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## Climatic forcing of Quaternary deep-sea benthic communities in the North Pacific Ocean

Moriaki Yasuhara, Gene Hunt, Thomas M. Cronin, Natsumi Hokanishi, Hodaka Kawahata, Akira Tsujimoto, and Miho Ishitake

**Abstract.**—There is growing evidence that changes in deep-sea benthic ecosystems are modulated by climate changes, but most evidence to date comes from the North Atlantic Ocean. Here we analyze new ostracod and published foraminiferal records for the last 250,000 years on Shatsky Rise in the North Pacific Ocean. Using linear models, we evaluate statistically the ability of environmental drivers (temperature, productivity, and seasonality of productivity) to predict changes in faunal diversity, abundance, and composition. These microfossil data show glacial-interglacial shifts in overall abundances and species diversities that are low during glacial intervals and high during interglacials. These patterns replicate those previously documented in the North Atlantic Ocean, suggesting that the climatic forcing of the deep-sea ecosystem is widespread, and possibly global in nature. However, these results also reveal differences with prior studies that probably reflect the isolated nature of Shatsky Rise as a remote oceanic plateau. Ostracod assemblages on Shatsky Rise are highly endemic but of low diversity, consistent with the limited dispersal potential of these animals. Benthic foraminifera, by contrast, have much greater dispersal ability and their assemblages at Shatsky Rise show diversities typical for deep-sea faunas in other regions.

Statistical analyses also reveal ostracod-foraminiferal differences in relationships between environmental drivers and biotic change. Rarefied diversity is best explained as a hump-shaped function of surface productivity in ostracods, but as having a weak and positive relationship with temperature in foraminifera. Abundance shows a positive relationship with both productivity and seasonality of productivity in foraminifera, and a hump-shaped relationship with productivity in ostracods. Finally, species composition in ostracods is influenced by both temperature and productivity, but only a temperature effect is evident in foraminifera. Though complex in detail, the global-scale link between deep-sea ecosystems and Quaternary climate changes underscores the importance of the interaction between the physical and biological components of paleoceanographical research for better understanding the history of the biosphere.

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### Introduction

Starting with pioneering studies by Hessler and Sanders (Hessler and Sanders 1967; Sanders 1968; Sanders and Hessler 1969), nearly fifty years of accumulated investigation into the deep-sea benthos have revealed some general ecological patterns. Abundance of deep-sea benthic communities decrease exponentially with depth (Rex et al. 2006;

Rex and Etter 2010), and it is widely believed that this and other abundance gradients are related to variation in particulate organic carbon flux to the seafloor (Smith et al. 1997; Rex et al. 2006; Rex and Etter 2010). Faunal composition also shows strong depth zonation (Carney 2005), and species diversity usually increases to a mid-bathyal maximum before decreasing again (Rex 1973, 1981; Rex

et al. 2005; Rex and Etter 2010). Perhaps most surprisingly, many taxa show latitudinal gradients of decreasing alpha diversity from the tropics to the poles, although the gradient may be stronger in the Northern Hemisphere (Rex et al. 1993, 2000, 2005; Culver and Buzas 2000; Stuart et al. 2003; Corliss et al. 2009; Yasuhara et al. 2009b; Rex and Etter 2010).

Despite these advances in documenting pattern, the underlying drivers that structure diversity and faunal patterns are still controversial (Stuart et al. 2003; Carney 2005; Rex et al. 2005; Yasuhara and Cronin 2008; Corliss et al. 2009; Yasuhara et al. 2009b; Tittensor et al. 2011). Uncertainty remains in part because these faunal patterns likely have complex causes, reflecting not only species' present-day tolerances for environmental factors (e.g., temperature, productivity) but also spatial and bathymetric differences in speciation, extinction, and dispersal (Rex et al. 2005; Jablonski et al. 2006), acting within a biogeographic template (McClain et al. 2009b; McClain and Barry 2010).

