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Response of epiphytic foraminiferal communities to natural eutrophication in seagrass habitats off Man O'War Cay, Belize

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Abstract

Eutrophication from a variety of anthropogenic sources is an increasingly prevalent problem in coastal waters, and is one of the factors contributing to the decline of seagrass ecosystems worldwide. This study investigated the impact of natural nutrient enrichment derived from nesting seabird colonies on Man O'War Cay, Belize, on the epiphytic foraminiferal communities living on the seagrass *Thalasssia testudinum*. Man O'War Cay, a small mangrove island in the central region of the barrier reef complex, hosts nesting colonies of magnificent frigate birds and brown boobies. Epiphytic foraminiferans were surveyed from five stations spaced at 10-m intervals along a 40-m transect in a seagrass meadow located off the eastern end of the island (March 2004). Low species diversity and high dominance of the encrusting, dendritic species *Cornuspiramia antillarum* characterized the epiphytic foraminiferal biota. Species diversity, as measured by the Shannon's H, and evenness, as measured by Buzas–Gibson's E, decreased in an offshore direction. The density of individuals per square centimeter of blade, however, increased in an offshore direction, with the lowest values observed at the station closest to the island, and the highest values recorded at the station farthest from the shore. The results obtained in this study indicate that epiphytic foraminiferal populations respond to nutrient enrichment, and thus may be useful indicators of ecosystem decline in subtropical–tropical, oligotrophic marine habitats.

Problem

Benthic foraminiferans have been widely used as indicators of eutrophication in coastal marine ecosystems (Alve 1995; Culver & Buzas 1995; Yanko *et al.* 1999; McGann *et al.* 2003). Seminal studies by Bandy *et al.* (1964a,b, 1965) investigating the impact of sewage outfalls on the benthic foraminiferal biotas off Southern California found offshore biotas in close proximity to the outfall plumes to be characterized by low species diversity and high population densities. Recent studies of the distribution of benthic foraminiferans around sewage outfalls in Santa Monica Bay found that the biotas were useful in delimiting impacted areas, and that certain species were of use as bioindicators of organic waste. In the north-west Atlantic, Thomas *et al.* (2000) found high dominance of the species *Ammonia beccarii* to be associated with nitrogen-rich effluent discharge from wastewater treatment plants into Long Island Sound. Eutrophication in coral reef ecosystems has also been associated sometimes with dramatic changes in the benthic foraminiferal communities; for example, the decline of larger endosymbiont-bearing taxa is often accompanied by increased dominance of smaller opportunistic species (Hallock *et al.* 2003).

Tropical and subtropical mangroves are often nutrient limited (Rützler & Feller 1996), and mangroves growing on islands with nesting and/or roosting colonies of birds are often more productive than those on adjacent islands without bird colonies (Onuf *et al.* 1977; Frederick & Powell 1994; Doyle *et al.* 2001). In Belize, the trees growing on nearby Twin Cays are characterized by a tree-height gradient, in which trees in the seaward fringe are uniformly tall (5–6 m), trees in the transition zone are shorter (2–4 m), and trees in the interior ponds are dwarfed in height (<1.5 m) (Feller *et al.* 2002). Tree height on Twin Cays has been shown to result from a complex interplay of nutrient availability and cycling, with trees in the fringe zone experiencing N-limitation, and the stunted growth of the interior dwarf stands resulting from severe P-limitation (Feller *et al.* 2002). In contrast, on nearby guano-rich Man O'War Cay, mangrove trees are more productive, have higher growth rates, and are considerably taller, reaching an estimated 10–15 m in height (Feller 1996).

Islands with nesting seabird colonies have been described as 'islands of enrichment,' because the guano-derived nutrient enrichment impacts not only the terrestrial habitat, but extends into the surrounding marine ecosystem as well (Frederick & Powell 1994). The scale of nutrient enrichment off islands with nesting colonies appears to be localized to a zone extending from 40 to 200 m offshore (Powell *et al.* 1991; Frederick & Powell 1994). Observed impacts include increased populations of phytoplankton in the water column (Lapointe *et al.* 2004), dense macroalgal growth (McGlathery 2001), increased productivity of seagrasses (Powell *et al.* 1991), and increased epiphyte loads on the seagrass blades (Tomasko & Lapointe 1991; Frankovich & Fourqurean 1997). At Man O'War Cay, Tomasko & Lapointe (1991) found heavy epiphyte loads on *Thalassia testudinum* to be associated with elevated concentrations of nutrients (ammonium, nitrite–nitrate, total dissolved inorganic nitrogen, and soluble reactive phosphate) in the water column. The translocation of accumulated nutrients from guano-rich Man O'War Cay into the surrounding seagrass habitats occurs via a number of routes, including inundation during daily tidal cycles (tidal range of 21 cm), overwash of the island during spring tides, periodic freshwater runoff during heavy rains, and the export of nutrient-enriched mangrove leaves and plant tissues (Onuf *et al.* 1977; Koltes *et al.* 1998).

The goal of the present study was (1) to survey the epiphytic foraminiferans living on *T. testudinum* off Man O'War Cay to determine whether the foraminiferans exhibit changes in their diversity and abundance with increasing distance from the island; (2) to compare these results with samples collected from off Man O'War Cay in June 2001 and February 2002; and (3) to contrast the Man O'War biotas with the epiphytic foraminiferans previously surveyed from other sites in Belize, all cays without nesting seabird colonies.

