

Population structures among epiphytal foraminiferal communities, Nevis, West Indies

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ABSTRACT – The taxocene of live epiphytal foraminifera was for one year monitored monthly on six phytal substrates in shallow water (<1 m) in two bays around Nevis, NE Caribbean Sea. Mosquito Bay was subject to a nutrient flux from a leaking septic tank. Long Haul Bay was comparatively undeveloped. SHE Community Structure Investigations (SHECSI) revealed that the populations on five plants had logarithmic series distributions of species abundances, the slopes of $\ln S$ vs. $\ln E$ for these five time-series being within -1 ± 0.3 . In three time-series, they were within -1 ± 0.05 .

Cluster analysis of twenty-five sediment samples in shallow water (<3 m) indicates that Nevis is largely surrounded by a single thanatacoenosis, for which SHECSI indicates a logarithmic series population structure. However, it is not possible to reconstruct perfectly the epiphytal population from the sediment thanatacoenosis. The thanatacoenosis included 40% allochthonous *Amphistegina gibbosa*, *Archaias angulatus* and *Asterigerina carinata*, washed in from offshore reefs, and few planorbulinids, although the latter dominates the biocoenosis on seagrass leaves in the backreef. *J. Micropalaeontol.* 27(1): 63–73, May 2008.

KEYWORDS: *Thalassia*, *Syringodium*, Caribbean, SHE Analysis

INTRODUCTION

It is axiomatic in ecology that in any multi-species population some species will be common and others rare (Magurran, 1988; Buzas & Hayek, 2005). The extent to which a community is dominated by a few species, or, conversely, the degree to which species abundances are distributed equitably, is termed the population structure (Hayek & Buzas, 1997). Although foraminifera have been studied for several centuries, relatively little is known about their population structures (Buzas, 2004). In particular, little is known about population structures in epiphytal foraminifera.

The Caribbean region is ideal for investigating population structures among epiphytal foraminiferal communities. Most shallow-water foraminifera in the oligotrophic Caribbean Sea are epiphytal (Cushman, 1922a; Brasier, 1975; Wilson, 1998, 2000), living on (a) the calcareous algae *Penicillus capitatus*, *Halimeda* spp. and *Dasycladus vermicularis*, and (b) the seagrasses *Thalassia testinudum* and *Syringodium filiforme* (Waszczak & Steinker, 1978). On seagrasses they inhabit (a) leaves and (b) exposed rhizomes and leaf bosses, which can bear distinctly different communities (Langer, 1993; Ribes *et al.*, 2000). Wilson (1998) found that, within the same square metre, even the leaves of *T. testinudum* and *S. filiforme* bear different assemblages. Assemblages in sediment in which the plants are rooted comprise primarily dead specimens washed from plants (Steinker & Clem, 1984). However, much information is lost during the transition from the epiphytal biocoenosis to the sediment thanatacoenosis (Martin & Wright, 1988). This paper compares population structures of the foraminiferal biocoenoses on phytal substrates with that of the thanatacoenosis in the associated sediment, and determines the extent to which knowledge of the population structure of the epiphytal assemblages helps in the interpretation of fossil sediment assemblages.

The dataset used herein was first reported by Wilson (2000), who examined shallow-water (<1 m) epiphytal foraminifera communities in two embayments around the island of Nevis,

northern Lesser Antilles (17° 10' N, 62° 35' W, Fig. 1), monitoring populations monthly for twelve months to produce time-series for populations on various plants. From Long Haul Bay (LHB, Fig. 2), a backreef bay on the northeast, windward coast, Wilson (2000) sampled populations on *P. capitatus* capitulae (heads), *T. testinudum* leaves and *T. testinudum* rhizomes and leaf bosses. From Mosquito Bay (MB), an open embayment on the northwest, leeward coast, he sampled foraminifera on *P. capitatus* capitulae, *Halimeda opuntia* and *S. filiforme* rhizomes and leaf bosses. At the time of sampling, MB was subject to an organic flux from a leaking septic tank.

Having calculated population densities, Wilson (2000) used time-series analysis (see Berryman, 1999) to analyse species' population dynamics on the different substrates. No evidence of seasonality was found (cf. Wilson & Dawe, 2006) and only one, poor example of periodicity (*Discorbis rosea* on *T. testinudum* leaves). However, it was found that in LHB the total foraminiferal community on each substrate, and the populations of dominant species, typically showed stationarity – i.e. their population densities fluctuated around a constant mean, linear regression not revealing any significant long-term trends. In contrast, in MB the overall community and populations of dominant species showed nonstationarity, per month population densities decreasing significantly over the year of sampling. Wilson (2000) ascribed the different population dynamics to the impact of the focused organic flux in MB. Shallow-water foraminifera respond quickly to an increased nutrient flux (Altenbach, 1992), which can affect the species composition of the community (Scott *et al.*, 2001; Hallock *et al.*, 2003).

Given the wealth of information that can be derived from Wilson's (2000) time-series of epiphytal foraminiferal populations in MB and LHB, they have been further analysed and examined in two papers. Wilson (2006c) found that the epiphytal population comprises a collection of taxonomic guilds *sensu* Jaksic (1981), a guild being a group of species that exploit the same class of environmental resources in a similar way (see

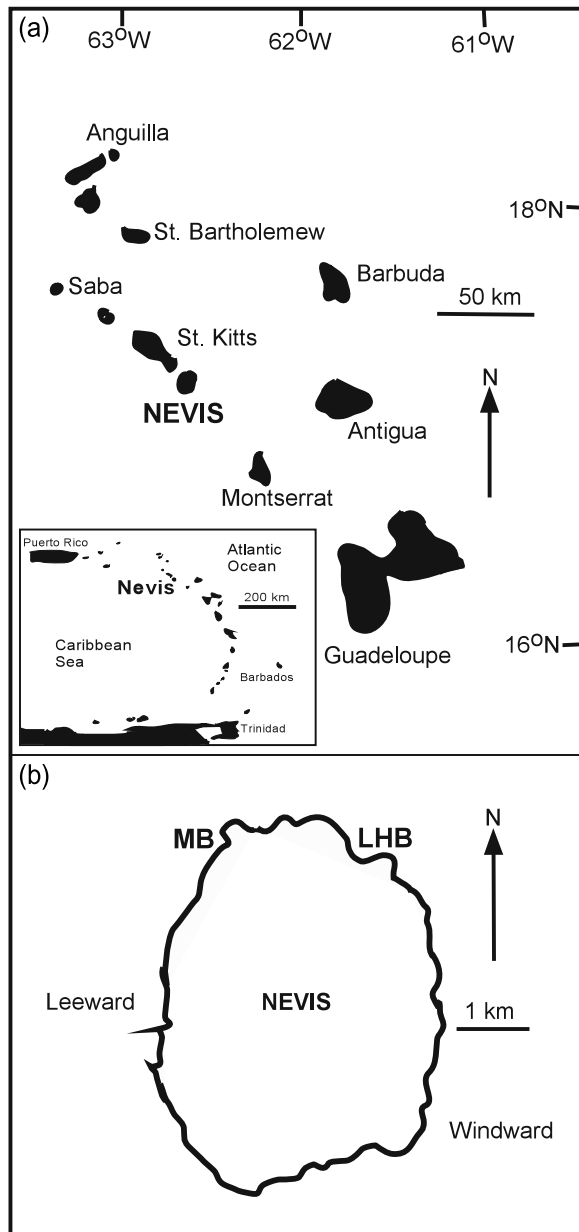


Fig. 1. (a) The northern Lesser Antilles, showing the location of Nevis. Inset: the Eastern Caribbean, indicating Nevis at the northern end of the Lesser Antilles island arc. (b) Nevis, showing the sample sites at Long Haul Bay (LHB) and Mosquito Bay (MB).