There is growing evidence from multiple taxonomic groups that climate change can be a consistent driver of deep-sea biodiversity and ecosystem patterns (Danovaro et al. 2004; Ruhl and Smith 2004; Hunt et al. 2005; Wollenburg et al. 2007; Ruhl et al. 2008; Yasuhara and Cronin 2008; Yasuhara et al. 2008b; Smith et al. 2009; Glover et al. 2010). Recent micropaleontological studies have demonstrated a link between glacial-interglacial Milankovitch cycles and deep-sea species diversity during the late Quaternary and mid-Pliocene, generally with a glacial-low and interglacial-high species diversity pattern (Cronin and Raymo 1997; Cronin et al. 1999; Yasuhara and Cronin 2008; Yasuhara et al. 2009b for ostracods; Ohkushi et al. 2000; Hunt et al. 2005 for foraminifera). However, almost all evidence for this link between Plio-Pleistocene climate cycles and deep-sea diversity comes from the North Atlantic Ocean, and it is not certain if such phenomena are truly global. One exception is the study of North Pacific deep-sea foraminifera by Ohkushi et al. (2000), which in this paper we reanalyze in conjunction with new ostracod data. Deep-sea foraminiferal faunal composition and abundance have been

used extensively to reconstruct late Quaternary paleoceanography, and thus it is well recognized that they can be related to climate cycles (Thomas et al. 1995; Nees et al. 1999; Ohkushi et al. 2000; Kawagata 2001; Rasmussen et al. 2002; Loubere and Fariduddin 2003; Ujié 2003). In this paper, we take micropaleontological records commonly used for paleoceanographic inference and subject them to a battery of paleoecological analyses in an attempt to disentangle potential environmental drivers of biotic change in the deep-sea benthic ecosystem.

Crustacean Ostracoda and unicellular Foraminifera are both important components of deep-sea benthos (Gooday et al. 1992; Shimanaga et al. 2000; Brandt et al. 2007; Yasuhara and Cronin 2008). Their calcareous shells are abundantly preserved, and both taxa have a rich fossil record accessible through deep-sea coring (e.g., Thomas and Gooday 1996; Cronin and Raymo 1997; Wollenburg et al. 2007; Yasuhara et al. 2008b, 2009a). Ostracods and foraminifera span similar size ranges, and in the deep sea, they are thought to exploit the same food source—particulate organic matter that sinks from shallower depths (Gooday 1994, 2003b; Didié and Bauch 2002; Cronin and Dwyer 2003; Schellenberg 2007; Yasuhara and Cronin 2008). Despite these and other similarities, these taxa differ importantly in several respects. Ostracods are composed of many thousands of cells and almost all marine ostracods reproduce sexually (Chaplin et al. 1994; Butlin et al. 1998; Ikeya and Kato 2000; Horne et al. 2002), whereas foraminifera are unicellular and have complex life cycles with sexual and asexual stages (Goldstein 1999; Gooday 2003b). Of particular evolutionary and ecological importance is the contrast in dispersal potential. Ostracods lack a dispersal stage, and most deep-sea taxa cannot swim (Brandt et al. 2007). In contrast, benthic foraminifera disperse widely and at least some species maintain genetic continuity over vast distances (Pawlowski et al. 2007; Alve and Goldstein 2010). Because these taxa are taphonomically similar but have different biological characteristics, comparing their patterns over time may help to test general ecological hypotheses. Nonetheless, with a