Study Area, Material and Methods

Study area

Man O'War Cay (16°52.5′ N, 88°07′ W) (Figs 1 and 2) is a small (~2 ha) oceanic-island mangrove cay located approximately 9 km north-west of Carrie Bow Cay (16°48′ N, 88°05′ W) and ~12 km from the mainland of Belize. These islands are among the approximately 400 mangrove and sand cays that lie at the western edge of the backreef lagoon in the central region of the Belizean Barrier Reef Complex (Macintyre & Aronson 1997). Due to its distance from the mainland, Man O'War Cay receives neither freshwater runoff nor terrigenous sediment, but rather is subject to intense evaporation during the dry season (November–March), and episodic inundation with freshwater during the wet season (April–October) (Rützler & Feller 1996; Macintyre & Aronson 1997). All three species of Caribbean mangroves [*Rhizophora mangle* Linnaeus 1753, *Avicennia germinans* (Linnaeus) Linnaeus 1764, and *Laguncularia racemosa* (Linnaeus) Gaertner 1807] are found on the island, which is home to nesting colonies of magnificent frigatebirds (*Fregata magnificens* Matthews 1914) and brown boobies (*Sula leucogaster* (Boddaert 1783)) (Stoddart *et al.* 1982; Trivelpiece & Ferraris 1987; Tomasko & Lapointe 1991). The shallow-water subtidal zone surrounding the island is vegetated by dense macroalgal growth, grading into a mixed species (*Thalassia testudinum* Banks & Solander ex König 1805 and *Syringodium filiforme* Kützing in Hohenacker 1860) seagrass meadow. Patches of unvegetated sediments are located to the south-east and west of the island (Fig. 2).

Most seabird species (96%) exhibit colonial breeding, and nest at sites that provide safety from predators, such as in trees, in marshes, or on islands (Coulson 2002). Many seabirds forage at great distance from their nesting sites, especially during the breeding season, periodically returning to the nests to incubate the eggs or feed the nestlings, thereby translocating nutrients from marine to terrestrial habitats (Coulson 2002; Weimerskirsch *et al.* 2003). Magnificent frigatebirds feed primarily on surface-dwelling fish and squid; brown boobies also feed on large quantities of squid and a wide variety of schooling fish (Brinkley & Humann 2001a,b; Nellis 2001; Shealer 2002). During the collecting season in March 2004, male frigatebirds with inflated gular pouches were observed sitting on the branches of the mangrove trees, as well as slowly circling above the island. Although typically characterized as kleptoparasites (stealing prey from other birds), the frig-

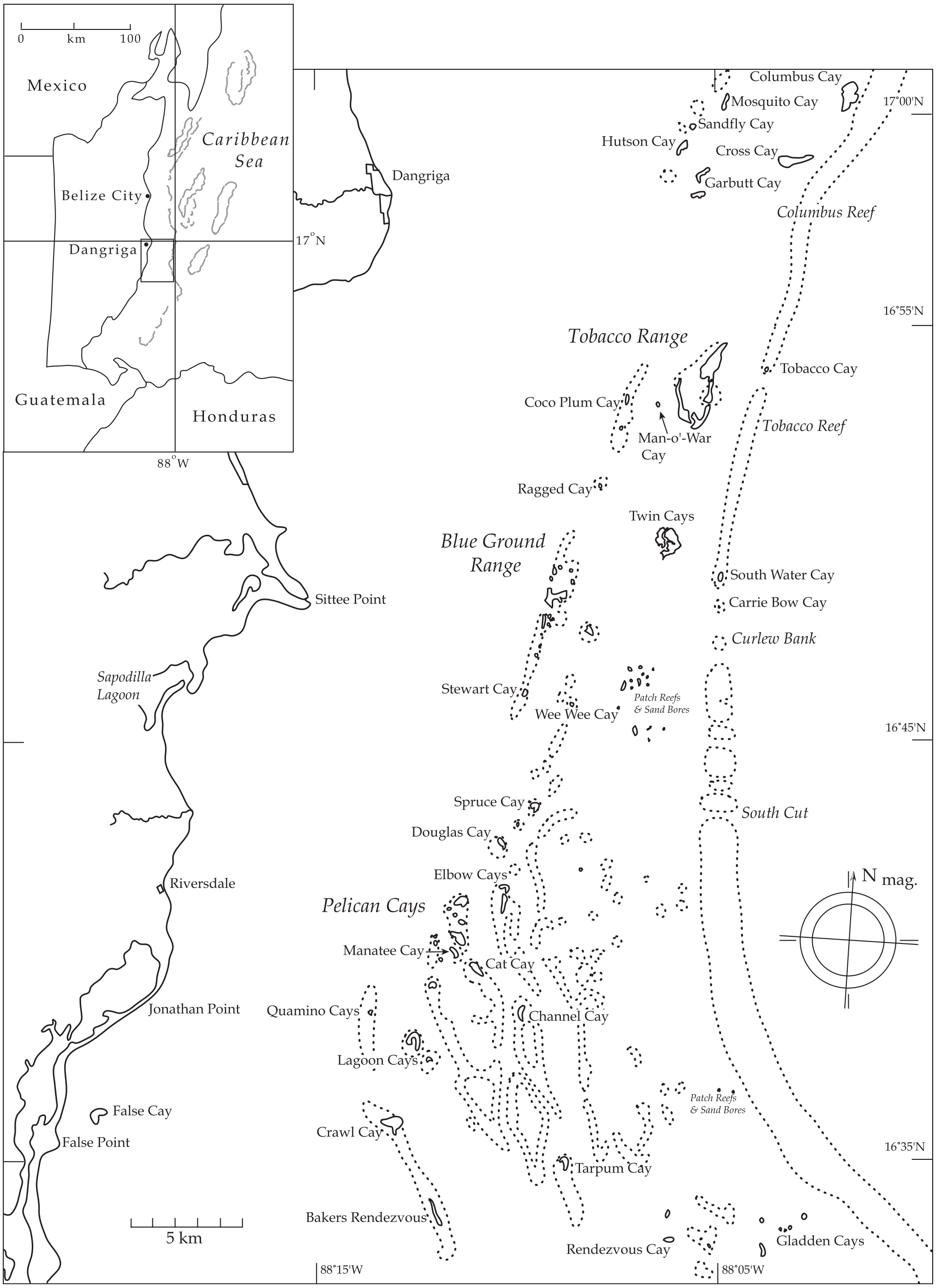

Fig. 1. Map of the central province of the Belizean Barrier Reef Complex showing the location of Man O'War Cay (arrow upper right quadrant). Other sites discussed include Twin Cays, Carrie Bow Cay, and the Pelican Cays.

atebirds at Man O'War Cay were observed to dive and pluck fish from the seagrass flat at the eastern end of the island, as it became progressively exposed during low tide (S. Richardson, unpublished observations).