Root, 1967). Wilson & Ramsook (2007) published the entire data set of Wilson's (2000) six time-series, and found that foraminiferal population densities on *P. capitatus* capitulae were three times higher in both bays than those on either *H. opuntia* or on exposed seagrass (*S. filiforme*, *T. testinudum*) rhizomes and basal leaf bosses. Mean population densities on *P. capitatus* capitulae were statistically indistinguishable in both bays. Thus, while the input of organic matter into MB has apparently affected the composition and population dynamics of the biocoenosis there, it has not affected the mean population densities there. Wilson & Ramsook (2007) concluded that *P. capitatus*, which has a lifespan of *c.* 45 days and supports denser

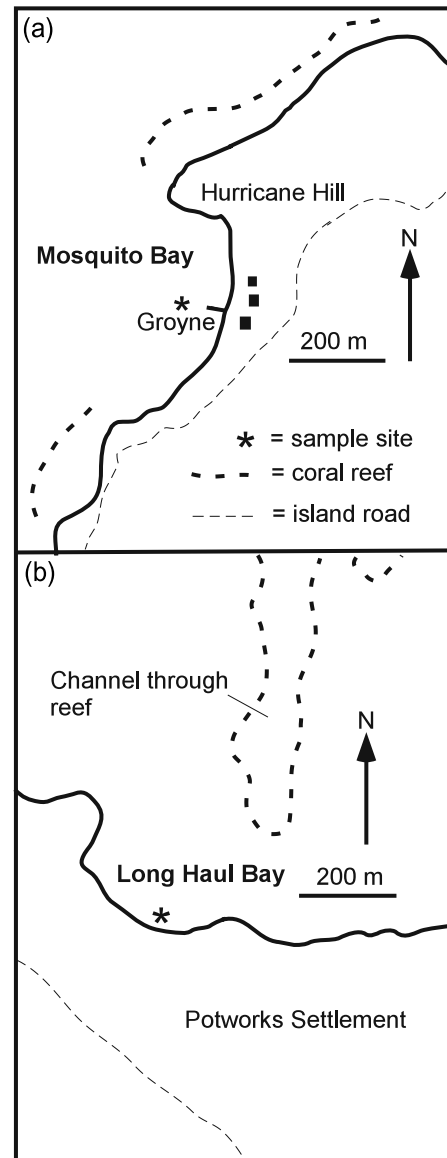


Fig. 2. Sketch maps of Long Haul Bay and Mosquito Bay, showing sites from which epiphytal samples were collected.

populations, contributes proportionally more foraminiferal tests to the sediment than do seagrass rhizomes, which support lower density populations and have life spans of several years. They suggested *P. capitatus* capitulae to support a permanently pioneering foraminiferal community that includes opportunists (Guild II of Wilson, 2006c), and seagrass rhizomes to be occupied by a climax community.

SHECSI ANALYSIS: AN OUTLINE

A taxocene is a taxonomically related set of species within a community, such as birds, gastropods or foraminifera (see Hutchinson, 1976). Many micropalaeontologists study the foraminiferal taxocene only. Therefore, knowledge of interactions between foraminifera and other taxa is slim at present. However, Magurran (1988, 2003) documented that, despite the possibility of interactions with other taxa, taxocenes have four

types of community structure, no matter what organisms are examined: geometric series, logarithmic series, logarithmic normal and broken stick. These form a series from least- to most-equitable species abundance distributions.

Hayek & Buzas (1997) determined that biological species richness S , diversity (measured using the information function $H = -\sum p_i \ln p_i$, where p_i is the proportional abundance of the i th species) and evenness (calculated from the equitability index $E = e^{H/S}$) are related through the decomposition formula

$$H = \ln S + \ln E \quad (1)$$

From this they developed SHE Analysis, one part of which uses cumulative population census figures, rather than a single vector of species' abundances, to determine the population structure (see also Buzas, 2004). Hayek & Buzas (1997) introduced the term SHE Analysis for Community Structure Identification (SHECSI) to describe that aspect of SHE Analysis that determines the population structure. In SHECSI the behaviour of accumulated values of $\ln S$, $\ln E$ and H when regressed linearly against the cumulative values of $\ln N$ (i.e. the logarithm of the cumulative number of specimens), and the expected asymptotic values of the information function $E(H)$, reveal three of the four common community structures.

- For the logarithmic series distribution $E(H) = \ln a + 0.58$, where a is the Fisher diversity index. For this series, H is constant. For a perfect logarithmic series, regression of $\ln S$ vs. $\ln E$ has a slope of -1 and an intercept of H .
- For the logarithmic normal distribution $E(H) = (1 - \gamma^2) \ln S$, where $(1 - \gamma^2) = 1 + \ln E / \ln S$ and $\ln E / \ln S$ is constant.
- For the broken stick distribution, $E(H) = \ln S - 0.42$ and E is constant at 0.66.

Thus, H , $\ln E$ and $\ln E / \ln S$ are each constant for a different species abundance distribution. Buzas & Hayek (2005) suggested that because of its simplicity, the constancy of the related indices and the regression formulation of $\ln S$ vs. $\ln E$, the logarithmic series should be the null model for the investigation of population structure. Buzas (2004) used logarithmic series relationships when investigating the community structure of foraminiferal assemblages in two Miocene beds in Maryland.

SHECSI is used here to determine community structures in the foraminiferal taxocene on phytal substrates in LHB and MB, Nevis, using the full dataset presented in Wilson & Ramsook (2007) and employing the logarithmic series as the null model.

MATERIALS AND METHODS

The geography and climate of the 50 km² volcanic island of Nevis are described thoroughly in Wilson (2006c) and Wilson & Ramsook (2007). At the time of sampling, both LHB and MB supported seagrass meadows and calcareous algae, but the vegetation in LHB was lusher, comprising a seagrass climax community of primarily *T. testinudum*. The seagrass meadow in MB comprised a pioneering community of primarily *S. filiforme* (details of seagrass ecology from Zieman & Zieman, 1989).

Samples were collected during 1994–1995 on the Thursday of the third week of each calendar month, and comprised sediment-trapping algae, seagrass rhizomes *sensu* Langer (1993) and seagrass leaves. When rough seas suspended sediments and

rendered the water cloudy, sampling was restricted to substrates that could be located and identified by touch. Cloudy water occurred more frequently in MB than in LHB.

From LHB *P. capitatus* capitulae were collected *c.* 10 m from shore within a seagrass meadow adjacent to a patch reef. *Thalassia testinudum* rhizomes and basal leaf bosses (leaves removed), and separate samples of *T. testinudum* leaves, were collected along the steep, shoreward edge of the meadow, all at *c.* 1 m depth.

Three substrates were sampled in MB: *H. opuntia* from a gabion at 30 cm depth at the bay head, and *P. capitatus* heads (capitulae) and exposed *S. filiforme* rhizomes and basal leaf bosses (leaves removed) from an area *c.* 200 m² and 1 m deep immediately seaward of the gabion. The gabion was destroyed when Hurricanes Luis and Marilyn struck in September 1995.

Sampling involved combining material from several individual plants to form 'pseudoreplicates' *sensu* Hurlbert (1984). All samples of *P. capitatus* comprised ten capitulae, and seagrass leaves of approximately 100 leaves.

The six samples collected each month (three each from MB and LHB) were stained by soaking for 24 hours in a solution of 70% isopropyl alcohol (the only preservative readily available on Nevis) and 2 g l⁻¹ rose Bengal. Rose Bengal stains those tests containing protoplasm (Walton, 1952).

The foraminiferal community on the leaves of seagrasses included many firmly attached planorbulinids. This substrate had to be prepared in a different way to the others, on which planorbulinids were rare. The preparation technique, described by Wilson (1998), entails drying the leaves until they crumble, then sieving them over a 125 µm mesh to remove fine particles. Stained foraminifera are picked from the >125 µm fraction.

Specimens were removed from the remaining five plant substrates by washing them under running water over a 63 µm mesh. The washed plants were examined for evidence of permanently attached foraminifera still in place. Few were found. The detached foraminifera were dried at *c.* 100 °C and sieved over a 125 µm mesh. Stained specimens were picked from the >125 µm fraction, and the per sample numbers of specimens N recorded.

