3. Scanning electron micrographs of epiphytic foraminiferans from Twin Cays, Belize. Scale bar=110 μm (Figs. a, d); 100 μm (Figs. b, c, e-i). **a** *Iridia* cf. *I. diaphana*; **b** *Pseudowebbinella goësi*; **c** *Crithionina* sp.; **d** *Planorbulina acervalis*; **e** *Hemidiscella palabunda*; **f** *Planogypsina* cf. *P. squamiformis*; **g** *Tretomphalus* sp.; **h** *Coscinospira antillarum*; **i** *Rosalina candeiana*.

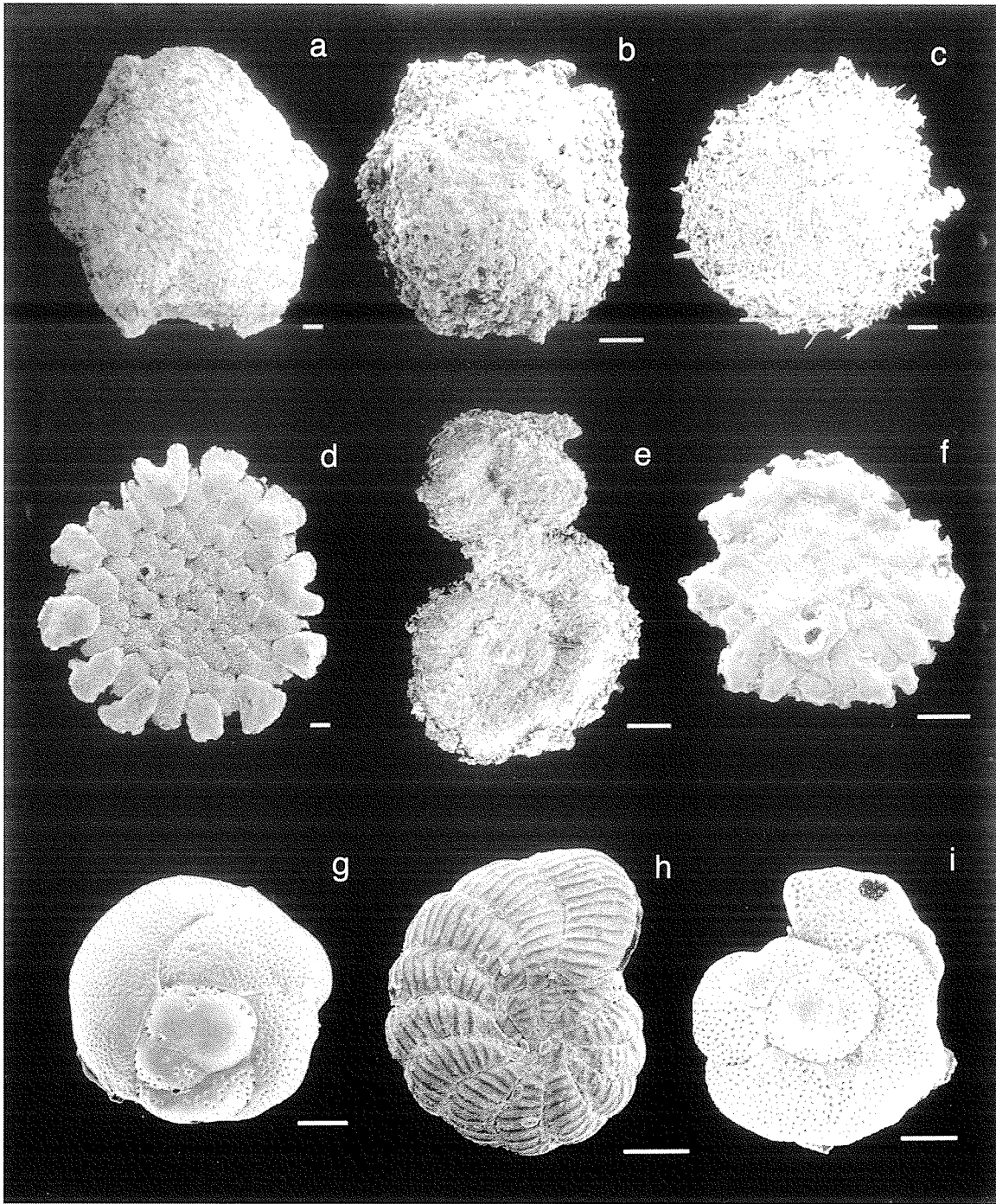


Plate 3

Plate 4. Scanning electron micrographs of epiphytic foraminiferans from Twin Cays, Belize. All scale bars=100 μm . **a, b** *Rotorbis auberii*; **c** *Flintinoides labiosa*; **d** *Textularia agglutinans*; **e** *Pseudohauerina occidentalis*; **f** *Triloculina bicarinata*; **g** *Criboelphidium poeyanum*; **h** *Sigmoihauerina atlantica*; **i** *Sorites dominicensis*.

