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Biodiversity and community structure of deep-sea foraminifera around New Zealand

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Abstract

The biodiversity and community structure of benthic foraminifera were estimated from 217 stations distributed in four geographic regions (north, south, east, west) around New Zealand. An analytical method accumulating sample values of species richness (S), the information function (H) and evenness (E) with increasing number of individuals (N) called SHE analysis was used to establish 16 foraminiferal communities and their community structure at shelf (0–200 m), bathyal (200–2000 m) and abyssal (>2000 m) depths. A decrease in S, H and E occurs from north to south and this latitudinal gradient extends to abyssal depths. An increase in S and H with depth occurs in the northern and southern areas. For $\ln S$, H and $\ln E$ against $\ln N$, regression lines on values obtained from SHE analysis at shelf, bathyal and abyssal depths all diverge in the southern area. Each of the other areas exhibits crossing of regression lines so that establishing the rank order of S, H or E with depth within an area requires consideration of N. For a log series pattern, H is a constant proportional to α, the parameter of the log series, and, based on the decomposition equation $\ln S = H + \ln E$, a regression of $\ln S$ against $\ln E$ yields a regression coefficient of -1 and an intercept of H. At depths of less than 1000 m, 2 of 8 communities have regression coefficient confidence intervals that include -1. At depths of greater than 1000 m, 7 of 8 communities intervals include -1. Thus, overall, the majority of cases, but especially those at depths greater than 1000 m, have a log series pattern.
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Keywords: Biodiversity; Community structure; Foraminifera; New Zealand

1. Introduction

A fundamental component of biodiversity studies is the relative species abundance vector (RSAV). The RSAV is the column of numbers composed of each species proportion at a site(s). The number of entries or rows in the column is called the rank of the vector which in turn is called the species richness (S). Formally, we have, then, the species proportion p_i, where $i = (1, 2, \ldots, S)$ and $\mathbf{p} = p_1, p_2, \ldots, p_S$. The statistical distribution of $\mathbf{p}$ or the RSAV is referred to as community structure (Buzas and Hayek, 2005). In this sense a community is simply a group of organisms, usually a taxonomic entity, of interest to the researcher. Thus, we may have a bivalve community, foraminiferal community and so forth. For the purposes of this paper, community,

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biofacies, assemblage and faunal zone are synonymous. Recently, because of renewed theoretical interest, a renaissance in research on species abundance has occurred (Hubbell, 1997, 2001; Volkov et al., 2003; Magurran, 2005; McGill, 2006; Shipley et al., 2006). The approach for the evaluation of biodiversity and community structure is a method of analysis developed by Buzas and Hayek (1996, 2005) that offers researchers a new tool for this renaissance. This methodology mathematically links accumulated values of density (N), species richness (S), information (H) and evenness (E). The entire procedure uses the acronym SHE analysis (Hayek and Buzas, 1997). The variables (S, H, E and N) are displayed on a single graph called a biodiversity-gram (BDG) (Hayek and Buzas, 2006).

The benthic foraminifera are and have been ubiquitous, abundant and speciose in the world of oceans for millions of years. In the modern environment as well as in the fossil record, thousands of species are described, and their distribution is well documented in space and time (Culver and Buzas, 1998). For studies of marine biogeography and biodiversity, in small and large amounts of space and time, they are ideal organisms. Like most other organisms, they exhibit a pattern of increasing species richness with decreasing latitude and often show an increase in species richness with depth (Gibson and Buzas, 1973; Murray, 1973, 2006).

The benthic foraminifera can provide the ideal organisms to examine the biodiversity and community structure of the deep-sea. However, much of the earlier work was conducted for taxonomic and biogeographic purposes and is not suitable for careful analysis.

In the deep-sea around New Zealand, the surveys of Hayward et al. (2001, 2002, 2003, 2006, 2007) from shelf to abyssal depths have remedied this situation. Exact locations of the stations and data are given in the Hayward et al. contributions. The purpose of this paper is to analyze this vast and unique New Zealand data set by SHE analysis for trends in biodiversity and community structure. We will do so by depth as well as by geographic area.

2. Methods

All samples used in this study come from the seafloor of the New Zealand region in the southwest Pacific between latitudes 33°S and 56°S (Fig. 1) and

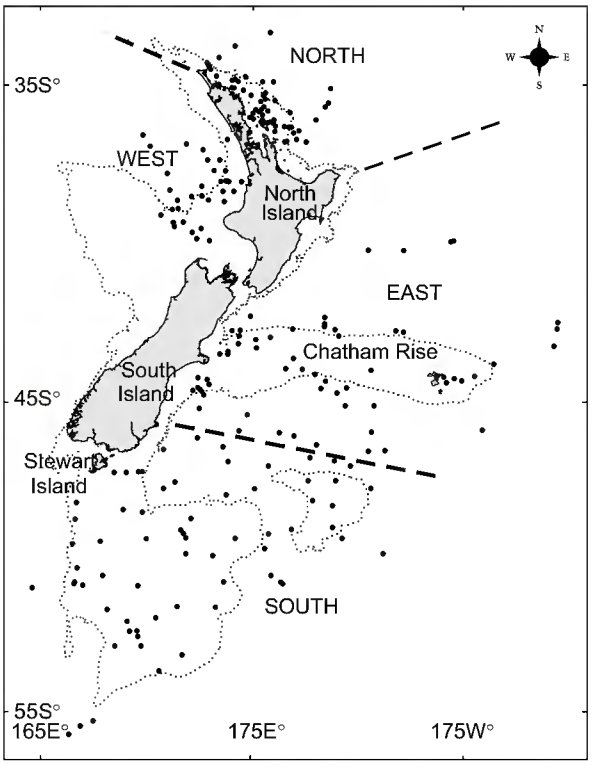

Fig. 1. Locations of benthic foraminiferal seafloor samples around New Zealand in the south-west Pacific. They have been grouped into four regions—north, west, east and south for comparitive analysis. The 1000 m depth contour is shown.

at mid-shelf to abyssal depths, between 50 and 5000 m (Table 1). The samples are grouped into four areas, located off the north, west, east and south coasts of the two main islands (North and South Islands) of New Zealand (Fig. 1). The sediment samples were obtained mostly from the archives held by the National Institute for Water and Atmospheric Research (NIWA), Wellington, supplemented by core top samples from several Ocean Drilling Program (ODP) sites. Except for the ODP sites, the samples analyzed were taken from the top few centimeters of gravity and piston cores or from surficial grab or dredge samples. Faunal slides (prefixed by F202) are housed in the collections of the Institute of Geological and Nuclear Sciences, Lower Hutt. Consequently, there was no opportunity to distinguish living from dead tests, and census counts are of total (living plus dead) faunas. We would, of course, have preferred to analyze live, dead and total populations separately. Horton and Murray (2006) discuss the advantages and disadvantages of using each of these populations. Ideally, observation of the living population over a

