OCEANIC-SCALE SPECIES DIVERSITY OF LIVING BENTHIC FORAMINIFERA: INSIGHTS INTO NEOGENE DIVERSITY, COMMUNITY STRUCTURE, SPECIES DURATION, AND BIOGEOGRAPHY

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ABSTRACT

Within-habitat (α) diversity of living benthic foraminifera in the Atlantic Basin increases as latitude decreases and generally increases with depth from shelf to abyss. Total populations (live + dead) show the same pattern and indicate that species are become more widespread with increasing water depth. Thus, within-habitat diversity increases with depth while regional (or γ) diversity is greater on the shelf (more communities). Community structure analysis indicates stasis and growth in shallower areas with stasis or decline in the abyss. The latitudinal gradient has existed for ca. 34 Ma; lower latitude deeper habitats have the longest species durations. For living populations an inverse relationship between density and diversity suggests scarcity of food is not sufficient to decrease diversity through extinction. For shallower-dwelling species, variability of solar energy can explain the latitudinal gradient. For deep-sea species, energy transfer from the surface, along with environmental stability over vast expanses, are plausible explanations for high diversity.

INTRODUCTION

Benthic foraminifera are abundant and speciose members of the meiofauna in all marine environments from marshes and bays to abyssal depths and are important in marine ecosystem functioning. Moreover, they have been so for millions of years. Consequently, they are ideally suited to record diversity patterns of modern oceans as well as those of the past.

When an individual of the living benthic foraminiferal population dies or reproduces the empty test is often preserved in the sediment and becomes part of the dead population. Because the dead population is more abundant, the total population (live + dead) usually resembles the dead population. Over time the dead population becomes the fossil population. Researchers, of course, hope that the transition from living to dead to fossil population faithfully records the structure and composition of formerly living foraminiferal communities.

Hessler & Sanders (1967) demonstrated that within-habitat (α) diversity of the macrofauna in the deep-sea was as high as in the shallower depths of the tropics. Buzas & Gibson (1969) also found high within-habitat (α) diversity for the total population of meiofaunal foraminifera at abyssal depths along the Gay Head to Bermuda transect in the North Atlantic. A related finding is that the latitudinal diversity gradient, the trend of increasing diversity with decreasing latitude (Fisher, 1960), is apparent not only on the shelf (e.g., Culver & Buzas, 1998, Dorst & Schönfeld, 2013, Jablonski et al., 2017) but also in certain deep-sea benthic macrofaunal groups (e.g., Rex et al., 1993, 1997) including the benthic foraminifera (Culver & Buzas, 2000, Dorst & Schönfeld, 2013).

The patterns noted above for benthic foraminifera were based on dead or total populations in the Atlantic Ocean basin (Buzas & Gibson, 1969; Culver & Buzas, 2000). The present study examines benthic foraminiferal diversity gradients in the Atlantic Ocean basin, from shelf, slope and abyssal depths, using data sets of living populations (rose Bengal-stained; Walton, 1952) from an extensive compilation by Murray (2015) that was used by Jones & Murray (2017) in their analyses of standing crop (density) of benthic foraminifera on an oceanic scale. If the same patterns are found for the living population as formerly found for the total population, then we can be confident of our diversity assessment throughout the Neogene (Miocene, Pliocene) and Quaternary to the present (e.g., Thomas & Gooday, 1996; Culver & Buzas, 2000).

In this article, we: 1) investigate whether a latitudinal species diversity gradient exists at shelf, slope and abyssal depths for within-habitat living populations of benthic foraminifera; 2) analyze differences in within-habitat diversity over shelf, slope and abyssal depths for the living population; 3) compare the within-habitat diversity patterns exhibited by living and dead or total populations; and 4) integrate these data with previous studies of benthic foraminiferal community structure, species durations and biogeography.

MATERIALS: NATURE AND ACQUISITION OF DATA

This study uses a subset of the data used most recently by Jones & Murray (2017) in their analysis of standing crop (density) values from the Atlantic basin. Jones & Murray (2017) extracted density data from a larger dataset compiled by Murray. This larger dataset was published in full in the electronic supplement to a book (Murray, 2006) and summarized in Murray (2015). This dataset included 2423 samples grouped by study (Murray, 2015) of which 1167 included counts of live specimens for each species encountered. The data from the Murray (2006) supplement (presented as multiple Excel workbooks) were collated into a single species by sample matrix (of count data) using the R programming environment (R Core Team, 2020). Each study encountered different species and in some cases used differing species names, either as a result of taxonomic revision or use of grouped species names (e.g., *Ammonia* group) or various taxonomic qualifiers (e.g., aff., spp., ?). As such, a manual quality control of the species names was undertaken by Murray to ensure that each species was represented by a single name in the final matrix. The cleaned dataset included a total of 1227 distinct "species". Grouped species counts (e.g., unidentified agglutinated), if used, were counted as a single species in analysis, potentially leading to some underestimation of species totals.