The specimens were sorted into species, identified using d'Orbigny (1839), Cushman (1918, 1921, 1922a, b, 1923, 1929, 1930, 1931) and Schnitker (1971), and the number of specimens per species per sample counted. Population diversity, measured using both species richness S and the information function H , and dominance, measured using the Equitability Function E , were calculated for accumulated values of N over all samples for each substrate. Linear regression of $\ln S$, H and $\ln E$ was conducted against $\ln N$, and goodness of fit determined using Pearson's product moment correlations. Regression of $\ln S$ vs. $\ln E$ was also conducted.

RESULTS

The accumulated values of N , S , H and E for each plant substrate in Long Haul Bay and Mosquito Bay are given in Tables 1 and 2, respectively, which also show the mean values of accumulated H ($=\bar{H}$). In Figures 3a–c (LHB) and 4a–c (MB) the accumulated values of $\ln S$, H and $\ln E$ are graphed against accumulated $\ln N$. Results for the two bays are presented separately.

Month	<i>Thalassia testinudum</i> rhizomes				<i>Thalassia testinudum</i> leaves				<i>Penicillus capitatus</i> capitulae			
	<i>N</i>	<i>S</i>	<i>H</i>	<i>E</i>	<i>N</i>	<i>S</i>	<i>H</i>	<i>E</i>	<i>N</i>	<i>S</i>	<i>H</i>	<i>E</i>
September	186	40	3.107	0.559					183	24	1.730	0.236
October	343	57	3.276	0.464	128	18	2.063	0.437	419	38	2.238	0.247
November	524	66	3.112	0.340	312	26	2.142	0.327	783	45	2.276	0.216
December	651	72	3.158	0.327	414	30	2.155	0.287	1086	51	2.307	0.197
January	975	74	2.728	0.207	720	31	2.058	0.253	1667	58	2.114	0.143
February	1082	75	2.647	0.188	920	34	2.000	0.217	2010	62	2.196	0.145
March	1403	76	2.439	0.151	1081	36	2.003	0.206	2307	66	2.196	0.136
April	1649	79	2.427	0.143	1235	40	2.068	0.198	2871	68	2.063	0.116
May	1896	82	2.437	0.139	1392	43	2.131	0.196	3005	69	2.115	0.120
June	2032	89	2.443	0.129	1517	47	2.171	0.186	3243	70	2.085	0.115
July	2199	91	2.476	0.131	1560	51	2.204	0.178	3385	73	2.106	0.113
August	2307	94	2.505	0.130					3633	75	2.057	0.104
\bar{H}	—	—	2.73	—	—	—	2.1	—	—	—	2.12	—

N, cumulative number of specimens; *S*, biological species richness; *H*, diversity; *E*, evenness.

Table 1. Accumulated values of *N*, *S*, *H* and *E* for each plant substrate in Long Haul Bay and the mean value of accumulated *H* ($=\bar{H}$)

Long Haul Bay

Thalassia roots. Examination of *H* (range 2.427–3.107) indicates that on this substrate it reaches a constant of *c.* 2.454 above *N*=1400. Hayek & Buzas (1997, table 14.2, fig. 14.2) found a similar convergence on a constant among forest trees in Bolivia, and limited their subsequent analysis to those samples beyond which *H* first attained its constant value. When this procedure is followed, analysis being restricted to the final six measurements in the *T. testinudum* time-series, *H* is almost constant ($H=1.56+0.119 \times \ln N$, $r=0.745$), the correlation between accumulated *H* and $\ln N$ not being significant at the 95% confidence level ($p=0.089$). As $\ln S$ vs. $\ln N$ increases ($\ln S=1.131+0.439 \times \ln N$, $r=0.968$, $p=0.002$) $\ln E$ vs. $\ln N$ decreases ($\ln E=0.438-0.322 \times \ln N$, $r=0.955$, $p=0.003$). Linear regression of $\ln S$ vs. $\ln E$, which for a logarithmic series would give an intercept of final accumulated *H* (i.e. 2.505) and a slope of -1 , actually gives an intercept of 1.88 and a slope of -1.29 . These data are not a perfect fit for a logarithmic series model. However, the constant value of cumulative *H* above the asymptote at *N*=1400, and the behaviour of $\ln N$ vs. $\ln S$ and $\ln E$, are

concluded to indicate a logarithmic series distribution of species abundances in this population.

Thalassia leaves. The accumulated values of *H* fluctuate between 2.0 and 2.31, but oscillate around a constant when regressed against $\ln N$ (slope -0.0306 , $r=0.257$, $p=0.473$), whereas $\ln S$ vs. $\ln N$ increases (slope=0.363, $r=0.970$, $p<0.005$) and $\ln E$ vs. $\ln N$ decreases (slope -0.333 , $r=0.970$, $p<0.005$). These last two regressions, although of opposite sign, differ only by 0.03. Regression of $\ln S$ vs. $\ln E$ gives $\ln S=2.066-1.036 \times \ln E$, the slope of which is almost -1 , and the intercept of which is close to the final accumulated value of *H* (2.20) and the value of $\bar{H}=2.12$. For *N*=1560 and *S*=51, $a=10.1$, so that for a logarithmic series distribution $E(H)=2.89$. Although $E(H)$ exceeds the final value of *H* by 0.69, the foraminiferal population structure on *Thalassia* leaves in LHB is concluded to be a logarithmic series.

Penicillus capitatus. Cumulative values of *H* have a wide spread (minimum 1.73, maximum 2.31). However, when regressed

Month	<i>Halimeda opuntia</i>				<i>Penicillus capitatus</i> capitulae				<i>Syringodium filiforme</i> rhizomes			
	<i>N</i>	<i>S</i>	<i>H</i>	<i>E</i>	<i>N</i>	<i>S</i>	<i>H</i>	<i>E</i>	<i>N</i>	<i>S</i>	<i>H</i>	<i>E</i>
September					164	27	2.500	0.451				
October	158	53	3.289	0.624	291	45	2.990	0.442	63	28	3.087	0.783
November	418	54	3.447	0.581	397	51	2.847	0.338	119	40	3.337	0.703
December	552	58	3.371	0.502								
January	789	67	3.352	0.426	525	57	2.947	0.334				
February	951	70	3.329	0.399	771	61	2.735	0.253	258	53	3.365	0.546
March	1190	77	3.323	0.360	1051	65	2.664	0.221	391	65	3.528	0.524
April	1329	79	3.322	0.351	1178	68	2.733	0.226	488	69	3.517	0.488
May	1452	83	3.367	0.349	1239	69	2.756	0.228	619	76	3.546	0.456
June	1574	86	3.382	0.342	1426	73	2.794	0.224	722	82	3.615	0.470
July	1734	88	3.338	0.320	1604	79	2.838	0.216	964	94	3.670	0.418
August	1894	91	3.361	0.317								
\bar{H}	—	—	3.35	—	—	—	2.78	—	—	—	3.46	—

N, cumulative number of specimens; *S*, biological species richness; *H*, diversity; *E*, evenness.