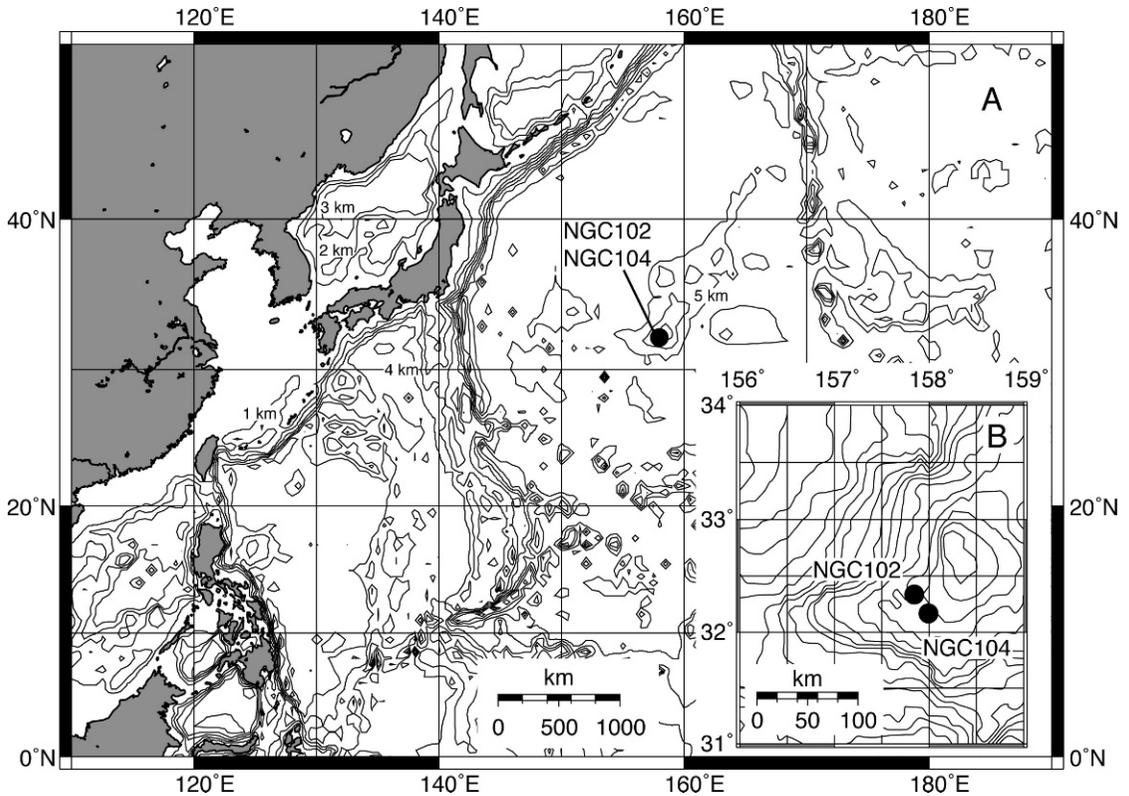


FIGURE 1. Locality map (A) and close-up of core locations (B).

very few exceptions (Steineck and Thomas 1996; Webb et al. 2009), studies do not jointly report both ostracod and foraminiferal faunal records from the same site.

Here we analyze Shatsky Rise benthic paleoecological records for the last 250 Kyr from two nearby cores NGC 104 and NGC 102 (Fig. 1). The North Pacific generally lacks the carbonate sediments that bear abundant benthic ostracods and foraminifera because the seafloor is below the carbonate compensation depth in most regions. Its relatively shallow bathymetry makes the Shatsky Rise (Fig. 1) an exception and thus provides a rare opportunity to investigate North Pacific deep-sea ecosystem dynamics using calcareous benthic microfossils. These microfossil data show glacial-interglacial shifts in overall abundances, and species diversities that are low during glacial intervals and high during interglacials. These patterns have been commonly documented in the North Atlantic Ocean, suggesting that the climatic forcing of the deep-sea ecosystem is widespread, and

possibly global in nature. In addition, we observe unique characteristics of remote oceanic plateau ecosystems and possible differences in environmental drivers of ecological (i.e., species diversity, faunal composition, and abundance) changes among taxonomic groups and regions.

### Materials and Methods

#### Cores and Chronology

Gravity core NGC 104 (32°10.04'N, 157°59.9'E) was collected at a water depth of 2665 m on the Shatsky Rise, northwestern Pacific, during the NH95-1 Cruise of RV *Hakurei-Maru*. This site is in the path of North Pacific Deep Water (Kawabe et al. 2009) and its water depth is close to the lysocline of this region (~2600 m) and well above the carbonate compensation depth. The sediments consist of calcareous ooze.

Marine isotope stages (MIS) 1–7 of the last 250 Kyr were examined for benthic ostracod faunal diversity, abundance, and composition. Large-volume (~50–100 g dry weight)

samples were wet-sieved and ostracods were picked from the  $>150\text{-}\mu\text{m}$  size fraction. This size fraction retains adults and juveniles from late molt stages from most deep-sea species (Yasuhara et al. 2009b). Specimens were identified to species level where possible, although species of *Krithe* were lumped together for analysis (species-level identification of this genus can be difficult and there are only a few species of this genus per sample). Benthic foraminiferal census data are from the nearby core NGC 102 ( $32^{\circ}19.84'\text{N}$ ,  $157^{\circ}51'\text{E}$ , 2612 m water depth) (Ohkushi et al. 2000), which is located only 23 km away (Fig. 1). Ohkushi et al. (2000) picked foraminiferal specimens from the  $>75\text{-}\mu\text{m}$  size fraction.

The chronology of core NGC 104 was established with correlation of the planktic foraminiferal (*Globorotalia inflata*)  $\delta^{18}\text{O}$  record to the composite oxygen isotope record from the LR04 stack (Lisiecki and Raymo 2005) (Fig. 2, Supplement Tables S1, S2) by using the software AnalySeries version 2.0.4.2 (Paillard et al. 1996). The chronologies of other cores used in this paper were also updated to the LR04 stack (Fig. 2, Supplement Tables S3, S4). Many sediment cores are now available on the Shatsky Rise (e.g., Ohkushi et al. 2000; Yamane 2003; this study) and comparison of their planktic foraminiferal  $\delta^{18}\text{O}$  records enabled us to improve the chronology of our analyzed cores. The correlation is based on obvious  $\delta^{18}\text{O}$  features that are common to many  $\delta^{18}\text{O}$  series from this region as well as the LR04.

