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LETTER

Species–energy relationship in the deep sea: a test using the Quaternary fossil record

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Abstract

Little is known about the processes regulating species richness in deep-sea communities. Here we take advantage of natural experiments involving climate change to test whether predictions of the species–energy hypothesis hold in the deep sea. In addition, we test for the relationship between temperature and species richness predicted by a recent model based on biochemical kinetics of metabolism. Using the deep-sea fossil record of benthic foraminifera and statistical meta-analyses of temperature-richness and productivity-richness relationships in 10 deep-sea cores, we show that temperature but not productivity is a significant predictor of species richness over the past *c.* 130 000 years. Our results not only show that the temperature-richness relationship in the deep-sea is remarkably similar to that found in terrestrial and shallow marine habitats, but also that species richness tracks temperature change over geological time, at least on scales of *c.* 100 000 years. Thus, predicting biotic response to global climate change in the deep sea would require better understanding of how temperature regulates the occurrences and geographical ranges of species.

Keywords

Deep sea, foraminifera, Quaternary, species–energy.

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INTRODUCTION

The deep-sea represents the most extensive ecosystem on Earth, with a remarkably high species richness (Levin *et al.* 2001; Snelgrove & Smith 2002) but the processes that generate and maintain this diversity remain very poorly understood (Levin *et al.* 2001). Among the ecological hypotheses proposed to explain global variation in species richness, the species–energy hypothesis has emerged as a leading contender (Hawkins *et al.* 2003; Willig *et al.* 2003). According to this hypothesis, species richness of a region is a function of the total or average amount of energy available, and thus a positive correlation is expected between richness and climate-related variables such as temperature. The energy-richness relationship has been investigated for a number of terrestrial and shallow marine organisms, ranging from trees to coral reefs (Fraser & Currie 1996; Roy *et al.* 1998; Hawkins *et al.* 2003), but remains very poorly known for deep-sea organisms.

Although general correlations between energy-related variables and large-scale patterns of species richness are becoming well documented (Hawkins *et al.* 2003), considerable uncertainty remains as to how available energy can be translated into species richness (Currie *et al.* 2004). Energy could regulate patterns of local or regional species richness thorough either ecological or evolutionary processes. Ecological regulation of richness results largely through the effects of climate on spatial occurrences of existing species. How species are distributed across environmental gradients could reflect physiological tolerances of species (Lennon *et al.* 2000) or potentially could be a consequence of changes in the total number of individuals as energy availability changes (the 'more individuals' hypothesis, Hutchinson 1959; Currie *et al.* 2004). Evolutionary regulation is primarily a consequence of climatic influences on regional speciation and/or extinction rates (Rohde 1992; Flessa & Jablonski 1996).

Although the species–energy hypothesis predicts a positive correlation between available energy and species richness, it does not specify the slope of this relationship. A more recent model that makes a specific prediction about how ambient temperature should relate to species richness was developed in the context of the metabolic theory of ecology (Allen *et al.* 2002; Brown *et al.* 2004). This model uses the temperature dependence of metabolism to predict that the natural logarithm of ectotherm species richness should be linearly related to 1000 divided by temperature (in Kelvin) with a slope of − 9 (Allen *et al.* 2002). Thus, this model invoked metabolism as an important regulator of patterns of species diversity. However, the model does not specify the mechanism(s) underlying the predicted relationship. Evolutionary processes such as temperature dependence of speciation rates could potentially be important here (Allen *et al.* 2002; Currie *et al.* 2004) but speciation and/or extinction rates are not directly included in this model and so it cannot make quantitative predictions about how climate would influence evolutionary rates. Alternatively, the slope predicted by the Allen *et al.* (2002) model could result from ecological processes such as the influence of temperature on interactions between species (Allen *et al.* 2003; Storch 2003).