Table 2. Accumulated values of *N*, *S*, *H* and *E* for each plant substrate in Mosquito Bay and the mean value of accumulated *H* ($=\bar{H}$)

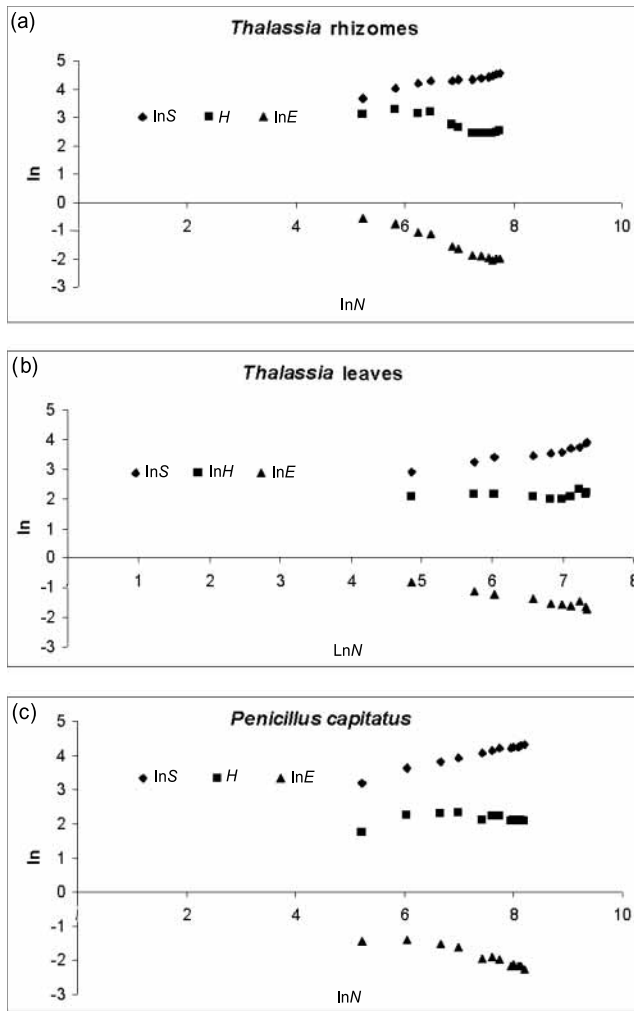


Fig. 3. Graphs of $\ln S$, H and $\ln E$ against cumulative $\ln N$ for epiphytial foraminifera on substrates in Long Haul Bay.

against $\ln N$, they fluctuate around a constant (slope -0.0374 , $r=0.275$, $p=0.386$), whereas $\ln S$ vs. $\ln N$ increases (slope $=0.354$, $r=0.992$, $p<0.005$) and $\ln E$ vs. $\ln N$ decreases (slope -0.312 , $r=0.914$, $p<0.005$). The slopes of these last two regressions are opposite in sign but almost equal (difference $=0.042$). Regression of $\ln S$ vs. $\ln E$ gives $\ln S=2.183-0.968 \times \ln E$, the slope of which is almost -1 , and the intercept of which is close to the final accumulated value of $H(2.06)$. The value of \hat{H} was 2.12 . For $N=3633$ and $S=75$, $a=13.37$, and the expected final H for a logarithmic series is $E(H)=\ln 13.37+0.58=3.17$. Although $E(H)$ exceeds the final value of accumulated H by 1.11 , the foraminiferal population on *P. capitatus* in LHB is, from these data, concluded to have a logarithmic series distribution.

Mosquito Bay

Halimeda opuntia. Regression of H against $\ln N$ indicates that, on *H. opuntia*, H fluctuates around a constant (slope $=0.005$). However, Pearson's product moment correlation shows only a poor and statistically insignificant fit between observed and expected values ($r=0.09$, $p=0.79$), indicating that values of H fluctuate as samples are progressively accumulated (maximum

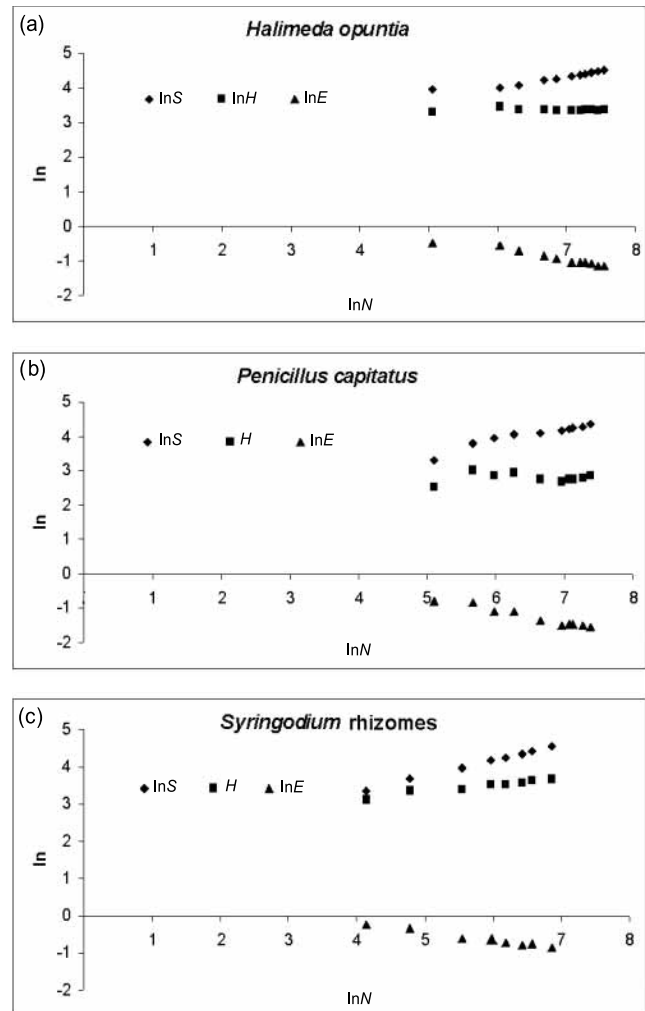


Fig. 4. Graphs of $\ln S$, H and $\ln E$ against cumulative $\ln N$ for epiphytial foraminifera on substrates in Mosquito Bay.

$H=3.45$, minimum $H=3.29$). In contrast, there are good fits when both $\ln S$ and $\ln E$ are regressed against $\ln N$ ($\ln S$, slope $=0.25$, $r=0.94$, $p<0.005$; $\ln E$, slope $=0.31$, $r=0.97$, $p<0.005$). The slopes of these regressions are opposite in sign and almost equal. The last observed value of H in the accumulated series is 3.36 , while $\hat{H}=3.35$. Regression of $\ln S$ against $\ln E$ for the *H. opuntia* community gives an intercept of 3.54 , and a slope -0.82 ($r=0.98$, $p<0.005$). Given $N=1894$ and $S=91$, $a=21.96$. Thus, the expected final H is $E(H)=\ln 21.96+0.58=3.67$. Although not a perfect fit, these results, and especially the fluctuation of H around an almost constant value, are concluded to indicate a logarithmic series distribution.

Penicillus capitatus. Cumulative H on this substrate varies between 2.5 and 3.0 . Regression of H , $\ln S$ and $\ln E$ against $\ln N$ indicates that cumulative H , although it fluctuates, does so around a constant (slope $=0.0199$, $r=0.108$, $p=0.77$), whereas $\ln S$ increases (slope $=0.393$, $r=0.958$, $p<0.005$) and $\ln E$ decreases (slope $=-0.373$, $r=0.972$, $p<0.005$). That the slopes of $\ln S$ and $\ln E$ are almost equal (difference 0.02) but opposite in sign is indicative of a logarithmic series distribution. The last observed

value of accumulated H is 2.84, while $\hat{H}=2.78$. Regression of $\ln S$ vs. $\ln E$ for the MB *P. capitatus* fauna gives an intercept of 2.83 and a slope of -0.958 ($p=0.0005$). For $N=1604$ and $S=79$, $\alpha=17.43$. Given these values, the expected final H for a logarithmic series is $E(H)=\ln 17.43+0.58=3.44$. Despite the 0.6 difference between $E(H)$ and final H , this population is concluded to have a logarithmic series structure.

***Syringodium filiforme*.** It is not possible to discriminate the community structure on this substrate unequivocally. The accumulated values of H , S and E are not constant. Regression of H , $\ln S$ and $\ln E$ against $\ln N$ shows that both H (slope=0.194, $r=0.97$, $p<0.005$) and $\ln S$ (slope=0.429, $r=0.99$, $p<0.005$) increase with increasing $\ln N$. However, the increases are not parallel, as would be the case for a broken stick population structure. Thus, E is not constant, the slope of $\ln E$ vs. $\ln N$ instead being -0.23 ($r=-0.99$, $p<0.005$). For a logarithmic series distribution, the slopes of $\ln E$ and $\ln S$ when plotted against $\ln N$ would be equal but opposite. This is not the case here.