The metric chosen for analysis of diversity is the Shannon (1948) information function, because this function includes not only species richness, but also species proportions. Single samples of sediment, each normalized to 10 ml, were analyzed and each is considered to represent a foraminiferal habitat. Consequently, this study is about within-habitat or α diversity and not of regional or γ diversity or between-habitat or β diversity (Whitaker, 1972). For a summary of the geologic, paleoceanographic and paleoclimatic utility of benthic foraminifera, their important role in marine ecosystem functioning, see Gooday et al. (2008), and for detail on the dataset analyzed as part of this paper, see Murray (2015) and Jones & Murray (2017).

The information function (Shannon, 1948) has distributional properties amenable for parametric statistical analysis. This well-known diversity measure is

$$H = - \sum_{i=1}^{S} p_i \ln p_i$$

where p_i is the proportion of the ith species. Reasonable estimates of species richness (S) as well as species proportions (p_i) are required for the calculation of H. In temperate areas about 200 to 500 individuals are required for the species effort curve (plot of accumulated S vs accumulated N) to become asymptotic (Hayek & Buzas, 2010). In tropical shelf areas, the species effort curve shows no sign of abatement even when thousands of individuals are accumulated (Buzas et al., 1977), but a representative estimate of species proportions (p_i) is obtained by using 200 to 400 individuals (Hayek & Buzas, 2010). Consequently, we chose N = 200 as a minimum number of specimens counted in a sample as the criterion for inclusion in this study. Of the 1167 samples in the compiled matrix, 411 met this criterion (Fig. 1).

Like Jones & Murray (2017), we divided the data into the depth categories: 1) shelf, <200 m water depth; 2) slope, 200 to 2000 m water depth; 3) abyss, >2000 m water depth. For examination of latitudinal gradient of within-habitat diversity within each of these depth categories, we performed a linear least squares regression using SYSTAT 13. While the entire data set ranges from high latitudes in both hemispheres (Jones & Murray, 2017), for counts >200 individuals, the data become partially restricted. For shelf data, counts >200 are restricted to stations from the northern hemisphere. For slope data, counts >200 are from stations in both hemispheres. For abyssal data, counts >200 are from stations in the southern hemisphere. For analysis of the diversity data in the three depth categories, the null hypothesis is that the means $\mu_{\text{(shelf)}} = \mu_{\text{(slope)}} = \mu_{\text{(abyss)}}$. To compare means we used the Analysis of Variance (ANOVA). We choose to reject the null hypothesis when $p < 0.05$. Levene's test for homogeneity of variance was applied in each case where relevant and each was non-significant.

Murray (2007) estimated that the number of hard-shelled modern species of benthic foraminifera to be ~3,200 to 4,200. However, this number ignored the many rare species. The

WoRMS database (https://www.marinespecies.org) currently lists 8,953 recognized and named Recent species. Further, Gooday (2019) noted that Murray's estimates do not include the many undescribed, single-chambered, soft-bodied (monothalamous) forms nor the "huge diversity" of unknown phylotypes (Lecroq et al., 2011). Delicate, loosely agglutinated tests are underrepresented in typical samples of benthic foraminifera owing to destruction during sampling and processing (Gooday et al., 1998) and, of course, below the calcium carbonate compensation depth (CCD), hard-shelled populations are dominated by agglutinated species (Gooday et al., 2008). Therefore, the benthic foraminifera investigated in the present study are hard-shelled fossilizable species from, in large part, the continental shelf and slope and the immediately adjacent abyssal plain (above the CCD) of the Atlantic Ocean basin. These are the taxa preserved in the fossil record and, consequently, their patterns of species diversity are of importance for understanding both modern ecosystem (Gooday et al., 1992) and paleoecosystem (Thomas & Gooday, 1996) functioning. The samples utilized in this study are derived from many data sets collected over six decades using several sieve sizes (>63 microns, >106 microns, >125 microns and > 150 microns). Jones & Murray (2017) discussed at length the potential influence of this methodological variation on standing crop. When size-fraction was included in statistical models as a covariate, it was not significant in explaining the standing crop. They concluded that between sample density variation is a result of environmental variation rather than the size-fraction used. Density variation due to the former is orders of magnitude larger than density variation due to the latter.

RESULTS

DIVERSITY PATTERN WITH LATITUDE

For depths < 200 m (continental shelf) in the northern hemisphere 158 samples met the criterion of counts >200 individuals (Table 1). Results of a least squares regression analysis are shown in Table 2. In the 200 – 2000 m depth category (continental slope), 171 samples with N > 200 are distributed over both the northern and southern hemispheres (Table 3). Results of two least squares regression analyses are shown in Tables 4 and 5. For the > 2000 m category (abyssal plain) in the southern hemisphere, 82 samples met the criterion of counts >200 (Table 6). Regression analysis results are shown in Table 7. In all depth zones and hemispheres assessed, there was widespread variability but an overall significant trend of decreasing within-habitat diversity of live foraminiferal populations with increasing latitude (Tables 2, 4, 5 and 7; Fig. 2).