Table 1
Results of SHE analysis from South of New Zealand

Biofacies	Stations depth	n	N	S	H	E	β_1	β_1 Confidence limits
1	S6–S15		200	28	2.72	0.55		
	Outer shelf	10	400	36	2.62	0.37	−0.72	$-0.84<\beta<-0.60$
	143–188 m		1000	52	2.49	0.23		
	$\mu = 169$ m		1300	58	2.44	0.20		
Regression equations:								
$\ln S = 1.27 + 0.39 \ln N$, $p = 0.00$, $R^2 = 0.97$; $H = 3.52 - 0.15 \ln N$, $p = 0.00$, $R^2 = 0.89$								
$\ln E = 2.25 - 0.54 \ln N$, $p = 0.00$, $R^2 = 0.99$; $\ln S = 2.89 - 0.72 \ln E$, $p = 0.00$, $R^2 = 0.98$								
2	S20–S27		200	27	2.78	0.58		
	Upper bathyal	8	400	35	2.81	0.46	−1.12	$-1.31<\beta<-0.92$
	435–565 m		1000	52	2.83	0.33		
	$\mu = 519$ m		1300	56	2.88	0.31		
Regression equations:								
$\ln S = 1.23 + 0.39 \ln N$, $p = 0.00$, $R^2 = 0.98$; $H = 2.57 + 0.04 \ln N$, $p = 0.22$, $R^2 = 0.48$								
$\ln E = 1.33 - 0.35 \ln N$, $p = 0.00$, $R^2 = 0.99$; $\ln S = 2.70 - 1.12 \ln E$, $p = 0.00$, $R^2 = 0.98$								
3	S42–S47		200	31	2.91	0.57		
	Lower bathyal	6	400	41	2.98	0.46	−1.26	$-1.64<\beta<-0.89$
	960–1244 m		1000	58	3.04	0.35		
	$\mu = 1076$ m		1300	65	3.10	0.32		
Regression equations:								
$\ln S = 1.31 + 0.40 \ln N$, $p = 0.00$, $R^2 = 0.99$; $H = 2.38 + 0.10 \ln N$, $p = 0.05$, $R^2 = 0.82$								
$\ln E = 1.07 - 0.31 \ln N$, $p = 0.00$, $R^2 = 0.98$; $\ln S = 2.76 - 1.26 \ln E$, $p = 0.00$, $R^2 = 0.98$								
4	S63–S68		200	35	3.00	0.58		
	Abyssal	6	400	48	3.05	0.44	−1.06	$-1.57<\beta<-0.55$
	3452–5000 m		1000	73	3.10	0.30		
	$\mu = 4352$ m		1300	82	3.13	0.28		
Regression equations:								
$\ln S = 1.11 + 0.46 \ln N$, $p = 0.00$, $R^2 = 0.99$; $H = 2.63 - 0.07 \ln N$, $p = 0.38$, $R^2 = 0.44$								
$\ln E = 1.52 - 0.39 \ln N$, $p = 0.00$, $R^2 = 0.95$; $\ln S = 3.01 - 1.06 \ln E$, $p = 0.00$, $R^2 = 0.94$								

n is the number of stations in the community (see Section 2 for how it is determined by SHECSI). N is the number of individuals used in the regression equations to calculate S, H and E. β_1 is from the regression equation $\ln S = \beta_0 + \beta_1 \ln E$.

considerable period of time is required to assess the vicissitudes of seasonal and yearly fluctuations, and only through use of the living population can we be certain that transport or other kinds of taphonomic loss or gain did not influence the dead or total population. However, long-term observations on living populations are usually not available. The total and dead populations are often equivalent, because the dead population is often an order of magnitude larger than the living population (Buzas, 1965). Many authors point out that the total or dead population can be thought of as integrating seasonal and temporal fluctuations (Scott et al., 2001), and because it often resembles downcore fossil assemblages, it is the most useful for environmental assessment (Culver and Horton, 2005). The community structure evaluated from fossil populations through SHE analysis thus far do resemble modern living and total populations (Buzas, 2004; Hayek et al., 2007). Thus, although we cannot be certain, we feel confident the analysis presented here is germane and representative of a living community measured over an extended period of time.

All samples were washed gently over a 63-micron sieve, and after drying of the residue, a microsplitter was used to obtain an amount containing approximately 200 benthic specimens. Most foraminiferal studies use 300 specimens; however, as Buzas (1990) has pointed out the number is arbitrary and only an increase of 0.01 gain in confidence of the estimate results by using 300 instead of 200. Moreover, the SHE methodology used here accumulates over samples so that for the final community evaluation estimates are made with well over 1000 individuals. All benthic foraminifera were picked from the microsplit, mounted on faunal slides, identified

and counted. All taxa were identified to species level, except unilocular forms, which were identified to generic level.

SHE Analysis (Buzas and Hayek, 1996, 2005; Hayek and Buzas, 1997), based upon an information-theoretic approach, is the methodological advance for comprehensive diversity evaluation of a community over space and time. Ecologists have long known that the statistical relationship between the number of species (S) and the number of individuals (N) is semi-log or log–log (for a discussion, see Hayek and Buzas, 1997). Consequently, as individuals are accumulated, the number of species increases, and the linear regression equation $\ln S = \beta_0 + \beta_1 \ln N$ is applicable. In biodiversity evaluations in addition to species richness (S) a measure of evenness (E) is also often employed to characterize the community. Some measures of evenness utilize in their formula the Shannon information function (calculated from the RSAV) commonly symbolized by H and also called compound diversity (Hazel, 1975). A commonly used measure is $E = e^H/S$, where e is the base of the natural logarithms (for a discussion, see Hayek and Buzas, 1997). Buzas and Hayek (1996) showed that the decomposition equation is $H = \ln S + \ln E$, and because $\ln S$ is known to be a function of $\ln N$, so are H and $\ln E$. They further showed that for commonly used statistical distributions a plot of $\ln E$ vs. $\ln N$ is a straight line. SHE analysis when performed for biofacies identification (SHEBI) uses this linear relationship for the determination of biofacies or communities by accumulating samples along a traverse (Buzas and Hayek, 1998). Within the straight line segments obtained from the SHEBI, the samples are treated as replicates from a single community. The entire canonical ensemble of values for $\ln N$, $\ln S$, H and $\ln E$ are displayed on a single graph called a Biodiversity-gram or BDG (Hayek and Buzas, 2006). Because the expected value of H is known for major statistical distributions (see, Hayek and Buzas, 1997) and $\ln N$ and $\ln S$ are observed, $\ln E$ is fixed by the decomposition equation given above. Consequently with this information, SHE analysis for community structure identification (SHECSI) determines the underlying statistical distribution. For example, the expected value of H for a log series distribution is $E(H) = \ln \alpha + 0.58$, where α is the parameter of the log series distribution and 0.58 is Eueler's constant (Bulmer, 1974). Because α is a known constant, H is also a constant, and the accumulation of H with the increase in $\ln N$ must plot as a straight line. When this is the situation, the regression equation $\ln S = \beta_0 + \beta_1 \ln E$ is equivalent to the decomposition equation given above, where $\beta_0 = H$ and $\beta_1 = -1$ for the log series distribution. Also, for the log series distribution and because of the restrictions imposed by the decomposition equation, when H is constant, the regressions $\ln S$ vs. $\ln N$ and $\ln E$ vs. $\ln N$ must have the same value for the slope but with opposite sign. Buzas and Hayek (2005) have suggested for this and other reasons that the log series is the ideal null model against which observations can be compared.