Using the last observed value of accumulated $H(3.67)$ to determine a logarithmic series structure likewise yields inconclusive results. Regression of $\ln S$ vs. $\ln E$, which would for a logarithmic series have a slope of -1 and an intercept of H , actually has an intercept of 2.95 but a slope of -1.83 ($r=0.99$, $p<0.005$). The predicted diversity for a logarithmic series when $N=964$ and $S=94$ is $E(H)=4.35$, which exceeds the final observed H by 0.68. The final predicted $E(H)$ for a logarithmic normal model, conversely, is 3.67, which is the same as the observed final value of accumulated H . However, the value of $\ln E/\ln S$ is not constant, as would be the case for a logarithmic normal distribution.

DISCUSSION

Comparison of phytal substrates

Buzas (2004) noted that there is not yet a consensus as to how far measures can depart from the ideal before the logarithmic series model is rejected for a particular population. Here, a population is accepted as having a logarithmic series distribution of species abundances if it shows three characteristics:

1. changes in the accumulative values of H are not significantly correlated with the rise in accumulated $\ln N$ at a 95% confidence level, but are instead shown by linear regression to fluctuate around an almost stationary value;
2. regression of $\ln S$ against $\ln E$ gives a constant approximating to the final value of accumulated H and a slope of approximately -1 ; and
3. the slopes of $\ln S$ and $\ln E$ vs. $\ln N$ are of opposite sign and approximately equal.

Because $H=\ln S+\ln E$, it follows that a population satisfying any one of the above conditions automatically satisfies the other two. Nevertheless, for completeness all three were examined. Application of these criteria to the foraminiferal populations on the six substrates sampled indicates that five (*P. capitatus* capitulae in both LHB and MB, *H. opuntia* in MB and both *T. testinudum* leaves and rhizomes in LHB) supported foraminiferal populations with a logarithmic series population structure. The foraminiferal assemblage on *S. filiforme* did not show a

good fit, the value of cumulative H failing to attain an asymptote. This may be because this population was represented by too few samples and specimens.

General one-way Analysis of Variance (ANOVA) and Bonferroni's comparison of means were applied to the time-series of accumulated values of H to investigate differences in diversity between foraminiferal communities in the two bays and on different plants. Mean accumulated H on MB *H. opuntia* did not differ significantly from that on MB *S. filiforme* rhizomes, but the mean H on both exceeded that on MB *P. capitatus*. Wilson & Ramscook (2007) found a similar pattern for epiphytal foraminiferal assemblages in this bay when comparing the means of monthly values of H , rather than the mean of cumulative values of H . In contrast, findings in LHB differed from those reported by Wilson & Ramscook (2007), who found that the mean monthly values of H were indistinguishable for all substrates. In this bay the mean diversity on *T. testinudum* rhizomes, measured using the mean of the accumulated values of H , exceeded that on both *P. capitatus* capitulae and *T. testinudum* leaves. However, the mean values of accumulated H on *P. capitatus* and *T. testinudum* leaves did not differ significantly. This suggests that Hayek & Buzas' (1997) SHECSI might indicate differences in diversity with a precision not found by simple comparison of mean monthly values of H . The mean H on *P. capitatus* in MB exceeded that on the same plant in LHB.

That seagrass rhizomes and short shoots, and *P. capitatus* capitulae, were sampled from both bays allows comparison of population structures on the same or similar plants at the two sites. However, because the foraminiferal community on *S. filiforme* did not readily fit any of the four population models, comparison here is restricted to foraminiferal populations on *P. capitatus*. Linear regression of accumulated H against $\ln N$ reflects how these two populations differ in diversity; in LHB, *P. capitatus* H is almost constant at $c. 1.8$, whereas in MB it is almost constant at $c. 2.65$. It is generally accepted that species richness S increases with the number of specimens N (Buzas *et al.*, 1977; Magurran, 1988, 2003; Hayek & Buzas, 1997). Regression of $\ln S$ against $\ln N$ indicates that on *P. capitatus* the rate of increase in species richness differed little (MB, slope of $\ln S$ vs. $\ln N=0.393$, $r=0.958$; LHB, slope=0.354, $r=0.992$), despite differences in overall diversity between the two bays. The rate of decline of $\ln E$ against $\ln N$ likewise differed little, despite the higher overall values of E in MB; on MB *P. capitatus* the slope of $\ln E$ vs. $\ln N$ was -0.373 ($r=0.972$), whereas in LHB it was 0.312 ($r=0.941$).

Comparison may also be made between communities on different substrates in the same bay. In LHB, the rate of increase of $\ln S$ against $\ln N$ on *P. capitatus* (slope=0.354) differed little from that on *T. testinudum* leaves (slope=0.363), but more markedly from that on *T. testinudum* rhizomes (slope=0.439; value above constant). These data might reflect the nature of the community; Wilson & Ramscook (2007) concluded that, whereas short-lived substrates such as *P. capitatus* support lower diversity, permanently pioneering communities, longer-lived substrates such as seagrass rhizomes support climax communities of greater diversity. The rate of decrease of $\ln E$ against $\ln N$ on *P. capitatus* (slope= -0.312) was little different from that on *T. testinudum* leaves (slope= -0.333) or rhizomes (slope= -0.322 ; value above asymptote). Thus, around Nevis, the rate

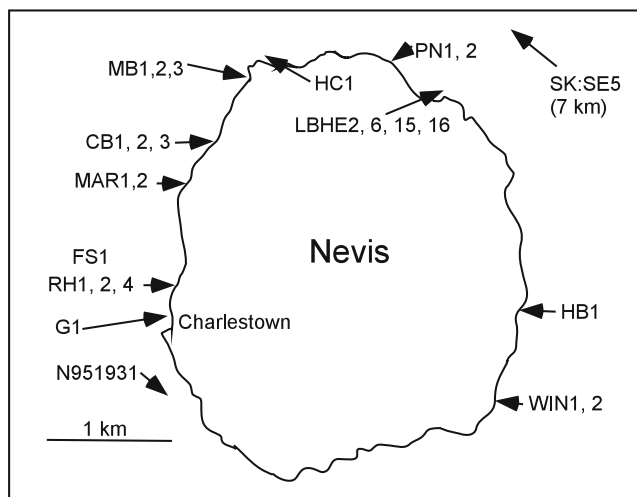


Fig. 5. Location of sediment samples around Nevis. Sample numbers from Wilson (2006b).

of increase of $\ln S$ is generally $c. 0.3$ to 0.4 , and the rate of decrease of $\ln E$ is $c. -0.3$ to -0.4 . However, these values are not universal constants. Buzas (2004) examined the population structure of the foraminiferal taxocene in two Miocene age beds in Maryland. While in one bed the slopes of $\ln S$ vs. $\ln N$ and $\ln E$ vs. $\ln N$ were 0.3 and 0.29 respectively, those in the other were 0.15 and -0.20 .

Population structure of the sediment thanatacoenosis

Wilson (2006a) documented the foraminiferal thanatacoenosis in twenty-five samples from shallow-water (<3 m) sediments around Nevis (Fig. 5, Table 3). Because nearshore seagrass meadows around Nevis are limited virtually to LHB and MB, bare sands were sampled at all locations, confounding the possible occurrence of live foraminifera in sediment bound by seagrasses (cf. Buzas *et al.*, 1977) by collecting samples from bare patches, such as anchor scars, within the seagrass meadows. As interest was focused on how the total sediment assemblage compares with the epiphytal biocoenosis, the samples were not stained with rose Bengal.