Nutrients are concentrated at colony sites by the defecation of both adults and nestlings (Powell *et al.* 1991; Frederick & Powell 1994). Excretion of nitrogenous wastes at colony sites can result in a considerable accumulation of guano; for example, a single Peruvian cormorant can deposit 1 kg of dry guano in single month (Welty & Baptista 1988). The nitrogenous wastes excreted by birds are comprised primarily of uric acid, with lesser

Fig. 2. Aerial photo of Man O'War Cay showing approximate location of transect sampled in off eastern end of island (A), and site of samples collected in 2001 and 2002 (B).

amounts of ammonia, urea, creatine, and amino acids, and discharged as a white or cream-colored paste that is rich in nitrogen (16%) and phosphorus (10%) (Welty & Baptista 1988). At Man O'War Cay, the leaves and branches of the mangrove trees were stained white with excrement, and a core of the underlying sediments revealed a thick layer of accumulated of guano (Wooller *et al.* 2003).

Field and laboratory protocols

In June 2001 and February 2002, blades of the seagrass *T. testudinum* were collected from a site approximately 15m off the north-eastern end of Man O'War Cay, Belize (Fig. 2B). In March 2004, a 40-m long transect was laid off of the eastern side of Man O'War Cay, along a ridge with a dense mixed stand of *T. testudinum* and *S. filiforme* (Fig. 2A). The initial transect station was located at latitude 16°53.069′ N, and longitude 88°06.407′ W, and trended approximately 128° SE. Stations were set up at 10-m intervals along the transect: station 1 (0 m), station 2 (10 m), station 3 (20 m), station 4 (30 m), and station 5 (40 m). At each station, samples of *T. testudinum* were collected for the analysis of the epiphytic foraminiferal biotas (n = 8 blades), and shoot densities of *T. testudinum* were counted in four 0.25-m^2 quadrats. The water depth at the time of collection (low tide) was less than 0.5 m at all stations.

Eight blades of roughly equivalent length were collected haphazardly (*sensu* Hayek & Buzas 1997) from within an area of approximately 1 m^2 of sea floor at each station. Seagrass blades collected from each station were stored separately, immersed in seawater in Ziploc bags, and stored 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.

Each blade was examined for live foraminiferans using a binocular, dissecting microscope. 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. All live individuals were counted on both sides of the blade, identified to species level, and tallied. Voucher specimens were removed from the blades and stored on microslides for subsequent comparison with the type Foraminifera collections housed in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Statistics

Descriptive statistical analyses and one-way ANOVAs were performed using Microsoft Excel X. The Shannon index of diversity (H') and the Buzas–Gibson measure of evenness (E) were calculated following the formulas cited in Hayek & Buzas (1997). An homogeneity of variance test (F_{max}) indicated that the sample variances for shoot density, blade width, blade length, and blade area were similar to each other (Fowler *et al.* 1998). For those data sets for which the F_{max} test showed that the sample variances were not similar – the total number of individuals per blade (N) and density (number of individuals per square centimeter) – the data were transformed using arcsinh transformation, due to the fact that both data sets included observations of zero (Fowler *et al.* 1998).

Results

The preliminary surveys of the epiphytic foraminiferal biotas living on *Thalasssia testudinum* off Man O'War Cay conducted in June 2001 (wet season) and February 2002 (dry season) yielded a low diversity biota with a total species richness of S = 13, low values of Shannon's H' and evenness (E), high dominance (~90% *Cornuspiramia antillarum*), and high population densities (Table 1). The results of the March 2004 study demonstrate that the epiphytic foraminiferans living on the seagrass *T. testudinum* change in both diversity and abundance with increasing distance from Man O'War Cay (Tables 2 and 3; Fig. 3). Overall, the community of epiphytic foraminiferans is represented by low species richness, with a total value of S = 15 and a mean value of S = 7.6; low diversity indices, with a mean value of $H' = 0.62$; high dominance, with a mean value of E = 0.28; and high population densities, with the mean number of individuals recorded at each station equivalent to N = 1194.

Table 1. Summary of epiphytic foraminiferal diversity and abundance data from *Thalassia testudinum* blades collected from site B, ~15 m off the north-eastern side of Man O'War Cay, Belize, in June 2001 and February 2002.