### Measures of Biotic State

From census data at these two sites—ostracods at NGC 104 and benthic foraminifera at NGC 102—we calculated variables related to the diversity, abundance, and composition of these faunas. Following many other deep-sea studies, we measured diversity as  $E(S_n)$ , the expected number of species in samples rarefied to  $n$  individuals. The sampling threshold,  $n$ , was set higher for foraminifera because they are typically more abundant than ostracods ( $n = 100$  for ostracods and  $n = 200$  for foraminifera; Supplement Tables S5, S6). For ostracods, diversities were calculated from

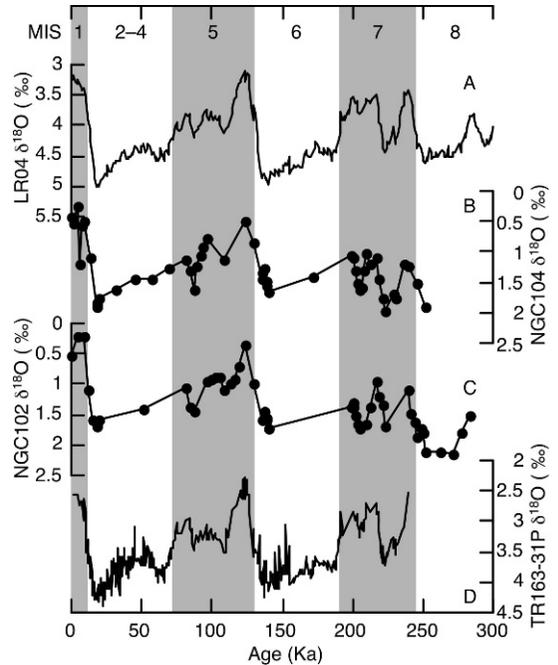


FIGURE 2.  $\delta^{18}\text{O}$  curves showing the result of LR04-based chronology (Supplement Tables S1–4): LR04 stack (A) and  $\delta^{18}\text{O}$  curves from the sites NGC 104 (B), NGC 102 (C), and TR163-31P (D). Ostracod, foraminiferal, and bottom-water temperature records are from cores NGC 104, NGC 102, TR163-31P, respectively.

three-sample moving sums of the census data set because of relatively low sample sizes, though results are similar if samples are not lumped.

We measured abundance as accumulation rates of benthic foraminifera (BFAR) and ostracods (BOAR), metrics commonly used for microfossils from cores (e.g., Thomas et al. 1995). These accumulation rates measure the number of individuals deposited per  $\text{cm}^2$  of ocean floor per thousand years, and are calculated as the product of the number of specimens per gram of sediment, the sediment bulk dry density, and the linear sedimentation rate (Supplement Tables S7, S8).

In order to explore changes in ostracod faunal composition, we performed nonmetric multidimensional scaling (MDS) on Bray-Curtis distances calculated from square-root transformed relative species abundances. We focused analyses on the first axis of this ordination because it was similar across data transformations (square-root, fourth-root, raw relative abundances) and across different

ordination methods (including detrended correspondence analysis). As such, we interpret it as capturing a primary signal of compositional variation through time in each fauna. Because the ostracods and foraminifera are from different samples, ordinations were performed separately for each group.

### Proxies for Environmental Change

We used proxies to infer three aspects of environmental conditions through this interval: productivity, seasonality of productivity, and bottom-water temperature. Productivity was measured as mass accumulation rate of  $C_{org}$  (MAR  $C_{org}$ ), which reflects particulate organic carbon flux to the ocean floor, and thus food supply for benthic organisms. MAR  $C_{org}$  is widely used as a paleo-productivity proxy (e.g., Maeda et al. 2002). Using organic carbon data from NGC 102 (Kawahata et al. 1999; Ohkushi et al. 2000), we computed MAR  $C_{org}$  values as  $1000 \times (C_{org}/100) \times DBD \times LSR$ , where  $C_{org}$  is weight percent of organic carbon, DBD is dry bulk density, and LSR is linear sedimentation rate (as per the updated age model, Supplement Table S3). Seasonality of productivity was measured as the relative abundance of the “phytodetritus group” of benthic foraminifera, *Epistominella exigua* and *Alabaminella weddellensis* (Sun et al. 2006). Productivity and seasonality proxies were not from the same exact samples as the faunal data, and so we used linear interpolation of the proxy curves to assign environmental values to faunal samples on the basis of their ages.