For the present study we used data from four designated areas around New Zealand: east, west, north and south (Fig. 1). In each area, we first applied the SHEBI procedure to determine the location of 16 communities and then analyzed each of these by the SHECSI procedure outlined above.

3. Results

3.1. Geographic areas at all depths

The area south of New Zealand is topographically highly variable. Because of this topography, there is no simple sampling scheme based on depth from shelf to abyss. Nevertheless, for analytical purposes we arranged the samples by depth, regardless of whether or not samples were contiguous. This sometimes allowed geographically distant samples, especially at shelf depths, to follow one another in the analysis. However, the benthic foraminiferal communities (biofacies) recognized by cluster analyses indicate that biofacies conform to a depth configuration, even though samples may not be contiguous (Hayward et al., 2006). Consequently, the scheme presented here is workable. Following Hayward et al. (2001), we use the depth classification proposed by Van Morkhoven et al. (1986). The depth scheme is as follows: inner shelf, 0–50 m; mid-shelf, 50–100 m; outer shelf, 100–200 m; upper bathyal, 200–600 m; mid-bathyal, 600–1000 m; lower bathyal, 1000–2000 m; abyssal, >2000 m.

As outlined in Section 2 SHE analysis has two facets: SHEBI and SHECSI. For an analysis with SHEBI we constructed a linear plot of $\ln E$ vs. $\ln N$, which was then used to delineate communities. The communities so identified were then analyzed for community structure by SHECSI . Only biofacies or communities defined by more than 4 stations were

included in the regression analysis, and results for select values of N are given in the tables.

In the southern area of New Zealand, we analyzed $S = 214$ species distributed among $n = 68$ stations. About half of the stations (44%) were grouped into 4 communities or biofacies. Table 1 and the BDG shown in Fig. 2 indicate that except for the outer shelf, H plots as a nearly straight line.

Although we provide regression equations for all three measures ($\ln S, H, \ln E$) against $\ln N$, the decomposition equation explains that only two of the three are necessary. For example, the slope for H vs. $\ln N$ equals the difference between the slopes for $\ln S$ vs. $\ln N$ and $\ln E$ vs. $\ln N$. The intercept in H vs. $\ln N$ equals the sum of the two intercepts for $\ln S$ vs. $\ln N$ and $\ln E$ vs. $\ln N$.

The regression of $\ln S$ with $\ln E$ as well as the predicted values of S, H and E at the given values of N are approximately equivalent across the outer shelf and at upper bathyal depths (Table 1, Fig. 2). At lower bathyal and abyssal depths, however, species richness increases so that there is a decrease from abyssal–lower bathyal to upper bathyal–outer shelf (Fig. 2, Table 1).

The patterns of results for the information function, H, are not so orderly. For the outer shelf biofacies, the slope for the equation for H vs. $\ln N$ is negative resulting in increasingly smaller values for

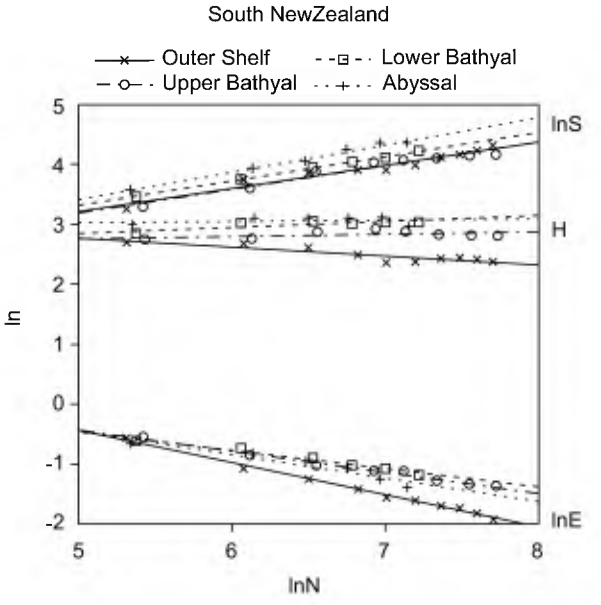

Fig. 2. Biodiversitygram (BDG) for area south of New Zealand. $\ln S$ is the natural log of the number of species, H is the information function. $\ln E$ is the evenness defined as $\ln E = H - \ln S$.

H as the number of individuals increases (Fig. 2, Table 1). At deeper biofacies, the slope of H vs. $\ln N$ is close to zero, making the plotted line essentially parallel to the $\ln N$ axis. As with species richness the deeper biofacies exhibit larger values of H as N increases and regression lines diverge.

As with the information function, the plot for evenness clearly differentiates the outer shelf from the other deeper biofacies that have higher values for evenness (Fig. 2). The regression lines for evenness also diverge as N increases. For higher densities the biofacies are more easily differentiated.

Overall, Fig. 2 shows an outward spread of data lines as N increases; at lower values of N there is less discrimination of S, H and E than at higher values. Examination of Table 1 indicates that at $N = 400$, the change in S from outer shelf to abyssal depths is 12 species; for H the change is 0.43 and for E, 0.07. However, at $N = 1300$, the changes are 24, 0.69 and 0.08, respectively.

The confidence intervals for the slope in each equation for $\ln S$ vs. $\ln E$, except that for the outer shelf, include the value -1, the theoretical constant from the log series distribution.

In the area north of the North island of New Zealand, 238 species distributed in 56 samples were analyzed by SHEBI. The analysis placed 51 samples or 91% into 4 biofacies.

The first biofacies contains $n = 33$ stations and extends from mid-shelf to upper bathyal depths (50–561 m). This wide span in depth encompassing a single community is not observed elsewhere around New Zealand or from any of the other studies subjected to SHE analysis so far. The remaining 3 biofacies each contain 6 stations (Table 2). Species richness is nearly identical for shelf to mid-bathyal depths (Fig. 3). However, species richness increases at lower bathyal and abyssal depths (Table 2, Fig. 3). The regression coefficients for the equation $\ln S$ vs. $\ln N$ for outer shelf, upper bathyal, lower bathyal and abyssal depths are similar (Table 2).

Values for H are more complicated, because the regressions for H vs. $\ln N$ are nearly horizontal at the two deepest biofacies, but have positive slopes at the two shallowest (Table 2). Consequently, at lower densities ($\ln N = 6$ or $N \approx 400$) the values of H can be differentiated for all four biofacies, but as $\ln N$ increases only the value for abyssal depths remains distinctly higher than the others (Fig. 3).

As with the H values, slopes for the $\ln E$ vs. $\ln N$ regressions at lower bathyal and abyssal depths are more similar than those at the shallower depths.