	June 2001	February 2002
species richness (S)	12	13
Shannon's H'	0.44	0.48
evenness (E)	0.12	0.13
total blade surface area [cm^2] (n = 12)	1076.7	806.5
mean blade surface area [cm^2] (n = 12)	89.7 (σ = 14.1)	67.2 (σ = 14.4)
N (total no. of individuals) (n = 12)	1962	4888
mean N per blade (n = 12)	1635 (σ = 65.2)	4073 (σ = 104.2)
mean density (N cm^{-2} blade surface area) (n = 12)	1.8 (σ = 0.7)	6.3 (σ = 2.3)

Table 2. Diversity indices for epiphytic foraminiferal biotas living on *Thalassia testudinum* collected at successive stations along transect A off eastern end of Man O'War Cay, Belize, in March 2004.

index	station 1 (0 m)	station 2 (10 m)	station 3 (20 m)	station 4 (30 m)	station 5 (40 m)	mean
species richness (S)	7	9	5	8	9	7.6
Shannon's H'	1.31	0.92	0.28	0.28	0.29	0.62
evenness (E)	0.53	0.28	0.26	0.17	0.15	0.28
no. of individuals (N)	86	751	1055	2233	1846	1194

The total number of individuals counted per station generally increased in an offshore direction, ranging from a low of N = 86 at station 1 to a high of N = 2233 at station 4 (Table 2). A parallel trend was observed in the mean number of individuals per blade (Table 4), with values increasing from stations 1 ($\mu = 11 \pm 14$) to 4 ($\mu = 231 \pm 77$). A one-way ANOVA of the transformed data indicates that the difference in the mean number of individuals per blade of the five samples (eight blades per sample) is statistically significant ($F_{4,35} = 2.64$, $P < 0.001$). A Tukey test of the results showed that statistically significant ($P = 0.05$) differences in the mean number of individuals per blade occur between stations 1 and all other stations, and between stations 2 and 4.

Perhaps more significantly, a distinct trend in increasing mean density of individuals per square centimeter of blade surface area was observed in an offshore direction along the transect, ranging from a low value of μ = 0.21 individuals·cm^{-2} at station 1 to a high value of μ = 4.2 individuals·cm^{-2} at station 5 (Table 5). A one-way ANOVA of the transformed data indicates that the difference in the mean density of individuals per square centimeter of blade of the five samples (eight blades per sample) is statistically significant ($F_{4,35} = 2.64$, $P < 0.001$). A Tukey test of the results showed that statistically significant ($P = 0.05$) differences in the mean number of individuals per blade occur between stations 1 and all other stations, stations 2 and 4, stations 2 and 5, stations 3 and 4, and stations 3 and 5. Or, more concisely, the only stations for which there were not significant differences in the density of individuals per square centimeter were stations 2 and 3 and stations 4 and 5.

Table 3. Relative abundance of epiphytic foraminiferal species living on *Thalassia testudinum* collected at successive stations along transect A off eastern end of Man O'War Cay, Belize, in March 2004.

species	station 1 (0 m)	station 2 (10 m)	station 3 (20 m)	station 4 (30 m)	station 5 (40 m)
Cornuspiramia antillarum (Cushman 1922)	33 ± 14	73 ± 40	94 ± 25	94 ± 31	95 ± 51
Cymbaloporetta squammosa (d'Orbigny 1839)	1.2 ± 1.1	0	0.09 ± 0.18	0.04 ± 0.09	0
Flintinoides labiosa (d'Orbigny 1839)	0	0.27 ± 0.50	0	0	0
Hemidiscella palabunda Bock 1968	0	0.13 ± 0.23	0	0	0
Iridia diaphana Heron-Allen & Earland 1914	41 ± 20	17 ± 23	2.4 ± 3.9	1.6 ± 3.3	1.6 ± 3.7
Neoconorbina cf. *terquemi* (Rzehak 1888)	0	0	0	0	0.11
Planorbulina acervalis Brady 1884	17 ± 13	2.5 ± 6.5	1.9 ± 2.6	1.7 ± 4.2	1.2 ± 4.3
Planogypsina cf. *squamiformis* (Chapman 1901)	3.5 ± 3.1	0	0	0	0
Pseudowebbinella cf. *goesi* (Höglund 1947)	0	1.6 ± 11	0	0.40 ± 3.2	0
Quinqueloculina sp.	0	0	0	0	0.05 ± 0.11
Rhizonubecula cf. *adherens* Le Calvez 1935	1.7 ± 2.5	2.5 ± 10	0	0.31 ± 0.33	0.16 ± 2.1
Rhizonubecula sp.	0	0.53 ± 6.4	0	0.04 ± 0.09	0
Rosalina candeiana d'Orbigny 1839	1.7 ± 2.5	2.1 ± 7.4	1.1 ± 1.0	1.2 ± 2.3	2.1 ± 3.2
Sorites dominicensis Ehrenberg 1839	0	0	0	0	0.11 ± 0.21
Allogromia sp.	0	0	0	0	0.11 ± 0.21
total	100	100	100	100	100

Confidence limits for cluster sampling were calculated following Hayek & Buzas (1997).

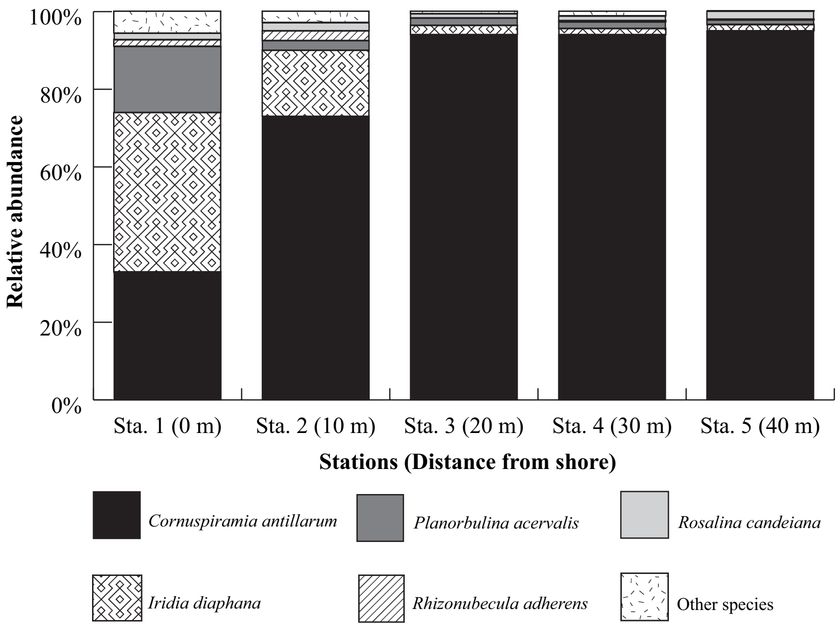

Fig. 3. Relative abundance of the most common species of epiphytic foraminiferans on *Thalassia testudinum* off Man O'War Cay, Belize, in March 2004. Percentage values for each species are listed in Table 4.