The relationships are not as clear in the southern hemisphere slope (Table 5) and the abyss (Table 7) as in other areas. Mean values for H indicate the shelf (Table 1; Fig. 2) and slope (Table 3; Fig 2) have more variability along the latitudinal gradient than the abyss (Table 6; Fig 2). Difference between maximum and minimum values (the range) of H on the shelf is 2.59 (Table 1), on the slope the range is 1.59 (Table 3) while for the abyss the range is 0.25 (Table 6).

DIVERSITY PATTERN WITH DEPTH

The samples analyzed in this study are arranged into three depth categories - shelf, slope and abyss (Table 8). Figure 3 indicates a significant and striking increase in mean H with depth

(Tables 8, 9) with mean values of H for <200 m, 200 – 2000 m and >2000 m of 1.94, 2.40, and 3.13, respectively).

DISCUSSION

Live, total and fossil populations exhibit the same patterns of within-habitat benthic foraminiferal diversity despite seasonality and relative rarity of live specimens and differences in population density or even presence of individual species in live populations owing to a variety of taphonomic circumstances (Murray, 1982, Mackensen et al., 1990). This characteristic of populations encourages the following discussion where we integrate the new data of this paper with published results of studies based on total and fossil populations. In this way, we can address the relevance and significance of oceanic-scale within-habitat diversity to biogeography, species durations and community structure.

DIVERSITY AND DEPTH

The live foraminiferal data of this paper indicate a significant increase in mean H with depth (Fig. 3). For the same depth categories, Jones & Murray (2017) obtained mean density values of 237.4, 199.3 and 64.2 foraminifera per 10 ml, respectively, for live populations. Different sieve sizes were used by researchers and may have introduced bias into the results. However, as Tables 1 and 6 indicate, most of the shelf sieve sizes were 63 μm and all from the abyss were 125 μm. Consequently, any bias would result in underestimating the difference in values of H between depths. The increase in within-habitat diversity with depth in live populations agrees with the pattern of increasing diversity with depth in total populations from 350 samples ranging in depth from 29 m to 5,001 m and extending from the Arctic to the Gulf of Mexico (Buzas & Gibson, 1969; Gibson & Buzas, 1973). In that survey, maximum values of H occurred in samples from abyssal depths. Culver & Buzas (2000) demonstrated a latitudinal diversity gradient for the total population at abyssal depth in both hemispheres of the Atlantic while Dorst & Schönfeld (2013) noted a similar pattern of diversity increase on the Atlantic shelf and slope off western Europe.

BIOGEOGRAPHY

The number of benthic foraminiferal biogeographic entities, provinces and their component communities, recognized by numerical and statistical analyses decreases with depth. This pattern has been observed in the western Atlantic Margin of North America (Buzas & Culver, 1980), the Gulf of Mexico (Culver & Buzas, 1981), the Pacific continental margin of North America (Buzas & Culver, 1990) and New Zealand (Hayward et al., 2010). This is because deeper-dwelling species are more widespread and, hence, although the within-habitat diversity may be greater in the abyss, the total number of species is smaller than in shallower areas (Buzas et al., 2014).

The widespread distribution of deep-dwelling versus shallow-dwelling species is also supported by molecular studies. Hayward et al. (2021) showed that the three species of the shallow water genus *Ammonia* thought to be world-wide in their distribution actually belong to 60 species each with a limited distribution. In marked contrast, molecular studies on a cosmopolitan abyssal-dwelling species (*Epistominella exigua*) indicate genetic homogeneity across regions of the Arctic, Atlantic, Pacific and Antarctic Oceans (Lecroq et al., 2009). The widespread abyssal species, *Cibicidoides wuellerstorfi*, does, however, exhibit some genetic differentiation between different areas (Burkett et al., 2020).

We noted earlier that shelf diversity data are from the northern hemisphere, abyssal data are from the southern hemisphere and slope data are from both hemispheres. Thus, we can compare hemispheres for the latter data only. The latitudinal diversity gradient is greater in the northern hemisphere (Fig. 2B) than the southern (Fig. 2C). A weaker southern hemisphere latitudinal gradient also characterizes the deep-sea macrofauna, reflecting a higher degree of regional variation in the south (Rex & Etter, 2010).

DURATION OF LATITUDINAL DIVERSITY GRADIENT

The latitudinal gradient in within-habitat diversity that we see today at all ocean depths has a long history. For abyssal depths, Thomas & Gooday (1996) suggested the pattern for increasing diversity with decreasing latitude in benthic foraminifera originated at the Eocene-Oligocene boundary ~34 Ma when the Earth transitioned from “greenhouse” to “ice-house” conditions. Neogene to modern
benthic foraminiferal populations from shelf environments of the temperate Atlantic Coastal Plain and the tropical Central American Isthmus indicate that not only has a latitudinal gradient of diversity (measured by Fisher’s alpha) been present for at least 10 Ma, but also that it has been increasing over time (Buzas et al., 2002a), by 40% at the temperate region and by 106% at the tropical region.