Table 2
Results of SHE analysis for north of New Zealand

Biofacies	Stations depth	n	N	S	H	E	β_1	β_1 Confidence limits
1	N56–N24		200	36	3.09	0.61		
	Upper bathyal	33	400	47	3.18	0.50	−1.39	$-1.44<\beta<-1.34$
	50–561 m		1000	68	3.28	0.39		
	$\mu = 223$ m		1300	75	3.30	0.36		
Regression equations:								
$\ln S = 1.52 + 0.39 \ln N$, $p = 0.00$, $R^2 = 0.98$; $H = 2.51 + 0.11 \ln N$, $p = 0.00$, $R^2 = 0.94$								
$\ln E = 0.99 - 0.28 \ln N$, $p = 0.00$, $R^2 = -0.98$; $\ln S = 2.92 - 1.39 \ln E$, $p = 0.00$, $R^2 = 0.99$								
2	N20–N15		200	33	2.78	0.46		
	Mid-bathyal	6	400	46	2.95	0.42	−2.28	$-3.39<\beta<-1.16$
	754–1242 m		1000	69	3.19	0.35		
	$\mu = 967$ m		1300	77	3.28	0.32		
Regression equations:								
$\ln S = 1.12 + 0.45 \ln N$, $p = 0.00$, $R^2 = 0.99$; $H = 1.35 + 0.27 \ln N$, $p = 0.01$, $R^2 = 0.93$								
$\ln E = 0.23 - 0.19 \ln N$, $p = 0.00$, $R^2 = 0.98$; $\ln S = 1.84 - 2.28 \ln E$, $p = 0.00$, $R^2 = 0.94$								
3	N14–N9		200	43	3.28	0.62		
	Lower bathyal	6	400	54	3.29	0.48	−1.04	$-1.20<\beta<-0.89$
	1295–2036 m		1000	77	3.30	0.35		
	$\mu = 1664$ m		1300	87	3.31	0.32		
Regression equations:								
$\ln S = 1.74 + 0.38 \ln N$, $p = 0.00$, $R^2 = 0.99$; $H = 3.17 + 0.02 \ln N$, $p = 0.47$, $R^2 = 0.37$								
$\ln E = 1.43 - 0.36 \ln N$, $p = 0.00$, $R^2 = 0.99$; $\ln S = 3.23 - 1.04 \ln E$, $p = 0.00$, $R^2 = 0.99$								
4	N6–N1		200	54	3.66	0.69		
	Abyssal	6	400	68	3.65	0.55	−0.86	$-1.31<\beta<-0.40$
	2550–3757 m		1000	90	3.63	0.40		
	$\mu = 3002$ m		1300	96	3.63	0.36		
Regression equations:								
$\ln S = 2.34 + 0.31 \ln N$, $p = 0.00$, $R^2 = 0.99$; $H = 3.77 - 0.02 \ln N$, $p = 0.71$, $R^2 = 0.20$								
$\ln E = 1.43 - 0.34 \ln N$, $p = 0.00$, $R^2 = 0.97$; $\ln S = 3.72 - 0.86 \ln E$, $p = 0.01$, $R^2 = 0.93$								

Explanation of symbols given in Table 1.

Again there is more discrimination at lower densities. In particular, evenness decreases with increasing N. That is, regardless of depths at a given value of N the evenness values are similar (Table 2, Fig. 3).

Regression coefficients for H vs. $\ln N$ are nearly zero for lower bathyal and abyssal depths. The confidence intervals for both slopes (β_1's) include −1 (Table 2). At the two shallower biofacies we observe crossing of regression lines (Fig. 3). Consequently, regardless of N for the deeper two biofacies, abyssal values for S, H and E are larger than lower bathyal values.

In the western area of New Zealand, we analyzed 149 species distributed in 32 stations ranging in depth from 60 to 2150 m. Of these 24, or 75%, grouped into 3 biofacies defined by more than 4 samples. The first biofacies ranges from mid to outer shelf depths (60–154 m). The slope of the regression on $\ln S$ vs. $\ln N$ is relatively large at 0.67 so that the predicted change in S from $N = 400$ to 1000 is 30 species (Table 3, Fig. 4). The slopes for $\ln S$ vs. $\ln N$ are nearly identical for mid-bathyal and lower bathyal depths. As Table 3 and Fig. 4 indicate, this difference in slopes means that at $N = 400$, S is smaller at shelf depths, but at $N = 1000$, S is nearly identical at all depths.

A similar situation exists for H. The regression coefficient for H vs. $\ln N$ at shelf depths is substantially higher than the other two (Table 3). At $N = 400$, the values of H at shelf depths are considerably lower than at the deeper biofacies, where H's are similar (Table 3, Fig. 4).

The values of E are lowest at shelf depths regardless of N. At values of $N = 400$, the deeper biofacies have similar E values, but the regression lines diverge, and at $N = 1000$, mid-bathyal has a higher E than lower bathyal.

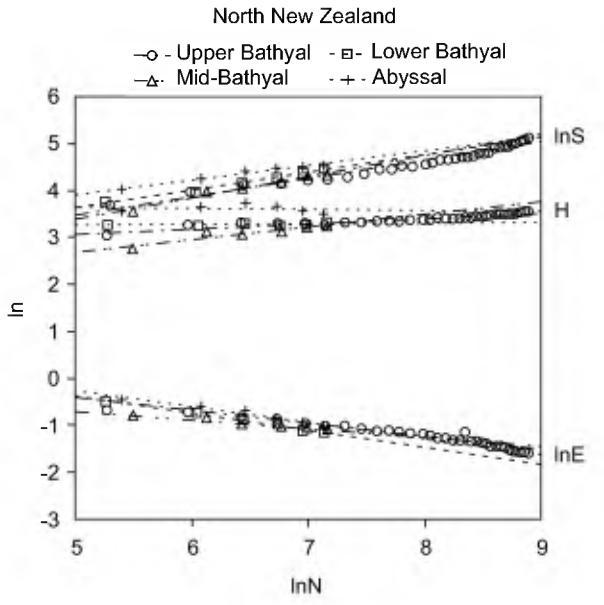

Fig. 3. BDG for area north of New Zealand. Symbols as defined in Fig. 2.

The BDG in Fig. 4 shows that the lower bathyal biofacies has a regression coefficient for $\ln S$ vs. $\ln E$ close to -1. The crossing of the regression lines indicates that the community structure must be considered when evaluating the biodiversity of the area west of Taranaki is evaluated.

The area east of New Zealand is dominated by the Chatham Rise (Fig. 1), which causes a complex topography. Here 251 species distributed in 61 samples were analyzed. This total number of species or gamma diversity is the highest of the areas studied. There are five biofacies composed of more than 4 samples. These 5 accounted for 32 of the total stations or 52% of the total.

The results for the SHE analysis are shown in Table 4. Plotting 5 regression lines results in an uninformative graph, so only three regressions are plotted on Fig. 5. The two lower bathyal plots were left off because the shallower one resembles the abyssal plot and the deeper one the upper bathyal.

The shallower lower bathyal and abyssal depths have higher species richness at low values of N than the other biofacies (Table 4, Fig. 5). However, the regression lines cross at higher values and species richness becomes similar.

The regression line for H at abyssal depths is almost horizontal and the form of the regression equation for $\ln S$ vs. $\ln E$ is equivalent to the decomposition equation. Note $\beta_0 = 3.05$, which is the value of observed H. For the biofacies at other depths, the regressions of H vs. $\ln N$ have positive slopes and there is separation at low values of N, but intersecting of lines at higher values of N (Fig. 5).

For evenness, the mid-bathyal and abyssal depths have higher values of E at low values of N, but the values become similar at higher values.

The community structure for abyssal depths is a nearly perfect log series pattern (Table 4). The confidence intervals for the slopes of mid-bathyal and the shallower lower bathyal do encompass -1. As noted, there is considerable difference among the regression equations at about $N = 1000$.