Spatial patterns of species richness observed today are the result of a variety of processes operating over different spatial and temporal scales, and separating the evolutionary effects from ecological/biogeographical dynamics remains a difficult problem. In particular, whether correlations between present day climatic variables and species richness are sufficient to demonstrate that current environmental factors are the main determinants of species richness of a region remains a subject of debate (Francis & Currie 1998, 2003; Qian & Ricklefs 2004; Ricklefs 2004). Alternatively, regional speciation and extinction dynamics could be the primary determinants of present day species richness gradients and the correlation with 'current' climatic variables may not necessarily reflect causality (Ricklefs 2004).

The deep-sea fossil record is characterized by generally continuous sedimentation, excellent chronology, and multitude of paleoceanographic proxies that allow for a detailed reconstruction of environmental and biotic history. Thus, this system is ideal for not only estimating how climate influences patterns of regional species richness, but also allows us to separate the influences of speciation/extinction dynamics from biogeographical controls. Here we take advantage of natural experiments involving climatic changes during the late Quaternary to test whether energy availability can predict species richness in the absence of strong evolutionary effects. In particular, using the fossil record of benthic foraminifera over the last 130 000 years, we explore the roles of temperature and productivity in determining species richness in the deep-sea. Because the duration of our study interval is very short relative to turnover rates of benthic foraminifera species (average duration of deep-sea benthic foraminiferal species is *c.* 20 million years, Douglas & Woodruff 1981), originations and extinctions have little or no effect on variation in species richness within this time span. Consequently, for this interval we can exclude evolution as a significant source of variation in species richness and are able to test whether changes in temperature and productivity lead to predictable changes in species richness primarily because of shifts in the distributions of species. In addition, these data allow us to test the predictions of the Allen *et al.* (2002) model over a much larger temporal span than previously attempted.

METHODS

We tested the relationship between temperature, productivity and species richness using published data from 10 deep-sea cores covering the last 130 000 years from both the Atlantic and the Pacific oceans. For each core sample, we obtained estimates of species richness and productivity, and inferred temperature by correlation to published bottom-water temperature curves. Then, analysing each core separately, we tested if species richness was predicted by temperature and/or productivity using multiple regression with generalized least squares (GLS) to account for temporal autocorrelation among samples. Finally, we summarized the overall relationship between temperature, productivity and species richness across all cores using a statistical meta-analysis of the multiple regression coefficients. Each of these steps is described in the following paragraphs.

We included cores from published studies that met the following criteria: (i) the numbers of species and individuals were reported for each sample, (ii) a reliable age model was provided, (iii) the core included samples within the interval 0 to 130 000 years ago, (iv) benthic foraminifera accumulation rate (BFAR), a proxy for productivity, was presented in a table or figure, and (v) the core location is currently situated in a deep-water mass. Because sustained ice cover may affect deep-water temperature (Bauch & Bauch 2001), we excluded cores likely to be under permanent sea ice during the last glacial maximum according to recent reconstructions (Sarnthein *et al.* 2003). The 10 cores that met these requirements are listed in Table 1.

In measuring species richness, raw data were generally not available to sample-standardize through rarefaction; instead we examined species richness as a function of sample size. We determined for each core the minimum sample size beyond which richness is nearly constant and omitted all samples with fewer than this number of individuals (usually *c.* 200). For two of the cores (cores 1 and 7 from Table 1), sample sizes were not given but the authors reported that samples came from the flat portion of the sampling curve ($n > 300$).

We used BFAR as a measure of productivity. This commonly used proxy has been shown to correlate with organic carbon flux to the sea floor in the modern ocean

Table 1 Ten deep-sea cores with benthic foraminifera assemblage data used in the present study