As noted previously, the overall diversity of the epiphytic foraminiferans living on *T. testudinum* off Man O'War Cay is relatively low. Species richness ranged from S = 5 at station 3 to S = 9 at stations 2 and 5. The highest value of Shannon's H' was observed at station 1 ($H' = 1.30$), dropping precipitously to a low value of $H' = 0.28$ at station 3 (Table 2). A similar decreasing trend moving offshore along the transect was observed in the calculated values of evenness, with the highest value observed at station 1 (E = 0.53) to the lowest (E = 0.15) at station 5 (Table 2).

Distinct differences in the relative abundance and dominance of certain epiphytic species were noted at each station (Tables 3 and 5). *Cornuspiramia antillarum* comprised a major component of the biota at all stations: this species was ranked as the second most abundant species at station 1 and the dominant species at stations 2–5 (Table 5). *Iridia diaphana* was the most abundant species

Table 4. Summary table of characteristics of *Thalassia testudinum* surveyed at each station along transect A off eastern end of Man O'War Cay, Belize, in March 2004.

	station 1 (0 m)	station 2 (10 m)	station 3 (20 m)	station 4 (30 m)	station 5 (40 m)
mean shoot density (n = 4)	9.5	30.3	29.0	22.8	27.8
SD	20.8	29.1	4.6	10.0	7.6
0.95 CL	12.2	11.6	1.8	4.0	3.0
mean blade width [cm] (n = 8)	1.3	1.3	1.3	1.1	1.0
SD	0.1	0.1	0.1	0.1	0.2
0.95 CL	0.1	0.1	0.0	0.1	0.2
mean blade length [cm] (n = 8)	24.2	35.5	38.9	34.8	27.8
SD	2.7	4.3	3.8	2.7	2.8
0.95 CL	2.3	3.6	3.2	2.2	2.3
mean blade surface area [cm^2] (n = 8)	61.4	90.5	93.1	76.1	55.9
0.95 CL	11.8	12.4	10.5	12.3	9.8
mean N per blade (n = 8)	10.8	93.9	131.9	279.1	230.7
SD	17.4	61.2	56.0	74.9	92.3
0.95 CL	14.5	51.0	46.7	62.5	77.0
density (no. of foraminifera cm^{-2} blade) (n = 8)	0.2	1.1	1.4	3.8	4.2
SD	0.4	0.7	0.5	1.5	1.7
0.95 CL	0.3	0.6	0.4	1.3	1.4

Mean shoot densities were counted in 0.25-m^2 quadrats.

Table 5. Rank abundance of the most common epiphytic foraminiferal species identified at each station along transect A off eastern end of Man O'War Cay, Belize, in March 2004.

station 1 (0 m)	station 2 (10 m)	station 3 (20 m)	station 4 (30 m)	station 5 (40 m)
1. *Iridia diaphana*	1. *C. antillarum*	1. *C. antillarum*	1. *C. antillarum*	1. *C. antillarum*
2. *Cornuspiramia antillarum*	2. *I. diaphana*	2. *I. diaphana*	2. *P. acervalis*	2. *R. candeiana*
3. *Planorbulina acervalis*	3. *P. acervalis*, cf. *adherens*	3. *P. acervalis*	3. *I. diaphana*	3. *I. diaphana*
4. *Planogypsina* cf. *squamiformis*	4. *R. candeiana*	4. *R. candeiana*	4. *R. candeiana*	4. *P. acervalis*
5. *Cymbaloporetta squammosa*, *Rhizonubecula* cf. *adherens*, *Rosalina candeiana*	5. *Pseudowebbinella* cf. *goesi*			

Only species occurring in abundances of >1.0% are listed. The exact values of relative abundance for each species are given in Table 3.

at station 1, and increased in abundance in an offshore direction. *Planorbulina acervalis* was ranked as the third most abundant species at stations 1–4 and the fourth most abundant species at station 5. Although *Planogypsina* cf. *squamiformis* was the fourth most abundant species at station 1, comprising 3.5% of the population, this species was not found at any of the other stations surveyed. The three other species found in low abundances (<2%) at station 1 – *Cymbaloporetta squammosa*, *Rhizonubecula* cf. *adherens* and *R. candeiana* – were also found in low abundances (<2%) at stations 2–5. Likewise, a few species had rare occurrences at the other stations sampled: *Flintinoides labiosa* (station 2), *Hemidiscella palabunda* (station 2), *Pseudowebbinella goësi* (stations 2 and 4), *Rhizonubecula* sp. (station 2), and *Sorites dominicensis* (station 5).

A summary of the general characteristics of the seagrass sampled at each station is given in Table 4. Mean shoot density ranged from 9.5 ± 12 shoots per 0.25 m^2 at station 1 to 30 ± 12 shoots per 0.25 m^2 at station 2. A one-way ANOVA of the data indicates that the difference in the mean shoot densities of the five samples, where n = 4 in each case, is statistically significant ($F_{4,15} = 3.06$, $P < 0.001$). A Tukey test of the results shows that statistically significant ($P = 0.05$) differences occur in the mean shoot densities between stations 1 and all other stations, stations 2 and 5, and stations 3 and 5.