Finally, we examine each of the four areas for biodiversiy patterns regardless of depth. Fig. 6 shows that $\ln S$, H and $\ln E$ all decrease significantly in the order north, west, east and south. The difference between north and south for all three variables is particularly striking. In the north at $N = 1000$, the estimated $S = 75$, $H = 3.33$ and $E = 0.37$ while in the south, $S = 60$, $H = 2.87$ and $E = 0.29$.

3.2. Depths in all geographic areas

As Figs. 2–5 and Tables 1–4 indicate not all areas contain each of the 5 depth categories used in this study. Nevertheless, examining each depth category in the areas in which each occurs is a worthwhile endeavor.

For the outer shelf (100–200 m) only two biofacies with more than 4 stations were recognized by SHEBI. These are west and south and are shown in Fig. 7. The community structure exhibited by the two is very different. As Fig. 7 shows, the regression lines cross at about $\ln N = 6.1$ or $N \approx 450$. Below that N, values for $\ln S$, H and $\ln E$ are larger for the south and above they are larger for the west.

At upper bathyal depths (200–600 m), the north and south areas exhibit similar community structure with slopes for H nearly constant. Values for $\ln S$, H and $\ln E$ are higher in the northern area. The community structure for the east, however, is dramatically different (Table 4, Figs. 5 and 8) with the slope value for the $\ln S$ vs. $\ln E$ regression reaching a value of -3.06 (Table 4), the highest observed in this study. For $\ln S$ and H, the regression line for east crosses those of north and south at different values of N, making predictions for which areas have higher values relative to N.

Table 3
Results of SHE analysis for west of New Zealand

Biofacies	Stations depth	n	N	S	H	E	β_1	β_1 Confidence limits
1	T11, T18, T27,							
	T23, T19, T28		200	22	2.28	0.46		
	Outer shelf	6	400	35	2.52	0.37	−1.91	$-2.62<\beta<-1.19$
	60–154 m		1000	65	2.83	0.28		
	$\mu = 112$ m		1300	78	2.92	0.26		
Regression equations:								
$\ln S = -0.45 + 0.67 \ln N$, $p = 0.00$, $R^2 = 0.99$; $H = 0.48 + 0.34 \ln N$, $p = 0.00$, $R^2 = 0.97$								
$\ln E = 0.93 - 0.32 \ln N$, $p = 0.00$, $R^2 = 0.95$; $\ln S = 1.66 - 1.91 \ln E$, $p = 0.00$, $R^2 = 0.93$								
2	T32, T33, T14,							
	T34, T15, T2,							
	T35, T36		200	41	3.22	0.62		
	Mid-bathyal	8	400	51	3.28	0.43	−1.35	$-1.54<\beta<-1.16$
	541–1120 m		1000	67	3.35	0.43		
	$\mu = 883$ m		1300	72	3.37	0.41		
Regression equations:								
$\ln S = 2.13 + 0.30 \ln N$, $p = 0.00$, $R^2 = 0.99$; $H = 2.80 + 0.08 \ln N$, $p = 0.00$, $R^2 = 0.88$								
$\ln E = 0.68 - 0.22 \ln N$, $p = 0.00$, $R^2 = 0.99$; $\ln S = 3.04 - 1.35 \ln E$, $p = 0.00$, $R^2 = 0.99$								
3	T37, T26, T16							
	T4, T38, T5,							
	T6, T39, T7,							
	T8		200	39	3.23	0.65		
	Lower bathyal	10	400	49	3.20	0.50	−0.89	$-1.00<\beta<-0.77$
	1233–2000 m		1000	66	3.16	0.36		
	$\mu = 1562$ m		1300	72	3.15	0.33		
Regression equations:								
$\ln S = 1.98 + 0.32 \ln N$, $p = 0.00$, $R^2 = 0.99$; $H = 3.44 - 0.04 \ln N$, $p = 0.00$, $R^2 = 0.57$								
$\ln E = 1.47 - 0.36 \ln N$, $p = 0.00$, $R^2 = 0.99$; $\ln S = 3.30 - 0.89 \ln E$, $p = 0.00$, $R^2 = 0.99$								

Explanation of symbols given in Table 1.

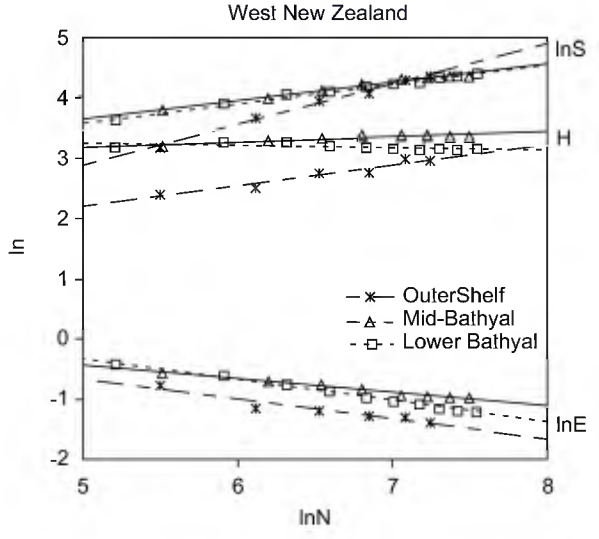

Fig. 4. BDG for area west of New Zealand. Symbols as defined in Fig. 2.

The north, west and east areas each have biofacies represented in the mid-bathyal depth range (600–1000 m). Fig. 9 shows that the regression equations predict that at lower values of N species richness is highest in the west and at higher values in the east. A prediction of similar values of $\ln S$ occurs at about $\ln N = 6.9$ or $N = 1000$. For H the western values are nearly constant while the slopes for north and east are nearly identical (Fig. 9, Tables 2–4). For $\ln E$, the north and west are also nearly parallel, but the west has larger values. The east has higher values of $\ln E$ at smaller N, but after about $\ln N = 6.9$ or $N = 1000$, the west is always the highest (Fig. 9).

At lower bathyal depths (1000–2000 m) all four areas are represented. The northern area again has the highest species richness: however, there is considerable crossing of regression lines at about $N = 1000$. Both the north and west values of H are