Bottom-water temperature data are available from the Pacific core TR163-31P (3°35'S, 83°57'W, 3205 m water depth), which is based on Mg/Ca ratios in benthic foraminifera (Martin et al. 2002). Site TR163-31P is far from the Shatsky Rise, but late Quaternary deep-ocean temperature shows concordant trends within the Pacific Ocean (Elderfield et al. 2010; Martin et al. 2002). Because the temperature curve is at a much higher resolution than the faunal data, it was smoothed with a cubic spline to eliminate high-frequency variation as described by Hunt et al. (2005), and the spline function was used to calculate temperatures for samples from their ages.

Correlation to a temperature curve from a distant location is reasonable here because changes in deep-water temperature are largely global, reflecting the temperature of waters sinking at high latitudes (Zachos et al. 2001; Sostdian and Rosenthal 2009; Elderfield et al. 2010). Deep ocean circulation propagates temperature changes in these source waters through most of the world ocean.

### Testing Environmental Drivers

We used regression models to test temperature, surface productivity, and seasonality of productivity because these factors have been considered as the promising candidates in studies of modern and fossil deep-sea environments (Thomas and Gooday 1996; Cronin and Raymo 1997; Gooday 2003a; Rex et al. 2000, 2006; Wollenburg and Kuhnt 2000; Carney 2005; Hunt et al. 2005; Yasuhara and Cronin 2008; Corliss et al. 2009; Yasuhara et al. 2009b; Rex and Etter 2010; Tittensor et al. 2011). Linear relationships with deep-sea species diversity have been reported for temperature (mainly positive) and seasonality of productivity (negative) (Hunt et al. 2005; Corliss et al. 2009). Both linear (mainly negative) and hump-shaped relationships have been observed for productivity (Wollenburg and Kuhnt 2000; Levin et al. 2001; Gooday 2003a; Tittensor et al. 2011). Furthermore, benthic abundance and faunal composition are also known to be related to at least some of these environmental parameters (Didié et al. 2002; Gooday 2003a; Carney 2005; Rex et al. 2006; Sun et al. 2006; Yasuhara et al. 2008b; Alvarez Zarikian et al. 2009; Rex and Etter 2010). Thus, we considered models covering all these combinations, using multiple regression to evaluate potential correlates of diversity, faunal composition, and abundance (Tables 1–6).

The independent variables in the regressions were temperature, productivity, and seasonality of productivity (in part, see below). Because hump-shaped relationships between diversity and productivity have been reported frequently in prior studies, we included a quadratic term for productivity in the models as well. Regression models were run separately for ostracods and foraminifera,

TABLE 1. Regression models of ostracod species diversity  $E(S_{100})$  as a function of temperature ( $T$ ), surface productivity ( $P$ : linear;  $P + P^2$ : potentially hump-shaped relationships), and seasonality of surface productivity ( $SP$ ).  $E(S_{100}) \sim 1$ : null model. AICc: small-sample Akaike Information Criterion.  $T$  Coef.,  $P$  Coef.,  $P^2$  Coef.,  $SP$  Coef.: coefficient for each variable. Bold:  $p < 0.05$ .

	Model	AICc	$T$ Coef.	$P$ Coef.	$P^2$ Coef.	$SP$ Coef.	$p$	$r^2$	Akaike weight
1	$E(S_{100}) \sim P + P^2 + SP$	76.3	—	<b>0.226</b>	<b>-0.008</b>	-0.019	<b>0.034</b>	0.320	0.244
2	$E(S_{100}) \sim P + P^2$	76.7	—	<b>0.201</b>	<b>-0.008</b>	—	0.055	0.223	0.200
3	$E(S_{100}) \sim T + P + P^2$	76.8	0.423	<b>0.220</b>	<b>-0.009</b>	—	<b>0.040</b>	0.309	0.198
4	$E(S_{100}) \sim 1$	77.9	—	—	—	—	—	—	0.112
5	$E(S_{100}) \sim T + P + P^2 + SP$	79.0	0.241	<b>0.229</b>	<b>-0.009</b>	-0.013	0.059	0.339	0.063
6	$E(S_{100}) \sim SP$	79.2	—	—	—	-0.013	0.278	0.049	0.059
7	$E(S_{100}) \sim T$	79.6	0.254	—	—	—	0.365	0.034	0.049
8	$E(S_{100}) \sim P$	80.5	—	0.002	—	—	0.943	0.000	0.031
9	$E(S_{100}) \sim T + SP$	81.9	0.114	—	—	-0.010	0.532	0.053	0.015
10	$E(S_{100}) \sim P + SP$	82.0	—	0.002	—	-0.013	0.560	0.049	0.015
11	$E(S_{100}) \sim T + P$	82.4	0.261	-0.003	—	—	0.665	0.035	0.012
12	$E(S_{100}) \sim T + P + SP$	84.9	0.114	0.000	—	-0.010	0.745	0.053	0.003

and within each taxon, separately across the three measures of biotic state: rarefied diversity, abundance (BFAR/BOAR), and composition (measured as the score on the first MDS axis). All models tested the ability of the environmental variables to predict biotic variables.