No.	Core	Reference	Ocean	Latitude	Longitude	Temp curve	Depth (m)	Sieve (μ)
1	M234414	Nees (1997)	North Atlantic	53.5 N	20.3 W	1	2201	125
2	DS97-2P	Rasmussen *et al.* (2002)	North Atlantic	58.9 N	30.4 W	1	1685	106
3	geoB1214	Schmiedl & Mackensen (1997)	South Atlantic	24.7 S	7.2 E	2	3210	125
4	geoB1710	Schmiedl & Mackensen (1997)	South Atlantic	23.4 S	11.7 E	2	2987	125
5	NP-36	Ujiié (2003)	Northwest Pacific	34.2 N	179.3 E	3	2664	73
6	NGC-102	Ohkushi *et al.* (2000)	Northwest Pacific	32.3 N	157.9 E	3	2612	75
7	MD88-779	Nees *et al.* (1999)	Southwest Pacific	47.8 S	146.5 E	3	2260	150
8	ERDC-112	Burke *et al.* (1993)	West Pacific	1.6 S	159.2 E	3	2169	250
9	BOFS-5K	Thomas *et al.* (1995)	North Atlantic	50.7 N	21.9 W	1	3547	63
10	BOFS-14K	Thomas *et al.* (1995)	North Atlantic	58.6 N	19.4 W	1	1756	63

'Temp curve' indicates which temperature curve from Table 2 was used to infer temperature in each core. 'Depth' is present day water depth, in meters. 'Sieve' refers to the sieve size (in microns) used to process the core samples.

(Herguera 2000). BFAR measures the number of benthic foraminifera deposited per cm^2 of ocean floor per thousand years, and is calculated as the product of the number of benthic foraminifera per gram of sediment, the sediment bulk dry density, and the linear sedimentation rate. For core 8 in Table 1, bulk dry densities were not reported and were assumed to be constant at a typical value for deep-sea carbonate (0.75 g cm^{-3}). All BFAR values were raised to the 0.64 power because a recent calibration study (Herguera 2000) found that the organic carbon flux to the sea floor was proportional to $BFAR^{0.64}$. Because BFAR calculations include an estimate of sedimentation rate, it can be affected by errors in a core's age model. However, using the number of benthic foraminifera per gram as an alternative productivity proxy yields similar results in the seven cores for which this information is available, suggesting that chronostratigraphic errors have little effect on our analysis.

Benthic foraminifera accumulation rate differs from other metrics of biological production in that it measures the rate at which consumers (benthic foraminifera), rather than producers accumulate biomass. In the deep-sea, there is no *in situ* primary production (with the exception of chemosynthesis in hydrothermal vent communities); the closest equivalent is organic carbon flux from productive shallower waters to the seafloor. BFAR is useful not only because it correlates with this organic carbon flux (Herguera 2000), but also because it increases with the number of individual benthic foraminifera and therefore is relevant for the 'more individuals' hypothesis linking productivity and richness (see Currie *et al.* 2004).

We tracked deep-sea temperature over the past 130 000 years using published data based on magnesium–calcium (Mg/Ca) paleothermometry, which has become an increasingly important temperature proxy in paleoceanographic studies (Dwyer *et al.* 1995; Martin *et al.* 2002; Archer *et al.* 2004). Because all deep ocean waters ultimately derive from density-driven sinking of very cold water in polar regions, bottom-water temperatures throughout the deep-sea are determined by the temperature of surface waters at these sites of deep water formation (Zachos *et al.* 2001). As changing climate raises or lowers surface water temperature at these high-latitude sites, these changes are propagated at depth through the global ocean circulation system. Consequently, temperature in the deep-sea is a relatively simple system that is much less affected by seasonal, latitudinal and geographical sources of variation that are so prominent in terrestrial and shallow marine ecosystems (Lear *et al.* 2000).

Published bottom-water temperature curves were available for three widely spaced late Quaternary deep-sea cores (Cronin *et al.* 2000; Martin *et al.* 2002) (Table 2). We smoothed each temperature curve using a cubic spline with the degree of smoothing determined by leave-one-out cross-validation (Härdle 1990). The spline was used to filter out noise and short-term variability, and also to estimate temperature for any time interval based on the predicted value of the spline function. Despite the thousands of

Table 2 Three cores with published bottom-water temperature curves based on Mg/Ca thermometry

No.	Core	Ocean	Latitude	Longitude	Depth (m)	Reference
1	Chain 82-24	North Atlantic	41.7 N	32.9 W	3427	Cronin *et al.* (2000)
2	M16772	Atlantic	1.4 S	12.0 W	3912	Martin *et al.* (2002)
3	TR163-31P	East Pacific	3.6 S	84.0 W	3205	Martin *et al.* (2002)

kilometres separating these cores and analytical differences in the methods used to estimate temperature, the three temperature curves are quite concordant over the past 130 000 years. Pair-wise correlations of splines interpolated every thousand years ranged from 0.52 to 0.82, supporting the notion that temperature changes in the deep-sea are largely global in extent, at least during the late Quaternary.