Table 4
Results of SHE analysis for east of New Zealand

Biofacies	Stations depth	n	N	S	H	E	β_1	β_1 Confidence limits
1	E32, E45, E3, E46, E63, E34, E47		200	20	2.19	0.42		
	Upper bathyal	7	400	34	2.56	0.36	−3.06	$-3.70<\beta<-2.42$
	289–511 m		1000	71	3.03	0.29		
	$\mu = 394$ m		1300	84	3.18	0.27		
Regression equations:								
$\ln S = -1.09 + 0.77 \ln N$, $p = 0.00$, $R^2 = 0.99$; $H = -0.62 + 0.53 \ln N$, $p = 0.00$, $R^2 = 0.98$								
$\ln E = 0.47 - 0.25 \ln N$, $p = 0.00$, $R^2 = 0.97$; $\ln S = 0.49 - 3.06 \ln E$, $p = 0.00$, $R^2 = 0.98$								
2	E33, E4, E26, E35, E48, E27, E12, E5, E13		200	21	2.69	0.70		
	Mid-bathyal	9	400	34	2.87	0.51	−1.50	$-1.99<\beta<-1.00$
	547–980 m		1000	67	3.12	0.34		
	$\mu = 735$ m		1300	78	3.17	0.31		
Regression equations:								
$\ln S = -0.66 + 0.70 \ln N$, $p = 0.00$, $R^2 = 0.98$; $H = 1.31 + 0.26 \ln N$, $p = 0.01$, $R^2 = 0.78$								
$\ln E = 1.97 - 0.44 \ln N$, $p = 0.00$, $R^2 = 0.98$; $\ln S = 2.58 + -1.50 \ln E$, $p = 0.00$, $R^2 = 0.94$								
3	E62, E36, E28, E49, E52		200	34	2.97	0.58		
	Lower bathyal	5	400	49	3.07	0.36	−1.29	$-1.74<\beta<-0.84$
	1003–1204 m		1000	79	3.19	0.31		
	$\mu = 1109$ m		1300	91	3.23	0.28		
Regression equations:								
$\ln S = 0.71 + 0.53 \ln N$, $p = 0.00$, $R^2 = 0.99$; $H = 2.23 + 0.14 \ln N$, $p = 0.04$, $R^2 = 0.90$								
$\ln E = 1.52 - 0.39 \ln N$, $p = 0.01$, $R^2 = 0.96$; $\ln S = 2.83 - 1.29 \ln E$, $p = 0.00$, $R^2 = 0.98$								
4	E51, E14, E7, E53, E39, E38		200	21	2.40	0.52		
	Lower bathyal	5	400	32	2.56	0.36	−1.55	$-1.94<\beta<-1.16$
	1462–1841 m		1000	56	2.77	0.28		
	$\mu = 1692$ m		1300	66	2.80	0.25		
Regression equations:								
$\ln S = -0.12 + 0.60 \ln N$, $p = 0.00$, $R^2 = 0.98$; $H = 1.29 + 0.21 \ln N$, $p = 0.02$, $R^2 = 0.89$								
$\ln E = 1.42 - 0.39 \ln N$, $p = 0.00$, $R^2 = 0.99$; $\ln S = 2.08 - 1.55 \ln E$, $p = 0.00$, $R^2 = 0.98$								
5	E29, E54, E65, E61, E8		200	33	3.05	0.66		
	Abyssal	5	400	46	3.05	0.47	−0.99	$-1.40<\beta<-0.59$
	2030–2332 m		1000	72	3.04	0.29		
	$\mu = 2245$ m		1300	82	3.04	0.27		
Regression equations:								
$\ln S = 0.96 + 0.48 \ln N$, $p = 0.01$, $R^2 = 0.96$; $H = 3.08 - 0.005 \ln N$, $p = 0.94$, $R^2 = 0.05$								
$\ln E = 2.12 - 0.48 \ln N$, $p = 0.00$, $R^2 = 0.99$; $\ln S = 3.05 - 0.99 \ln E$, $p = 0.00$, $R^2 = 0.98$								

Explanation of symbols given in Table 1.

the highest and have nearly zero slopes (Fig. 10, Tables 2, 3). The south and east have positive slopes for H, but the south has higher values. Values of $\ln E$ are similar for north, south and west. Only the east shows consistently lower values of evenness (Fig. 10).

Abyssal biofacies (>2000 m) are found in the north, south and east. The northern area has the highest species richness, information function and evenness (Fig. 11). The S, H and E for the east and south are nearly identical throughout the range of N. All three areas have nearly zero

slopes for H vs. $\ln N$, indicating that the abyssal communities exhibit a log series pattern of community structure.

If we concatenate the areas and examine S, H and E with depth categories, both $\ln S$ and H increase with depth (significant regression at the 0.05 level, Fig. 12). At $N = 1000$ we expect $S = 58$ at outer shelf depths and $S = 74$ at abyssal depths. Similarly, at $N = 1000$ we expect $H = 2.84$ at outer shelf depths and $H = 3.28$ at abyssal depths. Although $\ln E$ also increases with depth it does so only slightly and the regression is not significant.

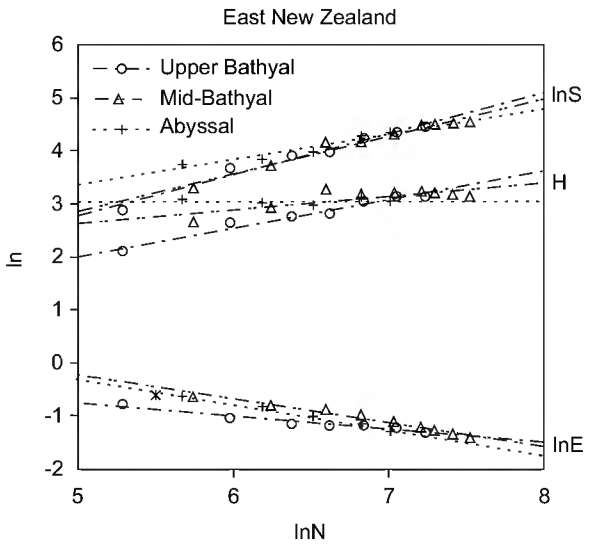

Fig. 5. BDG for area east of New Zealand. Symbols as defined in Fig. 2.

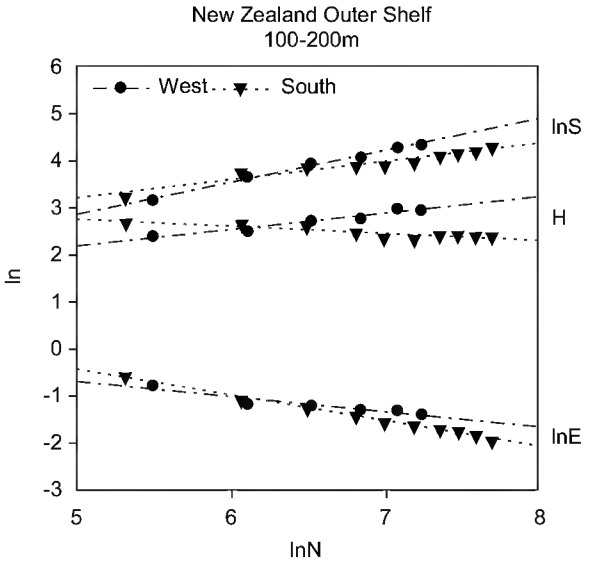

Fig. 7. BDG for outer shelf depths (100–200 m) south and west of New Zealand. Symbols as defined in Fig. 2.