The Akaike information criterion (AICc, to indicate the small sample version) was used to measure model support in a way that balances goodness-of-fit and model complexity, and Akaike weights were used to summarize proportional support for all candidate models (Anderson et al. 2000). AICc and related approaches facilitate consideration of all models to the degree to which they are supported by data without undo emphasis on rejection of a null hypothesis. We also considered parameter estimates averaged over all models, proportional to the support that each model receives (Anderson et al. 2000) (Tables 7, 8). This approach accounts for uncertainty in model selection and thus leads to appropriately broader confidence intervals

than relying only on the single, best-supported model.

We did not assess seasonality of productivity in the foraminiferal analyses (except those of the abundance) because it is not independent of foraminiferal diversity and composition. If the fauna is largely occupied by only a few phytodetrital species, rarefied diversity will be depressed and species composition will obviously be affected. Corliss et al. (2009) were able to use satellite-derived estimates of the seasonality in their study of modern foraminifera, but we currently lack downcore proxies that are independent of the benthic foraminiferal fauna.

Analyses reported here were implemented in the R programming language (R Development Core Team 2010), using functions from the R packages Vegan (Oksanen et al. 2010) for diversity and compositional analyses and MuMIn (Bartoń 2009) to perform the model averaging. Raw census data and Supplement Tables are deposited at Dryad (doi:10.5061/dryad.c1q30).

TABLE 2. Regression models of foraminiferal species diversity  $E(S_{200})$  as a function of temperature and surface productivity. Abbreviations as in Table 1. Bold:  $p < 0.05$ .

	Model	AICc	$T$ Coef.	$P$ Coef.	$P^2$ Coef.	$p$	$r^2$	Akaike weight
1	$E(S_{200}) \sim 1$	201.0	—	—	—	—	—	0.292
2	$E(S_{200}) \sim T$	201.0	2.531	—	—	0.133	0.076	0.291
3	$E(S_{200}) \sim T + P + P^2$	202.0	<b>3.614</b>	-0.639	0.017	0.108	0.198	0.167
4	$E(S_{200}) \sim T + P$	203.0	2.923	-0.067	—	0.275	0.088	0.095
5	$E(S_{200}) \sim P$	203.0	—	-0.001	—	0.991	0.000	0.085
6	$E(S_{200}) \sim P + P^2$	203.0	—	-0.434	0.013	0.366	0.069	0.069

TABLE 3. Regression models of ostracod faunal composition (nonmetric multidimensional scaling first axis: MDS1) as a function of temperature, surface productivity, and seasonality of surface productivity. Abbreviations as in Table 1. Bold:  $p < 0.05$ .

	Model	AICc	T Coef.	P Coef.	P <sup>2</sup> Coef.	SP Coef.	p	r <sup>2</sup>	Akaike weight
1	MDS1 ~ T + P + P <sup>2</sup>	-13.2	<b>-0.107</b>	<b>0.029</b>	<b>-0.001</b>	—	<b>0.010</b>	0.318	0.356
2	MDS1 ~ T	-11.5	<b>-0.113</b>	—	—	—	<b>0.024</b>	0.154	0.149
3	MDS1 ~ T + P + P <sup>2</sup> + SP	-10.4	-0.093	<b>0.028</b>	<b>-0.001</b>	0.001	<b>0.024</b>	0.323	0.088
4	MDS1 ~ P + P <sup>2</sup> + SP	-10.4	—	<b>0.027</b>	<b>-0.001</b>	0.003	<b>0.033</b>	0.257	0.086
5	MDS1 ~ P + P <sup>2</sup>	-10.3	—	<b>0.027</b>	<b>-0.001</b>	—	<b>0.044</b>	0.188	0.080
6	MDS1 ~ SP	-9.7	—	—	—	0.004	0.062	0.108	0.062
7	MDS1 ~ T + SP	-9.4	-0.088	—	—	0.002	0.064	0.168	0.053
8	MDS1 ~ T + P	-9.1	<b>-0.108</b>	-0.002	—	—	0.074	0.159	0.045
9	MDS1 ~ 1	-8.4	—	—	—	—	—	—	0.032
10	MDS1 ~ P + SP	-7.5	—	-0.002	—	0.004	0.157	0.116	0.020
11	MDS1 ~ P	-6.9	—	-0.003	—	—	0.370	0.026	0.015
12	MDS1 ~ T + P + SP	-6.8	-0.085	-0.001	—	0.002	0.136	0.171	0.014