The thanatacoenosis comprised 134 species of foraminifera, of which 20 each formed $>1\%$ of the total recovery. The principal differences between the epiphytal and sediment assemblages in shallow water in LHB were (a) the common occurrence of attached planorbulinids on seagrass leaves and their rarity in sediments, and (b) the greater percentage abundances of *Archaias angulatus*, *Amphistegina gibbosa* and *A. carinata* in the sediment than on plants. Because *A. gibbosa* and *A. carinata* are primarily reefal species (Todd & Low, 1976; Gischler *et al.*, 2003) and *A. angulatus* occupies the deeper backreef (Martin, 1986), the differences between the LHB biocoenoses and the shallow-water thanatacoenosis may be credited to shoreward transport of sediment during hurricanes (cf. Li *et al.*, 1997). In MB the epiphytal biocoenosis was dominated by *Triloculina rotunda*, with lesser *Tretomphalus bulloides*, while the sediment thanatacoenosis was dominated by *Discorbis rosea*. Given that epiphytal foraminiferal populations in MB showed nonstationary dynamics, the differences in MB may be ascribed to the impact of the

organic flux on the composition of the epiphytal biocoenosis, coupled with the influence of sediment transport by storms.

Cluster analysis by Wilson (2006a) revealed six clusters, but most comprised few samples, fifteen of the twenty-five samples from diverse locations around the island grouping as a generalized cluster. This was interrupted at various places (especially along the north coast and in Cades Bay, a small embayment south of MB) by other, smaller clusters. A greater percentage of *A. angulatus* is glauconitized on the western, leeward coast, including in MB, than along the windward. Wilson (2006b) ascribed this to a lower rate of sediment reworking by waves along the lower energy, leeward coast. Nevertheless, Wilson (2006a) found samples from the windward and leeward coasts to cluster together.

Buzas & Hayek (1998) suggested that a second form of SHE Analysis, SHEBI or SHE Analysis for Biofacies Identification, can be used to differentiate biofacies. Accumulated values of $\ln E$ along transects are sensitive indicators of biofacies boundaries, any increase in $\ln E$ indicating a change in biofacies. It might seem at first sight that this technique could be applied to the 25 Nevisian samples, which form a transect around the island. However, because SHEBI can be used only to recognize biofacies boundaries, and not recurrent species assemblages, it was not applied here. Instead, SHECSI was used to examine the foraminiferal population structure in the largest biofacies revealed from cluster analysis.

Samples were accumulated in order of increasing distance from the cluster centroid. Regression of accumulated H against $\ln N$ (Fig. 6) indicated a logarithmic series structure ($H=2.27+0.066\ln N$, $r=0.417$, $p=0.122$), while regression lines for $\ln S$ and $\ln E$ against $\ln N$ revealed almost equal and opposite slopes, with a good fit between the data and the calculated regression lines ($\ln S=1.729+0.344\ln N$, $r=0.942$, $p<0.005$; $\ln E=0.542-0.278\ln N$, $r=0.911$, $p<0.005$). The fifteen samples yielded 5503 foraminifera in 109 species, for which $a=19.27$. This equated to an expected final H of $E(H)=\ln 19.27+0.58=3.54$. When $\ln S$ was regressed against $\ln E$, it gave an intercept (2.65), close to both \hat{H} (2.78) and the final value of accumulated H (2.93), and had a slope (-1.081) very close to -1.0 . Thus, the foraminiferal thanatacoenosis in the cluster shows a logarithmic series distribution.

Two factors must be borne in mind when comparing the total sediment thanatacoenosis with the epiphytal biocoenoses.

1. The thanatacoenosis includes allochthonous species. Of the specimens recovered from the cluster, 40% comprised *Amphistegina gibbosa*, *Archaias angulatus* and *Asterigerina carinata* washed in from further offshore.
2. Whereas the sediment thanatacoenosis yielded only 0.3% planorbulinids, which live permanently attached to seagrass leaves, Wilson & Ramsook (2007) documented that the *Thalassia* leaf biocoenosis in LHB included 55% planorbulinids (*Planogypsina squamiformis*, *Planorbulina acervalis*, *P. mediterraneensis* and *P. retinaculata*). The paucity of planorbulinids in the sediment might be due to breakage of the fragile tests after death. Alternatively, planorbulinids might be transported out of the bay attached to the leaves on which they live; Stapel *et al.* (1996) found that seagrass blades are shed after $c. 30$ days, and that $c. 25\%$ of discarded above-ground seagrass biomass is transported seawards.