SPECIES DURATION

Species durations of benthic foraminifera (Buzas & Culver, 1984) show the same depth and latitudinal patterns as species diversity. Off the Atlantic coast of North America both partial durations (of living species) and species diversity are greater at lower latitudes and increased water depth: compare 16 Ma for <200 m (shelf) with 26 Ma for >200m (slope and abyss), and compare 7 Ma for <200 m Cape Hatteras to Newfoundland with 20 Ma for <200 m Florida to Cape Hatteras (Buzas & Culver, 1984). Similar patterns of durations and diversity were documented around New Zealand (Hayward et al., 2010)

COMMUNITY STRUCTURE

Also relatable to depth (shelf, slope, abyss) and, hence, diversity, is community structure, defined quantitatively by Buzas & Hayek (2011) and Hayek et al. (2019) as the mathematical statistical distribution fit to the observed relative abundance vector. Consideration of the decomposition equation for species richness, S, evenness, E, and H, plus their respective regressions on the accumulation of the number of individuals, N , leads to the establishment of three structural types of community. The types can be identified by a measure composed of the slope (β_{1H}) of the regression of accumulated H vs N within a community. A positive measure denotes community growth, zero denotes the existence of stasis, and a negative measure denotes the existence of a declining community. Global analysis of 72 communities with living and total populations were surveyed (Buzas & Hayek, 2011). For shelf and slope communities the measure is either mostly + or 0 while in the abyss either 0 or - . The average measure for the shelf is 0.13, slope 0.14 and abyss -0.06 (table 21 in Buzas & Hayek, 2011).

In summary, the variables considered above and their relative values (extracted from the new data of the current study and from related earlier studies on benthic foraminiferal distribution and diversity through time) are shown in the contrast between shallow (<200 m) and deep (> 200 m) categories presented in Table 10. The tabulation demonstrates that shallow and deep dwelling benthic foraminiferal communities are easily discriminated.

EXPLANATIONS FOR OCEANIC-SCALE DIVERSITY PATTERNS OF BENTHIC FORAMINIFERA

Within-habitat diversity is achieved through the interplay of species origination and immigration and species extinction and emigration over time (Buzas & Culver, 1998). To achieve high diversity, a community must maintain a relatively low extinction rate. Species density and the plethora of abiotic and biotic variables that determine its value (Jones & Murray, 2017) are important only as end values. Very low population densities may lead to extinction of species, thereby lowering diversity. Very high densities of organisms may lead to competition among species, and if there is competition among community members for a limited resource, then competitive exclusion demands a reduction in diversity. Relatively low extinction rates, then, suggest low overall ecological extinction from changes in abiotic and biotic variables and low competition among community members to ensure high diversities over time. The time component may require millions of years, fostering longer species durations in high diversity areas (Buzas & Culver, 1984).

Researchers have offered a variety of explanations for observed patterns of the latitudinal and depth diversity gradients (e.g., Pianka, 1966, Rohde, 1992, Rex & Etter, 2010; Jablonski et al., 2017, Gagne et al., 2020), and many of them are not mutually exclusive. Pontarp et al. (2019) have argued that the lack of consensus regarding the underlying causes for a latitudinal diversity gradient is due to the "verbal nature" of hypotheses and the fact that observed patterns can have multiple explanations. They proposed mechanistic linking of eco-evolutionary processes (selection, dispersal, ecological drift, and speciation) to the diversity gradient to better understand the contributions of these processes.

The great variability in values of H with latitude in shallower (< 200 m) areas shown in this study suggests a variety of drivers are likely responsible for individual values. Nevertheless, there is a significant trend of decreasing diversity with increasing latitude. Gagne et al. (2020) modeled global diversity for terrestrial and marine species. Their analysis for marine organisms (44,575 species) indicated maximum diversity in the tropics. Depth, water temperature and sunlight were the principal drivers. Curiously, their data set showed a decrease in diversity with depth, a reflection, perhaps, of the many organisms involved or just a consideration of gamma diversity. We do not consider depth as an environmental variable but, along with latitude and longitude, an attribute that locates a sample in space. It is the change in environmental variables associated with depth that is of primary interest. The variables water temperature and sunlight are reasonable and in accordance with advocates of solar energy or primary production as the principal driver of diversity (e.g., Rohde, 1992). Our data are not extensive enough to address the question of whether there is a decrease in species richness in the marine realm near the equator (Chaudhary et al., 2016; Woolley at al., 2016) or whether this is due to a knowledge gap (Menegotto & Rangel, 2018).

While Jones & Murray (2017) found an overall positive relationship between benthic foraminiferal density and particulate organic carbon (POC), on the shelf it was negative, prompting them to suggest predation not food was limiting density on the shelf. If predation on foraminifera (Culver & Lipps, 2003) affects all members of the community equally then, effectively, it limits density so that there is no species competition among community members. The lack of competition as judged by foraminiferal species with a community reacting in concert (pulsating patches) in shallow water was noted by Buzas et al. (2002b). However, for a latitudinal gradient, predation would have to be more severe at high latitudes to obtain the observed pattern. The presence of the gradient on the slope and in the abyss suggests a “trickle-down” ecologic economy where shallower vicissitudes are transferred to the deep ocean. The decreasing difference between maximum and minimum values of H from shelf to slope to abyss support this idea. The suggestion that the larger variability of environmental variables at the higher latitudes (particularly particulate organic matter flux to the sea floor) is responsible for the pattern is attractive (Hessler & Sanders, 1967; Thomas & Gooday, 1996; Rex & Etter, 2010; Cordier et al., 2022). Relative lack of variability explains why diversity is high in shallow tropical settings and nearly uniformly high in the abyss.