## Results and Discussion

### Oceanic Plateau Ecosystem

Modern Shatsky Rise ostracod and foraminiferal diversities are ~7 ( $E[S_{100}]$ ) and ~35 ( $E[S_{200}]$ ), respectively (Figs. 3, 4). For foraminifera, this diversity is comparable to that observed at similar latitude in the North Atlantic (Fig. 3), and it is also similar to foraminiferal diversity at another North Pacific oceanic plateau, Hess Rise (Fig. 3). In contrast, modern ostracod diversity is considerably lower on the Shatsky Rise than in the temperate North Atlantic (Fig. 3). The two faunas also differ in their levels of endemism. Most (>80%) foraminiferal species encountered at NGC 102 are known from elsewhere (Ohkushi et al. 2000), but all 19 ostracod species recovered at NGC 104 are currently undescribed and perhaps endemic.

It is conceivable that these modern faunal patterns relate to environmental conditions at Shatsky Rise. For example, compared to sites of similar depth and latitude in the North Atlantic, sites NGC 102 and 104 have lower dissolved oxygen levels (~2.5 ml/l versus

~6 ml/l) and slightly lower bottom-water temperature (~2°C versus ~3°C) (Garcia et al. 2006; Locarnini et al. 2006). However, dissolved oxygen concentrations usually affect marine benthos only when lower than ~2.0 ml/l in shallow-marine ecosystems (Diaz and Rosenberg 2008; Levin et al. 2009) and ~0.5 ml/l in the deep sea (Levin 2003) and many foraminiferal species can tolerate much lower levels.

A potentially more plausible explanation for these faunal patterns is the isolation of this oceanic plateau (~2000 km) surrounded by very deep seafloor (>5000 m) (Fig. 1). Although recent research suggests that ostracods can survive below the carbonate compensation depth (4400 m in northwestern Pacific [Berger et al. 1976]) and at least some abyssal species (or closely related species complexes) may have pan-abyssal distribution (Yasuhara et al. 2008a), they lack a dispersal stage and most taxa do not swim. Moreover, recent ecological and molecular studies suggest that ostracods, like nematodes and isopods, have lower gene flow and dispersal than foraminifera (Alve and Goldstein 2003; Brandt et al. 2007; Pawlowski et al.

TABLE 4. Regression models of foraminiferal faunal composition (nonmetric multidimensional scaling first axis: MDS1) as a function of temperature and surface productivity. Abbreviations as in Table 1. Bold:  $p < 0.05$ .

	Model	AICc	T Coef.	P Coef.	P <sup>2</sup> Coef.	p	r <sup>2</sup>	Akaike weight
1	MDS1 ~ T + P	-11.2	<b>-0.2121</b>	0.0060	—	<b>0.003</b>	0.339	0.476
2	MDS1 ~ T	-10.7	<b>-0.1768</b>	—	—	<b>0.003</b>	0.268	0.373
3	MDS1 ~ T + P + P <sup>2</sup>	-8.7	<b>-0.2053</b>	0.0004	0.0002	<b>0.009</b>	0.346	0.136
4	MDS1 ~ 1	-3.5	—	—	—	—	—	0.010
5	MDS1 ~ P	-1.1	—	0.0013	—	0.751	0.004	0.003
6	MDS1 ~ P + P <sup>2</sup>	0.2	—	-0.0113	0.0004	0.522	0.045	0.002

TABLE 5. Regression models of ostracod abundance (benthic ostracod accumulation rate: BOAR) as a function of temperature, surface productivity, and seasonality of surface productivity. Abbreviations as in Table 1. Bold:  $p < 0.05$ .