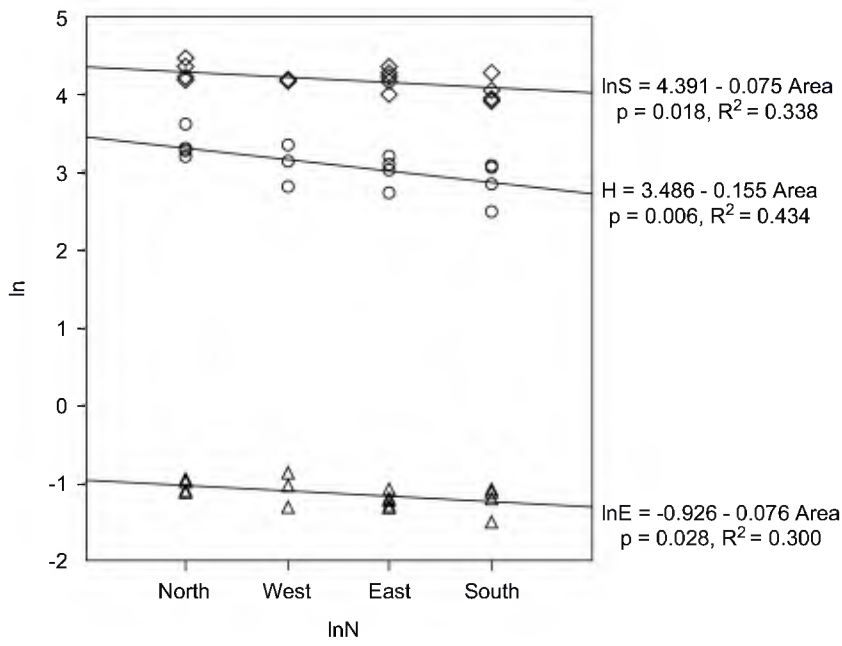

Fig. 6. Regressions of $\ln S$, H and $\ln E$ against areas. All depths included in each area. Values printed on graphs are from regression equations shown on the right of the graph. $\ln S$ and $\ln E$ were converted to numbers for ease of interpretation.

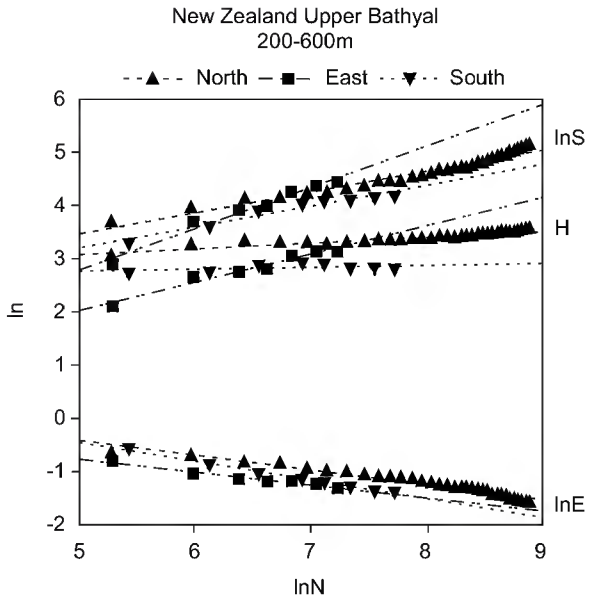

Fig. 8. BDG for upper bathyal (200–600 m) depths north, south and east of New Zealand. Symbols as defined in Fig. 2.

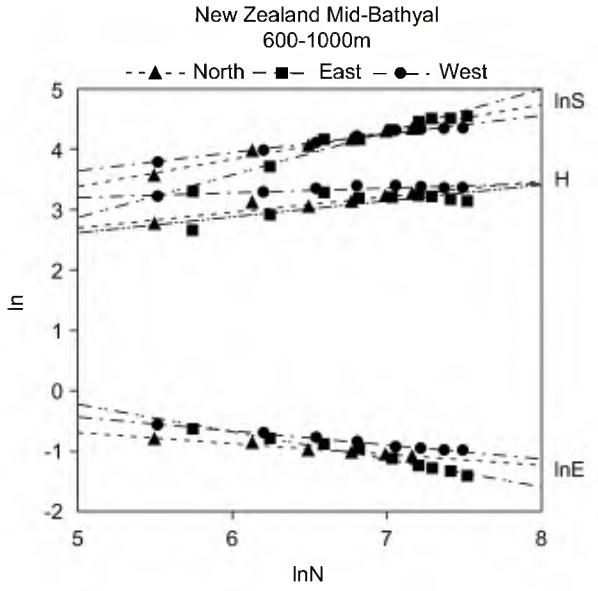

Fig. 9. BDG for mid-bathyal (600–1000 m) depths north, west and east of New Zealand. Symbols as defined in Fig. 2.

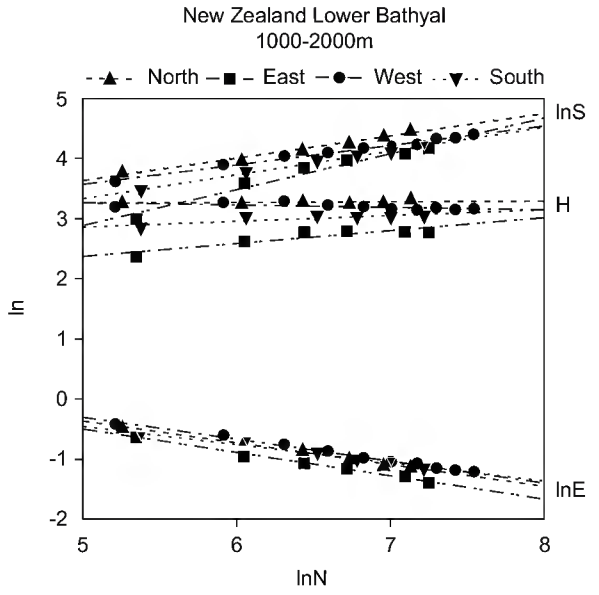

Fig. 10. BDG for lower bathyal (1000–2000 m) depths north, south, west and east of New Zealand. Symbols as defined in Fig. 2.

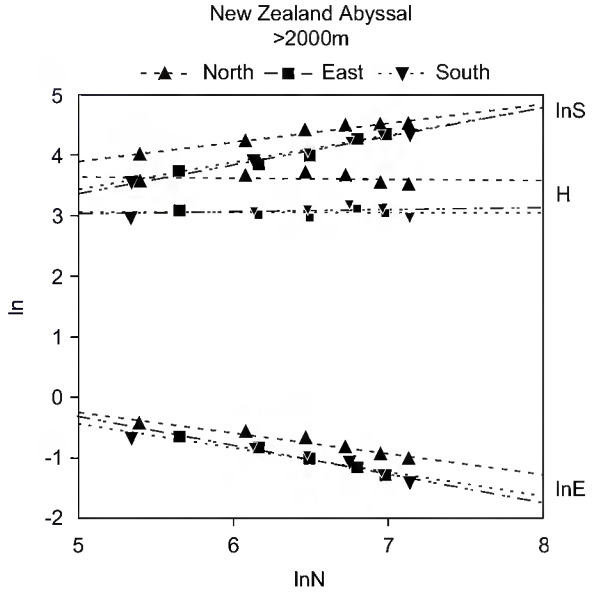

Fig. 11. BDG for abyssal (>2000 m) depths north, south and east of New Zealand. Symbols as defined in Fig. 2.

4. Discussion

Traditional biodiversity analysis examines each sample or station individually. Values for individual samples (a single value of N) then are analyzed for a trend, or several samples will be bundled together by a category such as depth, and the means from the categories will be compared (Ricklefs and Schluter, 1993; Gibson and Buzas, 1973).