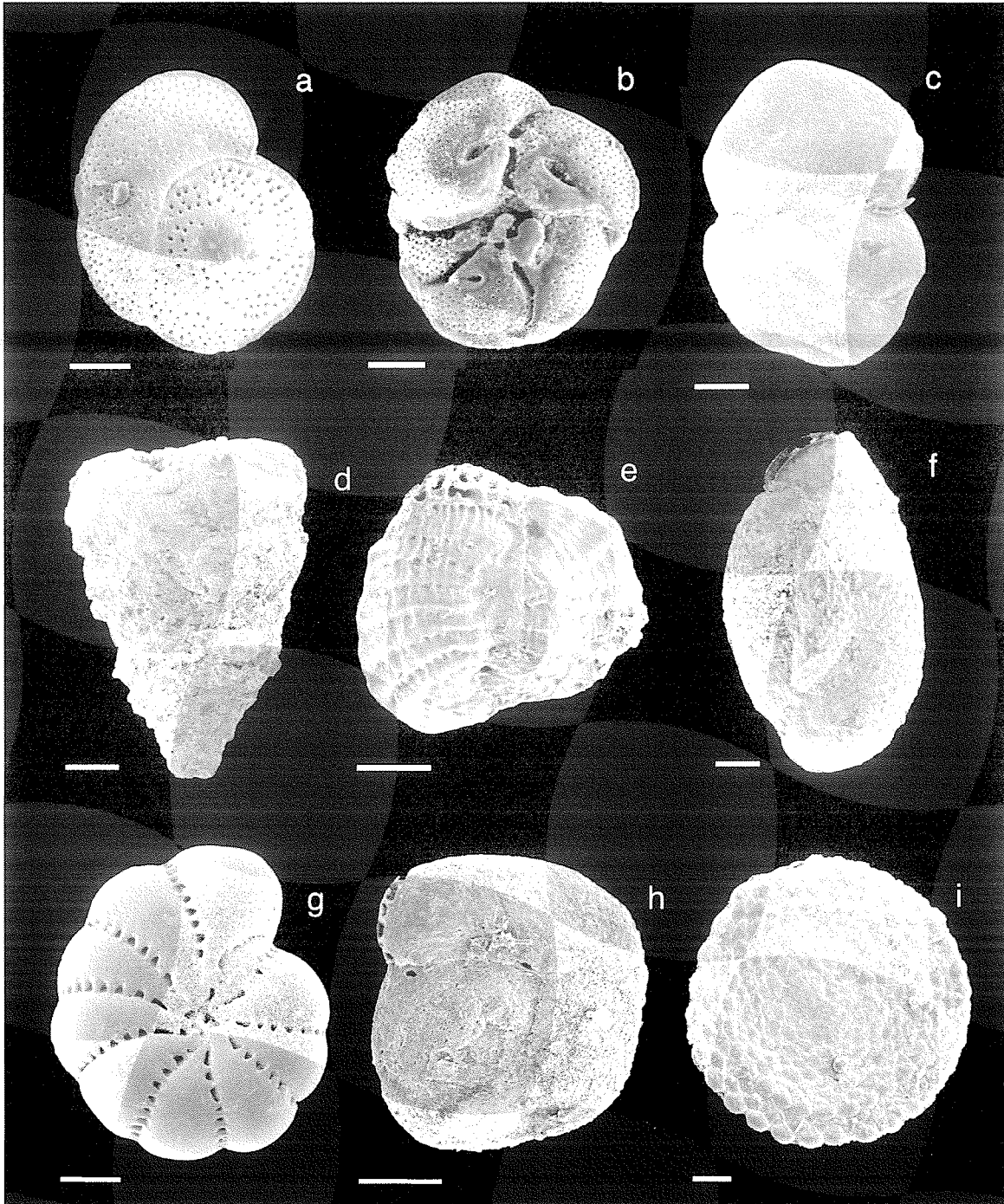


Plate 4