Sample number	Windward Coast										Leeward Coast															
	win1	win2	hb1	lbhc2	lbhc15	lbhc16	lbhc6	pn1	pn2	skse5	hcl	mb1	mb2	mb3	cb1	cb2	cb3	mar1	mar2	fs1	rh1	rh2	rh4	g1	n951031	
<i>Acervulina inhaerens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	2	0	0	0	0	0	0	0	0	0	0
<i>Agglutinella cf. robusta</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	4	6	0	0	1	3	0	0	0	0	0	0
<i>Agglutinella soriformis?</i>	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	
<i>Ammomassilina alveoliniformis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	
<i>Ammonia sobrina</i>	0	0	0	0	0	0	0	0	0	0	0	18	16	20	0	9	14	3	4	1	8	7	7	10	0	
<i>Ammonia tepida</i>	0	0	0	0	0	0	1	0	0	1	0	2	3	1	8	0	1	0	0	0	1	0	0	1	1	
<i>Amphistegina gibbosa</i>	33	46	75	69	8	10	14	32	23	20	51	43	15	12	8	6	5	28	32	53	18	39	25	40	12	
<i>Archaias angulatus</i>	16	24	43	18	5	5	19	74	73	3	68	106	29	34	10	18	5	59	68	72	36	15	37	17	12	
<i>Articulina atlantica</i>	1	0	0	1	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Articulina mayori</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	
<i>Articulina mucronata</i>	0	0	0	0	0	0	0	1	0	6	0	0	0	0	22	27	0	0	2	0	3	1	0	0	7	
<i>Articulina sagra</i>	0	0	0	3	0	1	4	0	0	0	0	0	2	6	0	0	12	0	0	0	0	0	4	1	1	
<i>Asterigerina carinata</i>	52	40	7	20	1	3	11	3	26	48	2	10	10	20	21	18	21	62	34	16	43	46	37	44	22	
<i>Bolivina striatula</i>	0	0	0	6	0	0	2	0	0	0	0	0	1	0	8	2	0	0	0	0	0	0	0	1	0	
<i>Borelis pulchra</i>	4	13	10	6	3	3	5	4	0	1	0	3	2	3	0	0	0	2	0	2	0	4	1	1	0	
<i>Broeckina orbitolitoidea</i>	2	0	0	0	0	0	0	0	1	7	0	2	1	5	7	4	3	4	2	3	5	8	4	2	5	
<i>Cancris sagra</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	0	0	0	0	0	0	0	0	0	
<i>Cibicides cf. robertsoniana</i>	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cibicides lobatulus</i>	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cibicides pseudoungerianus</i>	3	3	0	10	0	0	4	0	0	3	0	0	3	0	1	0	0	0	0	0	0	1	5	8	4	
<i>Cibicides sp. A</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
<i>Cibicides sp. B</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	
<i>Cibicides sp. C</i>	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cibicides sp. cf. mayori</i>	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
<i>Clavulina angularis</i>	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2	0	0	0	2	0	1	0	0	1	
<i>Cornuspira involvens</i>	0	0	0	0	1	0	1	0	0	0	0	0	1	0	2	2	0	0	0	0	0	0	0	0	0	
<i>Coryphostoma? limbata</i> var. <i>costulata</i>	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cymbaloporetta atlantica</i>	0	0	0	0	0	0	0	0	0	4	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	
<i>Cymbaloporetta bradyi</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cymbaloporetta squamosa</i>	1	0	0	6	0	0	3	4	25	6	0	1	2	3	2	4	0	1	1	0	4	3	2	1	0	
<i>Discorbis granulosa</i>	0	4	0	2	1	2	0	10	3	3	3	10	5	12	0	0	0	0	0	0	5	0	2	2	0	
<i>Discorbis mira</i>	15	5	6	19	15	9	14	1	3	8	1	1	11	20	12	11	8	3	0	0	9	5	1	14	9	
<i>Discorbis rosea</i>	17	149	274	87	77	169	110	27	67	78	7	70	55	86	21	13	22	145	119	145	119	96	66	157	11	
<i>Elphidium advenum</i>	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	3	0	1	0	1	2	1	0	0	4	
<i>Elphidium cf. poeyanum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	3	0	0	0	0	1	0	0	0	0	
<i>Elphidium discoidale</i>	0	1	0	0	0	0	1	0	0	5	0	2	7	11	12	9	8	20	14	3	12	6	15	9	12	
<i>Elphidium mexicana</i>	0	1	0	0	0	0	0	0	0	2	0	0	0	0	2	4	0	0	0	0	3	3	1	0	0	
<i>Elphidium poeyanum</i>	0	0	0	0	0	0	0	0	0	0	0	0	2	2	10	10	17	0	0	0	3	0	4	1	3	
<i>Elphidium sagrum</i>	0	1	0	1	0	1	0	0	0	0	0	4	0	10	5	4	1	9	7	5	5	9	7	10	0	
<i>Eponides antillarum</i>	0	0	0	0	0	0	0	1	2	1	0	1	3	1	0	4	1	0	5	1	3	2	1	1	0	
<i>Fissurina goreau</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Fursenkoina pontoni</i>	0	0	0	0	0	0	1	0	0	0	0	1	1	1	5	3	5	0	0	0	1	0	0	0	0	
<i>Glabratella brasiliensis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
<i>Globigerinoides ruber</i>	1	0	0	8	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	5	0	0	0	7	
<i>Hauerina bradyi</i>	4	0	1	0	0	1	4	0	0	2	0	1	6	4	8	1	7	0	0	0	0	3	1	0	3	
<i>Hauerina ornatissima</i>	6	1	0	2	2	0	5	0	0	2	0	1	1	2	0	0	0	0	0	0	0	0	0	1	4	
<i>Hauerina pacifica</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Heterostegina antillarum</i>	9	7	2	0	1	1	2	0	1	5	2	1	1	0	1	0	0	3	1	0	3	1	2	1	2	
<i>Massilina gualtieriana</i>	4	0	0	6	0	0	2	1	0	0	0	0	0	0	1	0	0	0	0	0	7	2	3	0	0	
<i>Massilina inaequalis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	28	5	0	0	0	0	5	0	6	0	
<i>Miliolid</i> gen. and sp. indet.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Miliolinella circularis</i>	1	0	1	1	4	0	10	0	0	0	0	1	0	0	15	11	8	0	0	0	1	3	0	0	0	
<i>Miliolinella labiosa</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Miliolinella suborbicularis</i>	11	0	0	7	0	0	11	0	0	15	0	2	1	4	8	7	3	0	0	0	2	0	4	0	5	
<i>Miliolinella vignerasi</i>	14	0	0	2	1	0	16	0	0	18	0	1	0	0	0	0	0	0	0	0	0	1	3	2	0	
<i>Monalysidium politum</i>	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	
<i>Neoconorbina terquemi</i>	0	0	0	3	0	0	0	0	0	0	0	0	0	0	5	5	0	0	0	0	0	0	0	0	0	
<i>Nodobacularella mexicana</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	3	0	3	2	5	7	1	2	0	0	
<i>Nodophthalmidium antillarum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	
<i>Nodosaria catesbyi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Nonion</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Nonionella cuevasensis</i>	1	0	0	3	0	0	3	0	2	13	0	2	1	2	2	0	0	2	3	0	0	1	0	0	0	

Sample number	Windward Coast												Leeward Coast												
	win1	win2	hb1	lbhe2	lbhe15	lbhe16	lbhe6	pn1	pn2	skse5	hc1	mb1	mb2	mb3	cb1	cb2	cb3	mar1	mar2	fs1	rh1	rh2	rh4	g1	n951031
<i>Nonionella grateloupi</i>	0	0	0	0	0	0	2	0	0	0	0	0	6	1	22	25	13	0	0	0	0	0	1	0	0
<i>Nonionella?</i> sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Peneroplis bradyi</i>	1	0	0	4	0	0	1	0	0	7	0	0	0	0	2	3	3	0	0	0	0	0	0	0	1
<i>Peneroplis carinatus</i>	6	0	10	0	0	1	4	4	14	0	0	14	0	11	5	4	0	38	44	23	28	12	24	17	0
<i>Peneroplis pertusus</i>	28	10	1	2	0	1	10	0	7	13	0	1	4	1	5	1	4	0	1	0	3	1	2	6	0
<i>Peneroplis proteus</i>	15	29	0	16	3	4	10	6	27	18	1	5	20	13	5	7	11	6	11	1	12	17	21	12	8
<i>Planogypsina squammitiformis</i>	4	0	0	3	3	0	0	0	0	1	0	6	1	3	1	9	4	0	0	0	0	1	0	0	0
<i>Planorbulina mediterraneensis</i>	8	0	0	0	2	1	2	0	1	0	0	0	1	0	7	36	4	0	0	0	0	1	0	0	1
<i>Planorbulina retinaculata</i>	5	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>Pyrgo denticulata</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	4	2	1	0	2	0	0	1	0	0	0
<i>Pyrgo jugosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	0	0	2
<i>Pyrgo subsphaerica</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	2	3	0	4	0	0	0	0	1	0	0	0
<i>Quinqueloculina auberiana</i>	0	0	0	0	0	0	0	0	0	0	0	11	2	11	0	0	8	50	23	0	11	9	0	0	0
<i>Quinqueloculina boschiana</i>	1	0	0	4	2	1	3	0	0	0	0	1	6	9	38	6	8	0	0	0	0	0	3	0	1
<i>Quinqueloculina carinistriata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0
<i>Quinqueloculina carinata</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	3	0	9	1	0	0	0	5	0	0	0	1
<i>Quinqueloculina</i> cf. <i>cruziana</i>	4	5	0	5	0	0	16	1	6	0	0	11	11	5	0	11	6	0	3	0	0	0	1	3	0
<i>Quinqueloculina</i> cf. <i>quadriateralis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Quinqueloculina crassicarinata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
<i>Quinqueloculina exsculpta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
<i>Quinqueloculina lamarckiana</i>	0	0	0	0	0	0	0	0	0	6	1	4	4	29	32	13	8	7	9	29	9	9	0	26	17
<i>Quinqueloculina longirostra</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Quinqueloculina parkeri</i> var. <i>occidentalis</i>	0	0	0	0	1	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0
<i>Quinqueloculina philippinensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0
<i>Quinqueloculina poeyana</i>	0	0	1	2	0	0	3	0	0	0	0	3	4	2	37	27	17	0	0	0	1	4	3	4	1
<i>Quinqueloculina polygona</i>	1	0	0	2	0	0	3	0	0	21	0	1	18	0	5	3	5	0	0	0	5	2	0	0	2
<i>Quinqueloculina seminula</i>	1	0	0	1	0	1	0	0	0	0	0	0	0	1	8	5	0	0	0	0	0	0	0	0	1
<i>Quinqueloculina</i> sp. C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Quinqueloculina</i> sp. cf. <i>Triloculina eburnea</i>	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>Quinqueloculina transversestriata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Quinqueloculina tricarinata</i>	5	0	0	11	2	0	12	0	1	0	0	1	0	12	60	7	17	0	0	0	8	0	7	0	0
<i>Quinqueloculina venezuelaensis</i>	3	0	0	0	0	0	3	2	0	19	0	8	3	3	17	8	2	16	6	0	23	22	11	18	17
<i>Rectobolivina raphana</i>	0	0	0	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Reophax bacillaris</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Reussella mortensi</i>	5	1	0	0	0	0	1	0	0	3	0	0	0	2	0	0	0	3	1	1	1	0	0	1	1
<i>Rosalina bahamaensis</i>	7	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
<i>Rosalina bradyi</i>	0	0	0	3	0	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rosalina floridensis</i>	0	0	0	1	0	0	1	0	0	9	0	2	11	14	40	37	25	1	0	0	1	4	7	0	3
<i>Rosalina orientalis</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3	0	2	0	0	0	0	0	0	0	0
<i>Rosalina subaraucana</i>	0	0	0	0	0	0	0	0	0	15	0	5	0	0	0	9	0	0	0	0	0	0	0	3	4
<i>Sagrina pulchella</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sigmavirgulina tortuosa</i>	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Sigmoilopsis arenata</i>	1	0	0	2	0	1	2	0	0	5	0	5	0	4	18	18	16	0	0	0	3	1	1	0	10
<i>Siphonaperta bidentata</i>	0	0	0	1	0	0	3	1	3	0	0	0	2	7	1	0	0	0	1	0	2	3	0	7	0
<i>Siphonina pulchra</i>	2	3	0	3	0	1	3	0	1	3	0	0	0	1	0	0	2	0	0	0	0	1	0	1	1
<i>Siphoninoides echinata</i>	2	1	0	0	0	0	2	0	0	4	0	0	0	3	0	0	0	0	0	0	1	0	0	0	1
<i>Sorites orbiculus</i>	37	3	2	0	5	1	12	0	2	7	0	2	0	6	6	7	0	0	0	0	26	4	1	9	5
<i>Spirillina vivipara</i>	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spirolina arietina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Spiroloculina angulata</i>	0	0	0	2	0	0	3	0	0	3	0	2	2	2	17	12	5	0	0	0	6	1	1	0	0
<i>Spiroloculina antillarum</i>	9	0	0	4	3	2	3	0	0	0	0	2	2	2	0	4	6	1	0	0	4	1	0	4	1
<i>Spiroloculina eximia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0
<i>Spiroloculina</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Textularia agglutinans</i>	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Textularia candeiana</i>	2	0	0	1	0	0	0	1	7	102	0	0	0	0	1	0	3	0	0	1	6	4	1	0	32
<i>Textularia</i> cf. <i>conica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Tretomphalus bulloides</i>	0	0	0	1	1	0	9	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
<i>Trichohyalus aguayoi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Triloculina bassensis</i>	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Triloculina</i> cf. <i>bertheliniana</i>	2	0	0	0	0	0	1	0	0	1	0	3	0	0	0	0	0	1	0	1	0	1	0	0	0