Numerous authors of research on benthic foraminifera (e.g., Gooday, 1988; Jorissen et al., 1995; Schmiedl et al., 1997), and on deep-sea communities in general (e.g., Smith et al., 2008), agree that food is an important limiting variable in the deep-sea (Buessler et al., 2007).). As might be expected, the density of foraminifera in the deep-sea is much lower than on the shelf and slope (Jones & Murray, 2017). Although we hypothesized that predation reduced densities so that competition was not important in shallower waters, the greater reduction of abyssal densities is evidently still not great enough to cause extinction (but see below the mid-

Pleistocene extinction event of elongate benthic species; Hayward et al., 2012). The low abyssal densities have not resulted in competition for food. Perhaps, the inputs from the surface water are so irregular in time and space (Gooday, 1988) that no one community member can have an advantage, allowing many species to cohabit within a community. However, recall that the status of abyssal community structures is at stasis or in decline so that abyssal communities are continually on the brink of extinction. The long species durations of abyssal communities, however, indicate extinctions are rare (background rate of ~2% myr^1 during the Cenozoic in benthic foraminifera; Hayward et al., 2012) but extinction events occur. For example, the extinction event in the abyssal foraminiferal biota at the Paleocene-Eocene Thermal Maximum (PETM), at 55.5 Ma (Bowen et al., 2015) was accompanied by a negative value signifying a declining community (Hayek et al., 2019). The extinction of many elongate benthic species (25% loss of deep-sea benthic diversity) in the late Pliocene to middle Pleistocene, mostly between 1.2 and 0.55 myrs ago, was likely caused by decrease of specific phytoplankton food flux during global cooling leading up to the mid-Pleistocene Climate Transition (Hayward et al., 2012). Foraminiferal species confined to the abyss have long species durations and many abyssal species are also distributed on the slope suggesting migration into the abyss from shallower depths (Hayward et al., 2010; Buzas et al., 2014). Such migration occurs with the macrofauna (Rex et al., 2005) and at shallower depths with the foraminifera (Buzas & Culver, 2009).

CONCLUSIONS

New data on shelf, slope and abyssal living benthic foraminifera in the Atlantic Ocean basin demonstrate a latitudinal gradient of within-habitat diversity with increase toward lower latitudes in all depth categories and an increase in diversity with depth regardless of latitude. Similar patterns are seen for dead and total (live plus dead) foraminiferal populations allowing integration of the new data with diversity, community structure, species duration, and biogeographic patterns of Neogene fossil benthic foraminifera. Surprisingly, while density at abyssal depths decreases owing to decreased food supply compared to the shelf and slope, within-habitat diversity is not affected and is high in the abyss.

ACKNOWLEDGEMENTS

We acknowledge the many authors who provided data to Professor John W. Murray. Dave Mallinson, Seth Sutton and Laura de Sousa kindly provided technical support. Reviews by Andrew Gooday and Bruce Hayward were very useful and much appreciated. This work was supported by the NERC National Capability funding to the National Oceanography Centre, as part of the Climate Linked Atlantic Section Science (CLASS) program (Grant Reference NE/R015953/1).

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TABLE CAPTIONS

TABLE 1. Foraminifera diversity (H) data for the shelf, <200 m depth. Note four cases include data from two publications. N = number of samples; H = Shannon's information function; S.D. = standard deviation.

TABLE 2. Results of regression on H vs latitude for <200 m depth.

TABLE 3. Foraminiferal diversity (H) data for the slope, 200 – 2000 m depth. N = number of samples; H = Shannon's information function; S.D. = standard deviation

TABLE 4. Results of regression on H vs latitude on the northern hemisphere slope, 200–2000 m depth.

TABLE 5. Results of regression on H vs latitude on the southern hemisphere slope, 200–2000 m depth.

TABLE 6. Foraminiferal diversity (H) data for the abyss, >2000 m depth. N = number of samples; H = Shannon's information function; S.D. = standard deviation.

TABLE 7. Results of regression of H vs latitude on the abyss, >2000 m depth.

TABLE 8. Mean values of H and standard deviations for samples at three depth categories. N = number of samples.

TABLE 9. Results of one-way ANOVA on depth categories: shelf, slope, abyss.