The mean total blade surface area (both sides of each blade) of the blades surveyed was the highest at the intermediate stations, with a maximum value recorded at station 3 (93 ± 10 cm^2) and the lowest values at stations 1 (61 ± 12 cm^2) and 5 (55 ± 9.8 cm^2). A one-way ANOVA of the data indicates that the difference in the mean blade surface area of the five samples, where n = 8 in each case, is statistically significant ($F_{4,35} = 2.64$, $P < 0.001$). A Tukey test of the results showed that statistically significant

($P = 0.05$) differences in mean blade surface area occur between stations 1 and 2, stations 1 and 3, stations 2 and 5, stations 3 and 4, stations 3 and 5, and stations 4 and 5.

The trend in mean blade length closely paralleled that observed in the mean blade surface area, with the highest values being seen at station 3 (39 ± 3.2 cm) and the lowest values observed at stations 1 (24 ± 2.8 cm) and 5 (28 ± 2.3). A one-way ANOVA of the data indicates that the difference in the mean lengths of the five samples (eight blades per sample) is statistically significant ($F_{4,35} = 2.64$, $P < 0.001$). A Tukey test of the results showed that statistically significant ($P = 0.05$) differences in mean blade length occur between stations 1 and 2, stations 1 and 3, stations 1 and 4, stations 2 and 5, stations 3 and 5, and stations 4 and 5.

Mean blade widths were observed to be widest at stations 1–3, with the highest value recorded at station 2 (1.28 ± 0.10 cm). The mean blade widths at the last two stations were observed to be slightly narrower, with the lowest value being recorded at station 5 (1.01 ± 0.16 cm). A one-way ANOVA of the data indicates that the difference in the mean widths of the five samples (eight blades per sample) is statistically significant ($F_{4,35} = 2.64$, $P < 0.001$). A Tukey test of the results showed that statistically significant ($P = 0.05$) differences in mean shoot densities occur between stations 2 and 4, stations 1 and 5, stations 2 and 5, and stations 3 and 5.

Discussion

Trends in species diversity

The range of diversity indices calculated for the epiphytic foraminiferal biotas off Man O'War Cay (Tables 1 and 2) is lower than that previously recorded for either Carrie Bow Cay or Twin Cays, both sites without nesting seabird colonies (Richardson 2004; S. Richardson, unpublished data). For example, the epiphytic foraminiferans off Carrie Bow Cay exhibited higher species richness, higher values of Shannon's H', and higher values of evenness in both June 2001 ($S = 17$, $H' = 1.89$, $E = 0.39$) and February 2002 ($S = 14$, $H' = 1.79$, $E = 0.43$). Even higher diversity indices characterize the epiphytic foraminiferans living on seagrasses in the mangrove channel and bays at Twin Cays, sampled in both the dry and wet seasons. In June 2001, the recorded values were $S = 19–31$, $H' = 1.5–2.2$, and $E = 0.27–0.68$, and in February 2002, the recorded values were $S = 19–24$, $H' = 1.2–2.4$, and $E = 0.17–0.44$ (Richardson 2004). In contrast, sites in the Pelican Cays exhibit lower values of species richness ($S = 5–11$), but somewhat higher values of Shannon's H' ($H' = 0.87–1.23$) and evenness ($E = 0.47–0.80$) (Richardson 2000).

The observed offshore decline in values of Shannon's H', but not in species richness, reflects an increasing offshore trend in dominance, as measured by low values of E (Table 2). Buzas–Gibson's E is a measure of equitability, and E is equal to 1 when all species occur in equal proportions (Hayek & Buzas 1997). The Shannon diversity index is a measure of uncertainty, thus samples with a high dominance will have low values of H' because the probability is high that an individual selected at random from the population will belong to the dominant species (Hayek & Buzas 1997). This facet of the Shannon diversity index explains why the values of H' declined from station to station off Man O'War Cay, although species richness remained relatively constant.

High dominance of *Cornuspiramia antillarum*

The observed offshore trend in increasing dominance results from high densities of the dendritic encrusting species *C. antillarum*, which comprised 73% of the population at station 2 and over 94% of the biotas sampled at stations 3–5. *Cornuspiramia antillarum* is an encrusting milioline species that forms an irregular, branching, tubular test up to several millimeters in diameter (Fig. 4). This species was first described as a common epiphyte on seagrasses collected from Jamaica and the Dry Tortugas, Florida, by Cushman (1922, p. 59), who commented that 'it is usually one of the first organisms to be attached to the leaf,' and that 'specimens were found in all stages of development, especially on the newer portion of the leaves.' Cushman (1922, p. 59) thus concluded that the growth rates of *C. antillarum* 'must be very rapid.' Later studies by Arnold (1967) noted that *C. antillarum* (identified as *Calcituba polymorpha* Roboz 1884) showed a wide tolerance for environmental variability; in culture, individuals fed on chrysophytes and diatoms, exhibited rapid growth rates, reproducing primarily by asexual modes of fragmentation or multiple fission.