Taking advantage of the nearly global nature of the deep-sea temperature signal, we matched each of the 10 cores with faunal data with its geographically nearest temperature curve (Table 1). The geographically matched temperature curve was used to estimate the temperature of each faunal sample on the basis of the faunal sample's age (by interpolating the temperature spline function). Our results are not sensitive to exactly which core with temperature data is matched to each core with faunal data; the three temperature curves are similar enough that our results are qualitatively unchanged if any one of them is used as the sole reference for all the faunal assemblages.

Within each core, we used temperature (T) and productivity (P) to jointly predict species richness (S) in a multiple regression ($S \sim P + T$). Because each core was analysed separately, we needed to assume that a consistent taxonomy was applied within, but not necessarily across, studies. In estimating the multiple regression coefficients, we used the following procedure to account for temporal autocorrelation among samples within a core (i) we estimated the multiple regression of richness on temperature and productivity using ordinary least squares; (ii) we then fit a set of autoregressive (AR) time series models (Box *et al.* 1994), of order one to five, to the residuals from ordinary least-squares regression; (iii) we chose the best AR model according to the Akaike Information Criterion; best-fit models ranged from first to third order; (iv) finally, we used GLS to estimate the same multiple regression, using the best-fit AR model to determine the expected correlation structure among residuals.

While multiple regression was used to assess the relationship between richness and energy variables considered jointly, we estimated the slope of the bivariate relationship between log-richness and $1000/T_k$ using reduced major axis regression. This method is preferred over least-squares when both variables are measured with non-negligible error (Sokal & Rohlf 1995). Nonparametric bootstrapping was used to calculate the standard error of reduced major axis slopes.

We undertook a statistical meta-analysis to summarize the overall effects of temperature and productivity on species richness. The meta-analysis allows us to compute an overall estimate (with standard error) of the multiple regression coefficients for temperature and productivity across all cores. Because of significant heterogeneity among the cores, we considered the cores to be a random rather than fixed effect, an approach that appropriately accounts for variation among cores in determining confidence intervals (CI) of summary estimates (Lipsey & Wilson 2001).

In order to explore the degree to which temperature and productivity variation were coupled over the past 130 000 years, we measured the product moment correlation between the two variables in each core and used a Wilcoxon signed rank test to determine if the median of these correlation coefficients differed from zero. To test if richness-energy relationships were influenced by the size fraction of benthic foraminifera studied, we regressed the multiple regression coefficients (weighted by the reciprocal of their sampling variance, Lipsey & Wilson 2001) against the sieve size used in each study.

RESULTS

The results of the meta-analysis provide strong statistical support for an overall significantly positive correlation between temperature and species richness in deep-sea foraminifera, although the nature and strength of the relationship varies considerably among cores (Figs 1 and 2a). Richness and temperature are positively related in seven of the 10 cores, four of which are statistically significant ($P < 0.05$). In contrast, none of the three negative richness-temperature relationships are significant (Fig. 2a, Table 3). We find similar variation among cores in terms of the productivity-richness relationship but, in contrast to temperature, the overall effect is negative and non-significant. Cores are nearly evenly split in terms of the direction of the relationship between richness and productivity: six cores show a positive relationship, one of which is significant, and four cores show a negative relationship, two of which are significant (Fig. 2b, Table 3).