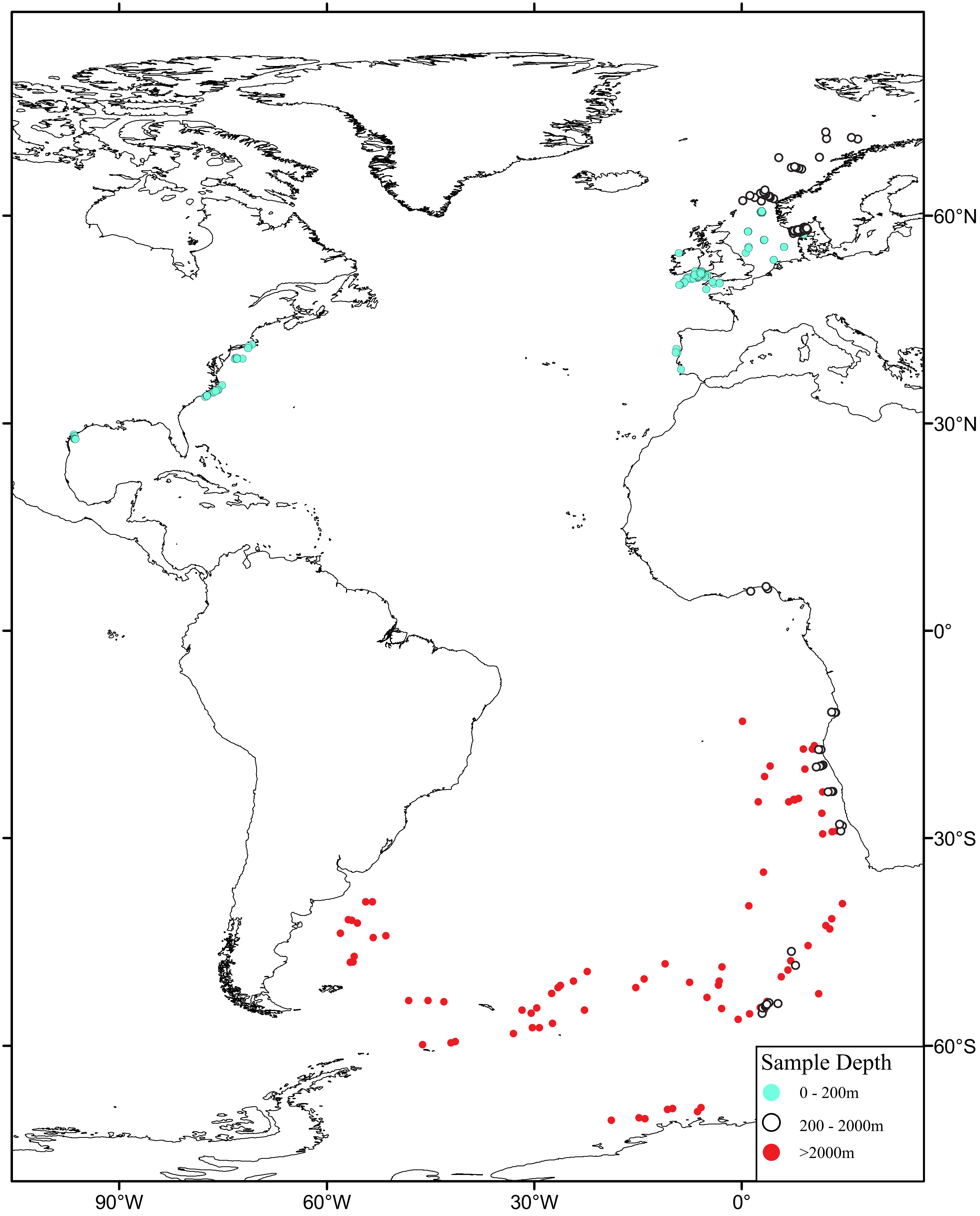
TABLE 10. Contrast of benthic foraminiferal diversity variables with depth: shallow = <200 m; deep = >200 m).