The extreme dominance (90–95%) of *C. antillarum* observed at stations 3–5 in 2004, and site B in 2001 and 2002, is much higher than the values previously recorded for this species at other non-bird cay sites in Belize (Table 6). In general, *C. antillarum* is absent from or occurs in low abundance (0–5.4%) at sites located in mangrove lagoons or channels, with the exception of Boston Bay, Twin Cays in February 2002, where *C. antillarum* comprised 17% of the population. Sites with a distinct open-water influence, such as nearby Carrie Bow Cay, appear to be characterized by moderate to high abundances (12–40%) of *C. antillarum*, with the exception of the site located on the coral

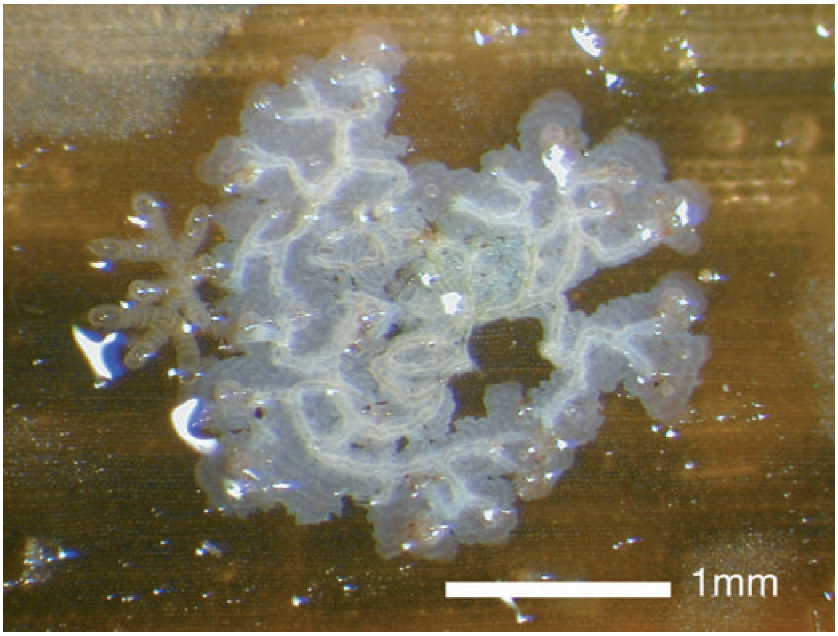

Fig. 4. Photomicrograph of a dendritic specimen of *Cornuspiramia antillarum* Cushman 1922 growing over the surface of calcareous algae encrusting a blade of *Thalassia testudinum* from Belize, Central America.

ridge at the entrance to Cat Cay lagoon, where this species comprised 75% of the population in August 1996.

The high dominance of *C. antillarum* at Man O'War Cay (stations 2–5 in 2004, June 2001, February 2002), and the ridge at the entrance to Cat Cay lagoon, Pelican Cays (August 1996), suggests that this species may have utility as a bioindicator of elevated water column nutrients when it comprises >70% of the epiphytic foraminiferal community. The lower dominance (34%) of *C. antillarum* at station 1 is interpreted as potentially being either an artifact of the low total number of individuals sampled (N = 86) or the extreme conditions in the intertidal zone at the edge of the guano island. Not only was seagrass cover sparse at this station, but high densities of macroalgae covered much of the benthos. Unfortunately, water samples collected for nutrient analyses during the course of the present study were lost in the power failures that occurred during the 2004 hurricane season in Florida; however, high levels of water column nutrients have been previously recorded off Man O'War Cay, relative to nearby islands without bird colonies. Tomasko & Lapointe (1991) recorded nutrient levels at Man O'War Cay that were an order of magnitude higher than those recorded at Twin Cays, and two orders of magnitude higher than Carrie Bow Cay. Shyka & Sebens (2000) also recorded elevated levels of water column nutrients (ammonium, nitrate + nitrite, and soluble reactive phosphorus) on the ridge outside Cat Cay lagoon in the Pelican Cays, a unique habitat where coral reef, mangrove, and seagrass ecosystems overlap (Macintyre *et al.* 2000).

Trends in population densities

The observed offshore trend in increasing mean densities of foraminiferans per square centimeter of seagrass blade is hypothesized to be a response to the increasing availability of food resources (Ward *et al.* 2003). As primary consumers, epiphytic foraminiferans feed predominantly on the microalgal and bacterial biofilm that forms on phytal substrates (Lee 1974; Novak 1984; Langer 1993; Richardson 2004, pl. 1, fig. b). Field studies by Lee *et al.* (1969) found actively reproducing populations of epiphytic foraminiferans to be associated with high densities of epiphytic diatoms on decaying macroalgae. Sessile epiphytic foraminiferans use pseudopodia extruded from peripherally located apertures to dislodge food items from the blade surface, while motile and facultatively sessile epiphytic foraminiferans graze along the blade surface (Langer 1993). The specific food preferences of most foraminiferal species are unknown; however, culture studies indicate that many benthic foraminiferans prefer specific species of diatoms, unicellular chlorophytes, cyanobacteria, and non-photosynthetic bacteria (Lee 1974; Anderson *et al.* 1991). Underwood (2002, p. 458) demonstrated that the community composition of benthic diatoms in tropical marine habitats change in response to enhanced nutrient supply, but concluded that 'our knowledge of the ecological niches of tropical diatom taxa is too limited to predict whether increased nutrient loading to reef and seagrass ecosystems would result in changes to species composition.'

Interestingly, in contrast to other sites previously surveyed (all islands without nesting bird colonies), the

Table 6. Comparative estimates of the relative abundance of the foraminiferal species *Cornuspiramia antillarum* from different localities in Belize, Central America.