Instead of examining diversity values at a single value of N, SHECSI analysis examines the values of $\ln S$, H and $\ln E$ as N accumulates (samples are added together). The results are plotted on a BDG

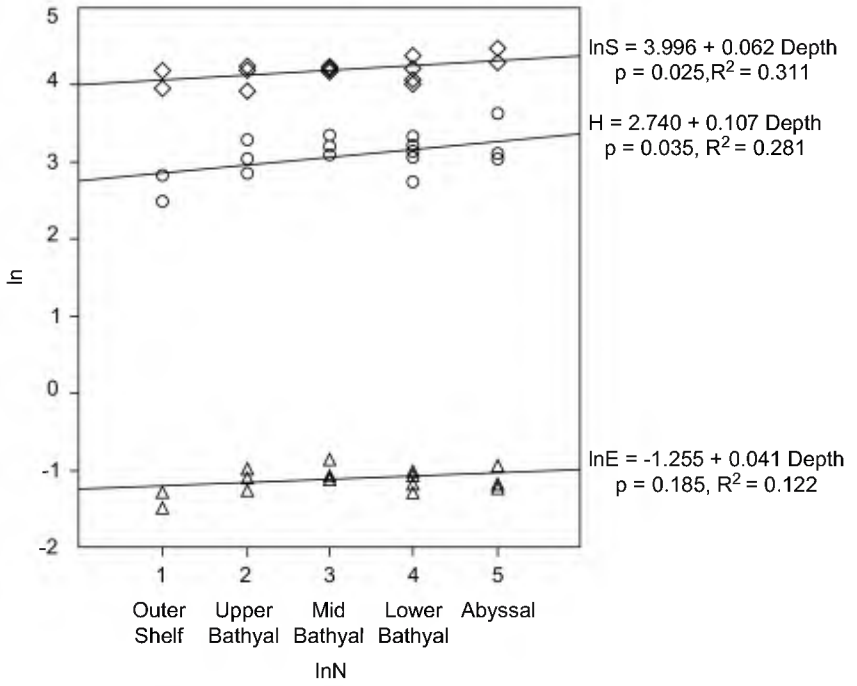

Fig. 12. Regressions of ln S, H and ln E against depths. All areas where data are available are included at each depth. Values printed on graphs are from equations shown on the right of the graph. ln S and ln E were converted to numbers for ease of interpretation.

with ln S, H and ln E on the Y-axis and ln N on the X-axis (Hayek and Buzas, 2006). If we examine just the ln S vs. ln N portion, we have a linear regression analysis often used for rarefaction in species richness studies (Hayek and Buzas, 1997). However, SHECSI also results in linear regression equations for H and ln E. The expected value for H is known for major statistical distributions and the decomposition equation provides the value for ln E. As N accumulates, the observed pattern formed by ln E vs. ln N defines the statistical distribution or community structure. The observed distribution can then be compared to the theoretical. For example, if ln E is constant, then H and ln S must be parallel as they increase with ln N (this is identified as a broken stick distribution). If ln S and ln E have the same value for their slopes but with different signs, then H must be constant (best described as a log series distribution).

SHECSI provides for rarefaction by linear regression of not only ln S, but also for H and ln E. More importantly, however, SHECSI provides a distribution function approach for examining community structure.

Both the traditional analysis of individual samples and SHE methodology indicate a trend over areas and depths around New Zealand. In general, the northern area has the highest values of S, H and E while the southern has the lowest. Thus, the well-known latitudinal diversity gradient with highest values at lower latitudes (Huston, 1994; Rosenzweig, 1995) is also present around New Zealand (Fig. 6), a trend noted by Hayward et al. (2006).

Fig. 12 shows there is also a trend of increasing S and H with depth. This pattern is apparent in the south (Table 1, Fig. 2) and north (Table 2, Fig. 3), but not in the west or east, a trend also noted by Hayward et al. (2006). The changes in S observed with depth in New Zealand are smaller than those observed in the western North Atlantic and Gulf of Mexico (Gibson and Buzas, 1973).

Higher biodiversity values at abyssal depths in the north relative to the other areas (Fig. 11) indicate the latitudinal diversity gradient is present even at depths of greater than 2000 m. This observation is in agreement with those of Gibson and Buzas (1973) and Culver and Buzas (2000) who observed the same phenomenon in the North and South Atlantic as well as in the northeastern Gulf of Mexico.

Because SHE analysis examines community structure dynamically over accumulated values of N, examination of foraminiferal communities well beyond the traditional biodiversity analysis is possible. Let us examine the insights gained.

In the northern area, SHEBI analysis indicates that biofacies or community 1 (Table 2) extends from the mid-shelf to upper bathyal depths an accumulation of $n = 33$ stations. This is the largest accumulation of stations observed thus far by the SHE technique. Cluster analysis in the same area identified 6 associations (Hayward et al., 2006). The changes in the relative abundance of the species with depth are evidently so continuous and small that the entire area can be regarded as adhering to a single statistical distribution or, by our definition, a single community, even though analysis of species composition indicates several associations. Around New Zealand, we identified 16 communities, and none of the others had accumulations of greater than 10 stations. These also are similar to associations determined by cluster analysis.

Because the species richness, S, is a function of the number of individuals, N, most foraminiferal researchers realize that comparisons of species richness requires measurement at a constant N or else rarefaction to a constant value. We have extended this concept to H and $\ln E$ as well and shown how they are all linked by a decomposition equation. Questions regarding comparisons or rank order of S, H or E with depth or area must consider not only the value of N, but also the community structure. At abyssal depths around New Zealand (Fig. 11) H is nearly constant, a log series pattern, so that $\ln S$ and $\ln E$ have equal but opposite slopes. Given this community structure, as the BDG in Fig. 11 shows, S, H and E are always greater in the north regardless of N. On the other hand, at mid-bathyal depths, only the east has a relatively constant value of H (Fig. 9). Consequently, at low values of N a rank order is distinguishable, while at higher values of N ($\ln 7$) values converge. The same pattern exists for the upper bathyal (Fig. 8) and is shown most dramatically on the outer shelf (Fig. 7). On the outer shelf, the southern area has a nearly constant value for H while, in the west, H vs. $\ln N$ has a positive slope. At lower values of N, S, H and E are greater in the south while at higher values of N, they are greater in the west (BDG, Fig. 7). The complexity of these patterns would not be apparent without SHECSI analysis.

The confidence intervals for the regression coefficients of 9, or 56% , of the 16 communities identified around New Zealand, include -1 (Tables 1–4). Because the methodology used here is relatively new, there are no studies to indicate the usefulness of the confidence belts about these values. However, it can be shown that for a log-normal distribution this slope will be closer to -4 or -5 rather than -1 (Hayek et al., 2007). Tables 1–4 show that while the slopes may be smaller or larger than -1, they are closer to -1 than -4 or -5. Most of the SHE evaluations of foraminifera from other areas outside of New Zealand, are from very shallow water where 9 of 12 communities have values close to -1 (see Buzas, 2004, for a review). Clearly, the foraminifera have a propensity for a log series pattern. Figs. 7–11 indicate that in New Zealand the 8 communities deeper than 1000 m (lower bathyal and abyssal) most often have confidence intervals that include -1 (7 of 8 = 88%). Communities from less than 1000 m have 2 of 8, or 25%. The only comparable data from depths greater than 1000 m come from Pleistocene sediments cored in the Arctic (Hayek et al., 2007). In 7 trials of observed communities in these cores all regression slopes were close to or less than -1. While more observations are needed, at present, it appears that benthic foraminifera in general are inclined toward a log series pattern and deep dwelling communities (>1000 m) are almost exclusively so.

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