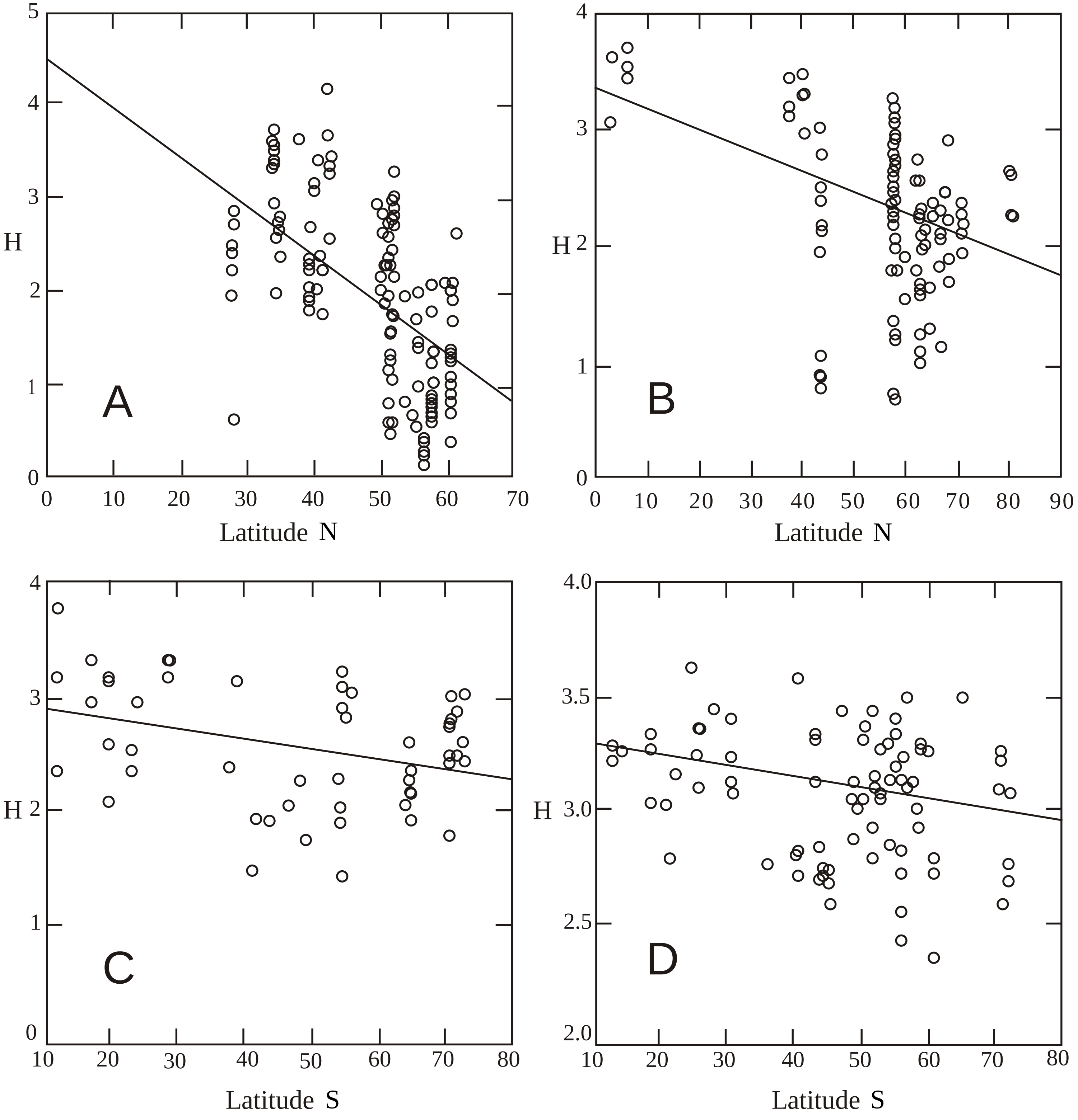
FIGURE CAPTIONS

FIGURE 1. Location of 411 samples (selected from 1167 used by Jones and Murray, 2017, in their study of foraminiferal density) with >200 individuals that were used for an examination of diversity using the information function (H). Modified from Jones and Murray (2017).

FIGURE 2. A, Plot of H versus northern degrees of latitude for shelf samples (<200 m). B, Plot of H versus northern degrees of latitude for slope samples (200–2000 m). C, Plot of H versus southern degrees of latitude for slope samples (200–2000 m). D, Plot of H versus southern degrees of latitude for abyssal samples (>2000 m).

FIGURE 3. Plot of mean H versus depth, 1.0 = shelf (<200 m), 2.0 = slope (200–2000 m), 3.0 = abyss (>2000 m).


60°N
30°N
0°
30°S
60°S
90°W
60°W
30°W
0°
Sample Depth
0 - 200m
200 - 2000m
>2000m


A
H
0
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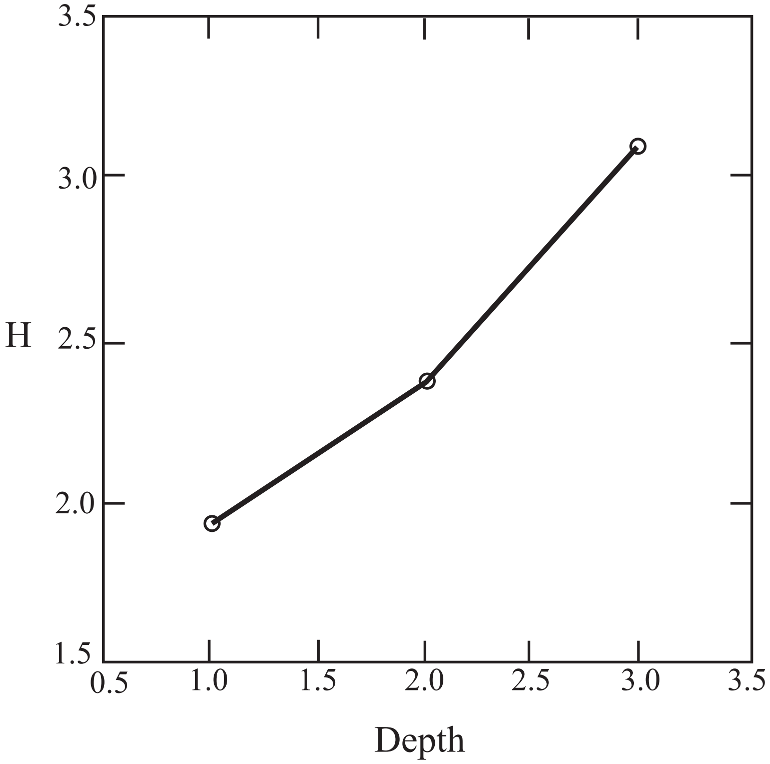
3.5
3.0
H
2.5
2.0
1.5
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Depth