locality	site characteristics	nesting bird colonies	date	relative abundance, *C. antillarum* (%)	reference
Man O'War Cay (station 1)	off mangrove cay	yes	March 2004	34	current study
Man O'War Cay (station 2)	off mangrove cay	yes	March 2004	73	current study
Man O'War Cay (station 3)	off mangrove cay	yes	March 2004	94	current study
Man O'War Cay (station 4)	off mangrove cay	yes	March 2004	95	current study
Man O'War Cay (station 5)	off mangrove cay	yes	March 2004	95	current study
Man O'War Cay (site B)	off mangrove cay	yes	February 2002	91	S. Richardson (unpublished data)
Man O'War Cay (site B)	off mangrove cay	yes	June 2001	90	S. Richardson (unpublished data)
Boston Bay, Twin Cays	mangrove lagoon	no	February 2002	17	Richardson (2004)
Boston Bay, Twin Cays	mangrove lagoon	no	June 2001	<1.0	Richardson (2004)
Sponge Haven, Twin Cays	mangrove channel	no	February 2002	5.4	Richardson (2004)
Sponge Haven, Twin Cays	mangrove channel	no	June 2001	2.4	Richardson (2004)
Dock, Twin Cays	mangrove channel	no	February 2002	<1.0	Richardson (2004)
Dock, Twin Cays	mangrove channel	no	June 2001	<1.0	Richardson (2004)
Cuda Cut, Twin Cays	mangrove channel	no	June 2001	<1.0	Richardson (2004)
Cuda Cut, Twin Cays	mangrove channel	no	February 2002	<1.0	Richardson (2004)
Carrie Bow Cay	reef flat off sand cay	no	February 2002	17	S. Richardson (unpublished data)
Carrie Bow Cay	reef flat off sand cay	no	June 2001	26	S. Richardson (unpublished data)
Cat Cay, Pelican Cays	ridge at entrance to mangrove lagoon	no	June 2001	39	S. Richardson (unpublished data)
Cat Cay, Pelican Cays	ridge at entrance to mangrove lagoon	no	August 1996	75	Richardson (2000)
Cat Cay, Pelican Cays	off mangrove cay	no	August 1996	38	Richardson (2000)
Manatee Cay, Pelican Cays	mangrove lagoon	no	June 2001	0	S. Richardson (unpublished data)
Manatee Cay, Pelican Cays	mangrove lagoon	no	August 1996	0	Richardson (2000)
Manatee Cay, Pelican Cays	ridge at entrance to mangrove lagoon	no	August 1996	40	Richardson (2000)
Little Cat Cay, Pelican Cays	entrance to mangrove lagoon	no	August 1996	24	Richardson (2000)
Fisherman's Cay, Pelican Cays	entrance to mangrove lagoon	no	August 1996	12	Richardson (2000)

All cays are labeled on index map in Fig. 1.

mean density of foraminiferans per square centimeter in February 2002 was more than three times the value calculated for June 2001, as well as representing the highest density value recorded to date. At other sites surveyed, the mean densities of epiphytic foraminiferans were higher in the wet season, possibly due to increased runoff, relative to the dry season (Richardson 2004). For example, in the wet season in June 2001, the mean densities recorded at stations in the Twin Cays ranged from 2.3 to 4.3 individuals·cm^{-2} of seagrass blade (Richardson 2004). In February 2002, during the dry season, the mean densities of epiphytic foraminiferans recorded at the Twin Cays stations were lower, ranging from 0.84 to 2.5 individuals·cm^{-2} of seagrass blade (Richardson 2004). The unusual density of foraminiferans recorded at Man O'War Cay in February 2002 occurred during the nesting season of the magnificent frigatebirds, which begins in mid-December and extends through early April, with eggs hatching in mid-to-late April (Trivelpiece & Ferraris 1987). Fewer birds were observed to be present in June 2001, relative to February 2002, although the numbers of individual birds present were not estimated.

Benthic foraminiferans as indicators of eutrophication

The response of epiphytic foraminiferans to eutrophic conditions in seagrass habitats has not been well documented. Studies by Fujita & Hallock (1999) found that increased epiphytization of *Thalassia* blades in Florida Bay favored colonization by taxa that cling to the epiphytic filamentous algae, such as *Archaias angulatus* (Fichtel & Moll 1798) and small species of milioline foraminiferans. Unfortunately, most pertinent studies to date (Brasier 1975; Martin & Wright 1988; Langer 1993) have utilized processing techniques to remove foraminiferans from the seagrass blades, such as scraping and sieving, that also damage fragile, encrusting species such as *C. antillarum* and *I. diaphana*.

The results of the present study indicate that the response of epiphytic foraminiferal communities to nutrient enrichment off Man O'War Cay falls within a zone of enrichment similar to that observed for seagrasses and their epiphytes off other islands with nesting bird colonies (Powell *et al.* 1991; Frederick & Powell 1994; Frankovich & Fourqurean 1997). Epiphytic foraminiferans as primary consumers that feed on the biofilm of microalgae and bacteria growing on seagrass blades, however, may exhibit somewhat different response patterns from those observed for primary producers. For example, a study of the seagrass epiphytes off Porjoe Key, a bird colony island in Florida Bay, showed algal epiphyte load to be highest at stations closest to the island (15 m), decrease in an offshore direction (30 m), and finally be replaced by a community of epiphytic metazoans at 45 m from the island (Frankovich & Fourqurean 1997).

Summary

Man O'War Cay, Belize, a small mangrove island that is home to nesting colonies of frigatebirds and brown boobies, provides a natural setting for studying the effects of eutrophication on seagrass meadows growing in oligotrophic, tropical–subtropical marine waters. The results of a survey of the epiphytic foraminiferal biotas living on the seagrass *Thalassia testudinum*, sampled along a transect off Man O'War Cay, yielded a low diversity biota, with a high dominance of the encrusting species *Cornuspiramia antillarum*. Species diversity, as measured by Shannon's H', decreased in an offshore direction along the transect and evenness, as measured by Buzas–Gibson's E, also decreased in the same direction. Population densities, however, were seen to increase from station to station, with the lowest number of foraminiferans per square centimeter observed at the station closest to the island, and the highest densities observed at the station farthest from the island. The results of this study suggest that the epiphytic foraminiferans living on seagrasses may be useful indicators of eutrophication in tropical–subtropical seagrass ecosystems.

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