The summary estimate of the slope of log-richness vs. $1000/T_k$ in our data (−10.69) is close to the value of −9 predicted by the Allen *et al.* model (Fig. 2c). However, there is considerable variation in slope among cores leading to a large CI, and the summary estimate is particularly influenced by one core with a large positive slope (Fig. 2c; core 9 in Table 3). Omission of this particular core shifts the summary estimate to −14.82, with a 95% CI of (−18.9 and −10.75). This slope does not quite overlap the theoretical prediction of −9 but the CI overlaps the range found in other empirical tests of this model (Brown *et al.* 2003).

Our results are unchanged if, instead of using AR models, we model temporal autocorrelation using moving average, mixed AR/moving average, or continuous time AR processes (Box *et al.* 1994). In addition, no substantial differences are observed if we transform the temperature and richness to match the predictions of the Allen *et al.* (2002) model ($\ln[S] \sim 1000/T_k + P$ or $\ln[S] \sim 1000/T_k + \ln[P]$).

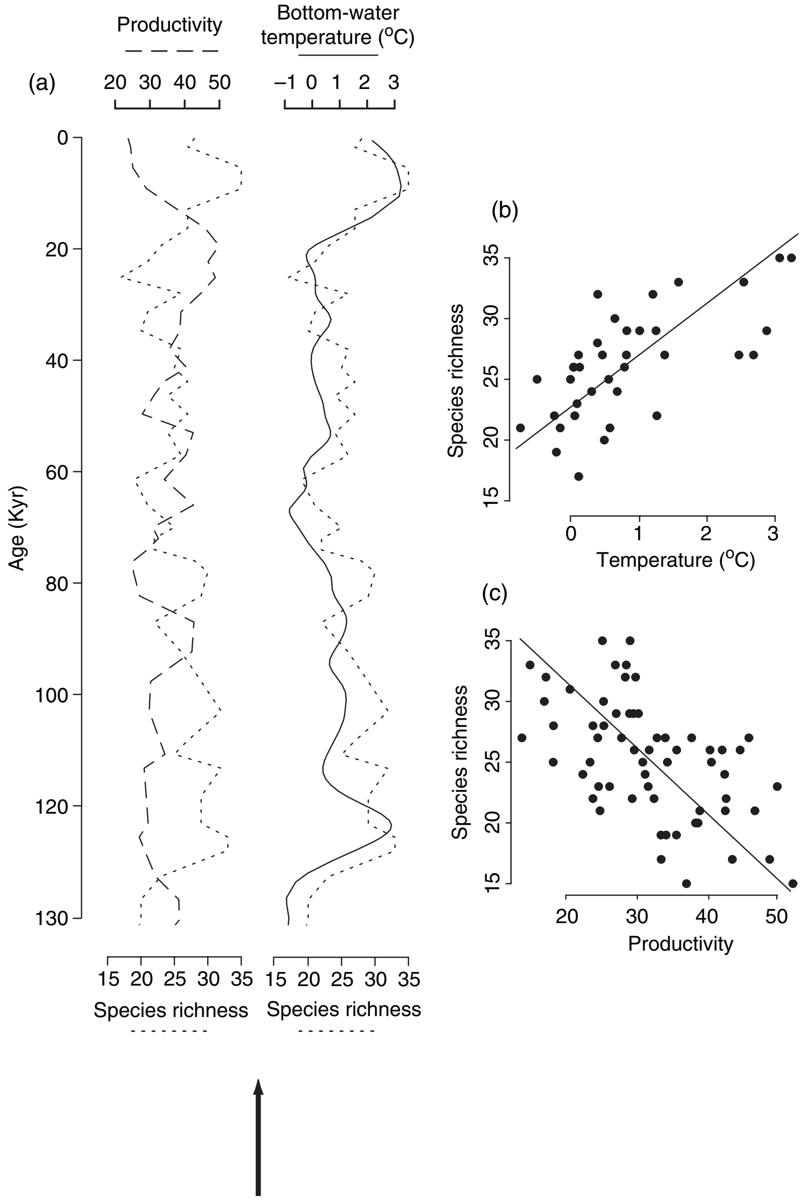

Figure 1 Temperature, species richness and productivity records for one core from the South Atlantic Ocean (core 4 in Table 1). (a) Downcore variation in species richness plotted with a smoothed temperature curve and productivity as measured as the benthic foraminifera accumulation rate. Vertical axis shows sample ages in thousands of years; see text for details. Species richness as a function of temperature (b) and productivity (c). Lines indicate the reduced major axis for each bivariate plot.