Author	**Locality**	**Latitude**	**N**	**Mean H**	**S.D.**
1. Mackensen et al. 1985	Norwegian Sea	60 °N	17	1.24	0.484
2. Alve and Murray 1995	Skagerrak	52 °N	5	1.48	0.483
3. Murray 1985	North Sea	52 to 57 °N	29	0.88	0.457
4. Murray 1979 Scott et al. 2003	Celtic Sea	52 °N	50	2.02	0.734
5. Murray 1979	English Channel	50 °N	9	2.28	0.526
6. Diz et al. 2004 Seiler 1975	Spain, Portugal	42 to 48 °N	11	3.34	0.57
7. Murray 1969 Poag et al. 1980	East USA	39 to 41 °N	14	2.19	0.258
8. Murray 1969	Cape Hatteras	35 °N	6	2.52	0.258
9. Lueck and Snyder Murosky and Snyder 1994	North Carolina	34 °N	10	3.44	0.098
10. Phleger 1956	Gulf of Mexico	28 °N	7	2.18	0.318

Sieve size (µm)
125
63
63
63
63
63
63
63
63
63

Effect	**Coefficient**	**Standard error**	**R^2**
Constant	4.442	0.309	0.304
Latitude	-0.051	0.0006	

Analysis of Variance

Source	**N**	**SS**	**df**	**MS**	**F**	**p**
Regression	158	41.196	1	41.196	68.293	0.000
Residual		94.102	156	0.603		

Author	Locality	Latitude	N	Mean H	S.D.
1. Ahrens et al. 1997	Greenland	80 °N	6	2.54	0.185
2. Mackensen et al. 1985	Norwegian Sea	62 to 71 °N	39	2	0.441
3. Alve and Murray 1995	Skaggerak	52 to 58 °N	50	2.45	0.57
4. Hess and Jorissen 2009	Biscay	43 to 44 °N	11	1.89	0.812
5. Seiler 1975	Portugal	32 to 40 °N	8	3.26	0.162
6. Schiebel 1992	Gulf of Guinea	3 to 5 °N	5	3.48	0.248
7. Schmiedl et al. 1997	East S. Atlantic	11 to 29 °S	15	2.93	0.475
8. Harloff and Mackensen 1997	Argentine Basin	37 to 49 °S	6	2.17	0.645
9. Mackensen et al. 1993	South Atlantic	46 to 55 °S	11	2.47	0.594
10. Murray and Pudsey 2004	Larsen Shelf	64 °S	8	2.26	0.209
11. Mackensen et al. 1990	Weddell Sea	70 to 72 °S	12	2.66	0.341

Sieve size (μm)
63
125
63
150
63
63
125
125
125
63
125

Effect	**Coefficient**	**Standard error**	**R^2**
Constant	3.335	0.228	0.114
Latitude	-0.017	0.0004	

Analysis of Variance

Source	**N**	**SS**	**df**	**MS**	**F**	**p**
Regression	119	7.39	1	7.39	14.599	0.000
Residual		43.831	117	0.375		

Effect	**Coefficient**	**Standard error**	**R^2**
Constant	2.931	0.183	0.082
Latitude	-0.007	0.004	

Analysis of Variance

Source	**N**	**SS**	**df**	**MS**	**F**	**p**
Regression	52	1.173	1	1.174	4.44	0.039
Residual		43.831	117	0.375		

Author	Locality	Latitude	N	Mean H	S.D.
1. Schmiedl et al. 1997	East S. Atlantic	11 to 29 °S	19	3.27	0.183
2. Harloff and Mackensen 1997	Argentine Sea	39 to 48 °S	11	3.03	0.311
3. Mackensen et al. 1993	S. Atlantic	35 to 55 °S	28	3.07	0.248
4. Harloff and Mackensen 1997	Scotia Sea	50 to 57 °S	17	3.16	0.329
5. Mackensen et al. 1990	Weddell Sea	69 to 70 °S	7	3.02	0.268

Sieve size (µm)
125
125
125
125
125

Effect	**Coefficient**	**Standard error**	**R^2**
Constant	3.313	0.093	0.052
Latitude	-0.004	0.002	

Analysis of Variance

Source	**N**	**SS**	**df**	**MS**	**F**	**p**
Regression	82	0.317	1	0.317	4.41	0.039
Residual		5.753	80	0.072		

Area	Depth	N	Mean H	S.D.
Shelf	<200 m	158	1.94	0.928
Slope	200–2000 m	180	2.4	0.636
Abyss	>2000 m	82	3.13	0.274

Source	**N**	**SS**	**df**	**MS**	**F**	**p**
H	420	76.589	2	38.294	74.719	0.000
Error		213.716	417	0.513		

Variable	**Shallow**	**Deep**
Density	high	low
Diversity with increasing latitude	decrease	decrease
Diversity with depth	low	high
Species distribution	narrow	widespread
Communities	many	few
Community structure	stasis, positive	stasis, negative
Species duration	low	high
Duration of current latitudinal gradient	at least 10 Ma	34 Ma