Sample number	Windward Coast										Leeward Coast														
	win1	win2	hb1	lbhe2	lbhe15	lbhe16	lbhe6	pn1	pn2	skse5	hc1	mb1	mb2	mb3	cb1	cb2	cb3	mar1	mar2	fs1	rh1	rh2	rh4	g1	n951031
<i>Triloculina</i> cf. <i>bicarinata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Triloculina</i> <i>linneiana</i>	0	0	0	0	0	0	8	0	0	2	0	0	0	1	1	1	3	0	0	0	4	6	2	2	1
<i>Triloculina</i> <i>oblonga</i>	0	0	0	0	0	0	4	0	0	1	0	0	0	0	0	3	2	0	0	0	4	1	2	0	0
<i>Triloculina</i> <i>planciana</i>	7	0	0	0	0	0	0	0	0	3	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
<i>Triloculina</i> <i>rotunda</i>	0	0	0	0	4	0	10	0	0	0	0	0	12	6	43	40	26	0	0	0	0	5	1	0	2
<i>Triloculina</i> sp. B	0	0	0	0	0	0	0	15	5	0	7	1	0	0	0	1	1	0	4	0	1	0	0	1	0
<i>Triloculina</i> sp. 1 cf. <i>oblonga</i>	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Triloculina</i> sp. 2 cf. <i>oblonga</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Triloculina</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Triloculina</i> <i>trigonula</i>	1	0	0	1	0	0	1	0	0	2	0	0	3	10	21	63	32	0	0	0	3	0	0	0	5
<i>Vertebralina</i> <i>cassis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
' <i>Spiroloculina</i> ' sp. cf. <i>scrobiculata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

Samples are arranged in a series that progresses anticlockwise around the island. Sample numbers from Wilson (1998).

Table 3. Foraminifera in sediment samples around Nevis.

CONCLUSIONS

Epiphytal foraminiferal populations were monitored monthly on six phytal substrates in shallow water (<1 m) in two bays around the island of Nevis, in an environment where the sediment assemblage consists mainly of dead specimens washed from associated plants, or allochthonous specimens washed inshore during storms. SHE Community Structure Investigations (SHECSI) revealed that, of six epiphytal foraminiferal time-series examined, five had logarithmic series distributions of species abundances. The sixth (*Syringodium filiforme* rhizomes) was apparently represented by too few foraminifera in too few samples to indicate a population structure definitively. The main indicator of a logarithmic series distribution is that cumulative H , when regressed against cumulative $\ln N$, is constant. None of the populations showed a perfect fit to this parameter, but, for five, H fluctuated around a constant. In a perfect time-series, the slope of a regression of $\ln S$ against $\ln E$ is -1 . For all five time-series for which cumulative H fluctuated around a constant, the slope of $\ln S$ vs. $\ln E$ was -1 ± 0.3 . In four time-series the slope was -1 ± 0.2 and, for three time-series

(*Penicillus capitatus capitulae* and *Thalassia testinudum* leaves in Long Haul Bay, *P. capitatus* capitulate in Mosquito Bay), it was within -1 ± 0.05 .

SHECSI analysis was used to investigate the foraminiferal population in the main cluster (thanatacoenosis) inferred from cluster analysis, which proved to have a logarithmic series population structure. However, care must be taken when attempting to reconstruct the epiphytal population from the sediment thanatacoenosis. At least 40% of the thanatacoenosis comprised allochthonous *Amphistegina gibbosa*, *Archaias angulatus* and *Asterigerina carinata*. Simply ignoring these allochthonous components while analysing the sediment assemblage would not yield a population structure closer to that among the epiphytal community. Whereas the thanatacoenosis yielded few planorbulinids, these dominated the biocoenosis on seagrass leaves.

The results presented here support Buzas' (2004) contention that most nearshore foraminiferal communities have a logarithmic series structure. However, these results are for epiphytal communities of the foraminiferal taxocene in an oligotrophic area where the shallow-water sediment contains few live foraminifera. Comparison between the epiphytal communities and the thanatacoenosis in the sediment indicates that, while the latter may have a logarithmic series population structure, it need not reflect the nearby epiphytal populations. In particular, the addition of allochthonous specimens, and the destruction or removal of more fragile ones, can distort the signal.

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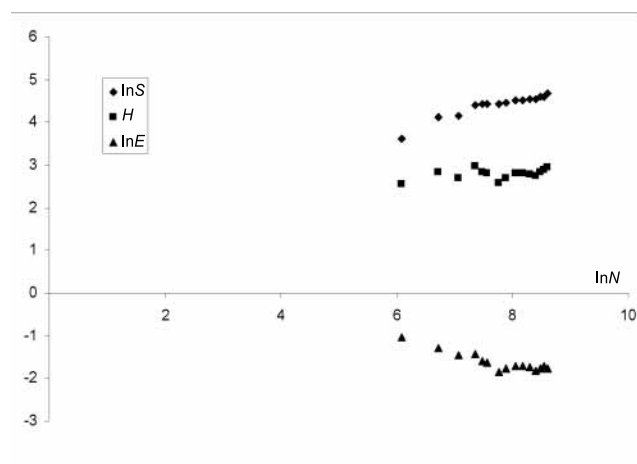


Fig. 6. Accumulated values of $\ln S$, H and $\ln E$ against $\ln N$ for sediment samples around Nevis.

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