Finally, the effects of temperature and productivity on species richness are not altered if the number of individuals in each sample (n) is added as a third predictor variable to the multiple regression ($S \sim P + T + n$), suggesting that variation in sample size is not spuriously affecting our results.

Temperature and productivity variation were not tightly coupled over the last 130 000 years in the cores we analysed. The correlation coefficient between these variables ranged from −0.68 to 0.77, with a median (−0.15) that is not significantly different from zero ($P = 0.49$).

The effects of temperature on species richness varied significantly with sieve size; those cores processed with larger sieves tended to have higher (positive) temperature coefficients ($P = 0.04$). In contrast, sieve size had no significant effect on the relationship between productivity and species richness ($P = 0.35$).

DISCUSSION

Our findings show that overall, changes in temperature lead to predictable and significant changes in the species richness of deep-sea benthic foraminifera, suggesting that temperature has a major causal influence on the number of species present in an area. As far as mechanisms relating deep-sea temperatures to species richness are concerned, we can rule

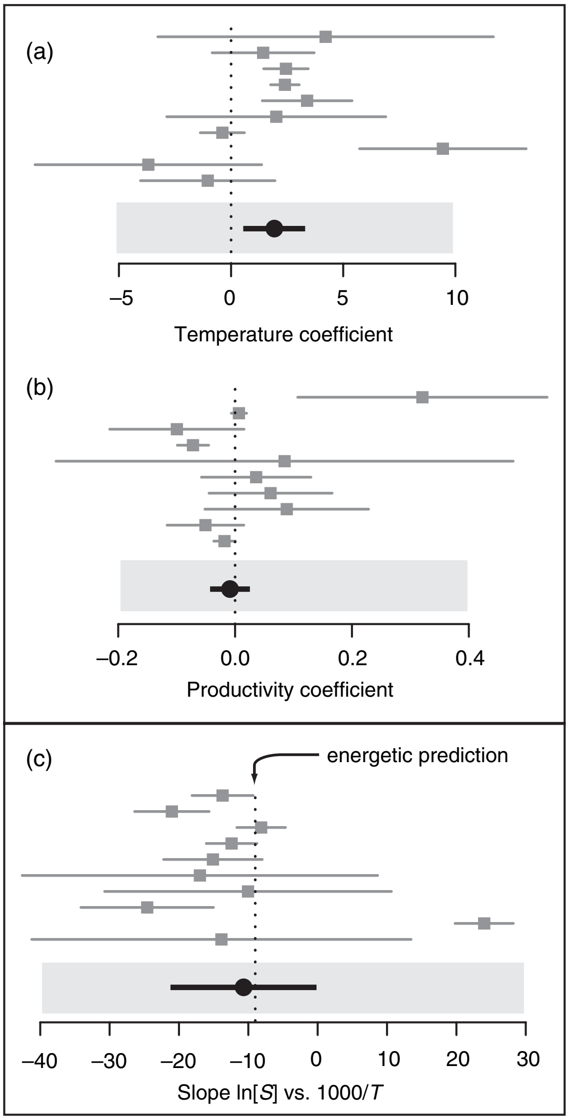

Figure 2 Results of meta-analysis of multiple regressions of species richness on temperature (a) and productivity (b), and reduced major axis slope of the natural logarithm of species richness as a function of $1000/T_k$ (c). In each panel, grey squares show coefficients for individual cores with 95% CI, and the summary estimate over all cores is shown by the larger black circle (with 95% CI) within the shaded area at the bottom. The summary estimate is significantly positive for temperature (a) but not significant for productivity (b). The prediction based on the energetics of metabolism is shown as the dotted line (c). In all three panels, the cores are plotted in the same order, from top to bottom, in which they are listed in Table 1.

out speciation and/or extinction as the drivers of richness changes in these cores; the duration of the study interval is too short relative to evolutionary rates of benthic foraminifera for these processes to play a significant role. Thus, the influence of temperature on richness in these cores must be the result of changes in the spatial occurrences of species, either because of shifts in geographical or bathymetric range limits, or changes in the patchiness with which species fill their distributional ranges. The causes of such distributional changes remain uncertain but could reflect species-specific physiological tolerances to temperature. Alternatively, changes in spatial occurrences of species could also be mediated by changes in total abundance as invoked by the 'more individuals' hypothesis (see Currie *et al.* 2004) or the metabolic model of Allen *et al.* (2002). Our summary estimate of the slope of log-richness vs. $1000/T_k$ is generally consistent with the predictions of the Allen *et al.* (2002) model suggesting that biochemical kinetics of metabolism could play a role in mediating species response to climate change. However, the CI associated with this summary estimate is quite broad and further studies are required to adequately test the Allen *et al.* model in the deep sea. In addition, our results demonstrate that the temperature-richness relationship predicted by the Allen *et al.* (2002) model can be produced by ecological processes (see Storch 2003) rather than the more commonly invoked mechanism of temperature-dependent speciation rates (Allen *et al.* 2002; Currie *et al.* 2004).

In contrast to temperature, the relationship between richness and productivity in the deep sea is clearly complex. Although previous research supports a causal connection between productivity and abundance of some benthic foraminifera species (e.g. Thomas & Gooday 1996; Wollenburg & Kuhnt 2000), our results suggest that these compositional differences may not have a simple relationship with species richness. This is further supported by the fact that empirical studies of modern deep-sea assemblages have revealed no consistent relationship between productivity and richness (Thomas & Gooday 1996; Gooday 1999; Levin *et al.* 2001; Glover *et al.* 2002; Lambshead *et al.* 2002; Snelgrove & Smith 2002). It is possible that part of the variation in the productivity-richness patterns in the present study and others is caused by an underlying hump-shaped relationship between diversity and productivity in the deep sea (Levin *et al.* 2001), but this is difficult to test here because BFAR values are not directly comparable across studies that use different sieve sizes.

In terrestrial and shallow marine environments, temperature is often tightly correlated with other measures of energy availability (e.g. primary production) because of a common dependence on solar insolation. In contrast, biological production in the deep sea comes primarily from organic particulates sinking from shallower water, resulting in the

Table 3 Summary of results of GLS multiple regression predicting species richness as a linear function of temperature and productivity

No.	Core	n	GLS coefficient temperature	GLS coefficient productivity	GLS R^2	RMA slope $\ln(S)$ vs. $1000/T_k$
1	M234414	32	4.22 (3.82)	0.32 (0.11)	0.25	−13.71 (2.15)
2	DS97-2P	125	1.43 (1.16)	0.01 (0.01)	0.03	−21.03 (1.77)
3	geoB1214	17	2.45 (0.51)	−0.10 (0.06)	0.63	−8.15 (1.73)
4	geoB1710	37	2.40 (0.33)	−0.07 (0.01)	0.79	−12.41 (1.88)
5	NP-36	20	3.39 (1.02)	0.08 (0.20)	0.42	−15.10 (3.53)
6	NGC-102	15	2.02 (2.49)	0.04 (0.05)	0.10	−16.98 (13.84)
7	MD88-779	17	−0.39 (0.50)	0.06 (0.05)	0.14	−10.05 (10.68)
8	ERDC-112	24	9.44 (1.89)	0.09 (0.07)	0.63	−24.58 (4.62)
9	BOFS-5K	54	−3.69 (2.58)	−0.05 (0.03)	0.23	24.01 (2.18)
10	BOFS-14K	33	−1.04 (1.53)	−0.02 (0.01)	0.11	−13.88 (13.86)
	summary		1.92 (0.70)	−0.01 (0.02)		−10.69 (5.4)

GLS, generalized least squares.
RMA, reduced major axis.
Each row gives the results from each core, with the number of samples (n), estimated coefficients for temperature and productivity (with standard errors), and the R^2. The final column shows the bivariate reduced major axis slope of $\ln(S)$ as a function of $1000/T_k$, where T_k is the temperature in Kelvin. The last row gives the meta-analysis summary estimate (with standard error). Meta-analysis finds that an overall significantly positive ($P < 0.05$) relationship between temperature and richness, but no consistent effect of productivity on richness.

loose and variable relationship between temperature and production seen in the 10 cores analysed here. As a consequence, it is unlikely that the overall correlation between temperature and richness in the deep-sea is spuriously driven by correlations between temperature and other production-related variables.

The significant temperature-richness relationship in these data is also highly unlikely to be due to preservational bias or choice of paleoenvironmental proxies. The cores we used were generally located well above the lysocline (the depth at which substantial calcium carbonate dissolution takes place). In our analyses, preservation can be an issue only if samples from periods with relatively colder bottom water have consistently worse preservation than warmer periods and hence artifactually lower diversity. However, there is no indication of such a systematic bias in preservational quality in the cores used here. As far as temperature and productivity estimates are concerned, we used standard proxies common in paleoceanographic studies (Martin *et al.* 2002; Rasmussen *et al.* 2002).

Despite the overall significantly positive effect of temperature on richness, our results also reveal considerable regional variation in this relationship. Similar geographical heterogeneity in the strength of energy-richness (or climate-richness) relationships is also present in terrestrial systems but the underlying causes remain poorly understood (Hawkins *et al.* 2003). In our data, some of this among core variation is attributable to the sieve size used in the original study. The stronger positive effect of temperature in cores processed with larger sieve sizes could potentially indicate that larger-bodied foraminifera species respond more readily to temperature changes than smaller-bodied species. This hypothesis is consistent with previous studies of shallow marine bivalves showing that geographic range shifts in response to climate change occurred preferentially in large-bodied species (Roy *et al.* 2001). In addition, random noise associated with estimating richness and productivity, and regional deviations in bottom-water temperature can all contribute to differences between cores. Finally, historical contingencies can also lead to some of the differences seen among individual cores (Ricklefs 2004). Even though our study interval is too short for evolutionary change to drive the changes in species richness within each core, species compositions of individual cores differed because of the differences in evolutionary and geological histories of different regions and bathymetric zones. The possibility that these differences in species composition can contribute to the divergent ecological responses to changes in temperature and productivity warrants further investigation. Causality aside, the considerable heterogeneity in energy-richness relationships documented in this and other studies (e.g. Hawkins *et al.* 2003) suggests that general tests of species–energy hypothesis may benefit from a meta-analytic approach such as that employed here (see also Arnqvist & Wooster 1995; Hillebrand 2004).

Species assemblages in the deep-sea have different evolutionary histories compared with terrestrial and shallow marine biotas, and are only indirectly linked to the climatic variables that influence diversity in other environments (Rex *et al.* 2000). Yet, we find the same positive relationship between temperature and species richness in deep-sea foraminifera as has been demonstrated in many terrestrial and shallow marine groups (Roy *et al.* 1998; Hawkins *et al.* 2003). Moreover, our results show that this temperature-richness relationship is not simply a characteristic of modern ecosystems, but that species richness in the deep-sea tracks changes in climate over geological time. In this respect, our results are consistent with previous regional paleontological studies that have shown a tight coupling between climate and ostracode diversity in the deep North Atlantic basin (Cronin & Raymo 1997; Cronin *et al.* 1999). Existing models of deep-sea diversity generally consider energy in the form of productivity as an important determinant of species richness (Levin *et al.* 2001; Snelgrove & Smith 2002), but the role of temperature has remained surprisingly neglected. Further analyses of temperature-richness relationship in other groups of deep-sea organisms should provide important insights into the processes that maintain the remarkably high species richness in the deep sea.

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