	Model	AICc	T Coef.	P Coef.	P <sup>2</sup> Coef.	SP Coef.	p	r <sup>2</sup>	Akaike weight
1	BOAR ~ P + P <sup>2</sup>	196.0	—	<b>1.141</b>	<b>-0.028</b>	—	<b>0.000</b>	0.417	0.475
2	BOAR ~ T + P + P <sup>2</sup>	197.0	1.155	<b>1.124</b>	<b>-0.028</b>	—	<b>0.001</b>	0.439	0.218
3	BOAR ~ P + P <sup>2</sup> + SP	198.0	—	<b>1.137</b>	<b>-0.028</b>	0.020	<b>0.001</b>	0.421	0.131
4	BOAR ~ T + P + P <sup>2</sup> + SP	198.0	2.157	<b>1.095</b>	<b>-0.027</b>	0.070	<b>0.001</b>	0.471	0.129
5	BOAR ~ P	202.0	—	<b>0.278</b>	—	—	<b>0.004</b>	0.238	0.021
6	BOAR ~ T + P	204.0	1.123	<b>0.259</b>	—	—	<b>0.011</b>	0.259	0.009
7	BOAR ~ P + SP	204.0	—	<b>0.291</b>	—	0.033	<b>0.014</b>	0.249	0.007
8	BOAR ~ T + P + SP	204.0	2.370	<b>0.273</b>	—	0.088	<b>0.012</b>	0.309	0.007
9	BOAR ~ 1	208.0	—	—	—	—	—	—	0.001
10	BOAR ~ T	209.0	1.920	—	—	—	0.161	0.063	0.001
11	BOAR ~ T + SP	210.0	2.929	—	—	0.068	0.228	0.094	0.000
12	BOAR ~ SP	211.0	—	—	—	-0.002	0.968	0.000	0.000

2007; Lecroq et al. 2009; Brandão et al. 2010). As a result, deep-sea ostracod taxa may only rarely reach and colonize this oceanic plateau, depressing its diversity. Lacking genetic connection to other deep-sea populations, the colonizing populations would have diverged to produce a mostly endemic ostracod fauna. Much higher diversities and lower levels of endemism than those in the Shatsky Rise are known from the North Atlantic and Southwest Pacific Ocean basins (Whatley and Ayress 1988; Jellinek and Swanson 2003). In addition, the diversity and degree of endemism of ostracods at Shatsky Rise are similar to those on isolated North Pacific seamounts (Larwood and Whatley 1993; Boomer and Whatley 1995; Whatley and Boomer 1995), but low ostracod abundance of these seamounts prevents direct comparison of diversity to Shatsky Rise. No Shatsky Rise ostracod species is identical to any species reported from these seamounts. Benthic foraminiferal assemblages at Shatsky Rise retain

typical levels of diversity and low endemism presumably because their dispersal potential keeps these populations demographically connected to deep-sea populations elsewhere. This hypothesized cause for Shatsky Rise faunal patterns can be tested with faunal data from other North Pacific oceanic plateaus and seamounts.

#### Glacial-Interglacial Ecosystem Changes

*Species Diversity.*—Both ostracod and foraminiferal diversities are generally higher during interglacial periods (MIS 1, 5, 7) than in glacial periods (MIS 2–4, 6) (Fig. 4). Positive diversity peaks correspond well to the peak interglacial periods represented by the global stack of the deep-sea foraminiferal  $\delta^{18}\text{O}$  curve (Lisiecki and Raymo 2005) (Fig. 4). Thus, the microfossil data reveal that deep-sea species diversity has been modulated by orbital-scale climate changes not only in the Atlantic and but also in the Pacific, suggesting

TABLE 6. Regression models of foraminiferal abundance (benthic foraminiferal accumulation rate: BFAR) as a function of temperature, surface productivity, and seasonality of surface productivity. Abbreviations as in Table 1. Bold:  $p < 0.05$ .

	Model	AICc	T Coef.	P Coef.	P <sup>2</sup> Coef.	SP Coef.	p	r <sup>2</sup>	Akaike weight
1	BFAR ~ P + SP	558.0	—	<b>425.6</b>	—	<b>51.0</b>	<b>0.000</b>	0.857	0.483
2	BFAR ~ T + P + SP	560.0	-576.3	<b>434.2</b>	—	41.9	<b>0.000</b>	0.861	0.186
3	BFAR ~ P + P <sup>2</sup> + SP	561.0	—	<b>451.8</b>	-0.8	<b>51.3</b>	<b>0.000</b>	0.858	0.121
4	BFAR ~ T + P	562.0	-1183.7	<b>427.8</b>	—	—	<b>0.000</b>	0.841	0.089
5	BFAR ~ T + P + P <sup>2</sup> + SP	563.0	-641.5	<b>481.1</b>	-1.4	41.3	<b>0.000</b>	0.863	0.045
6	BFAR ~ P	563.0	—	<b>401.2</b>	—	—	<b>0.000</b>	0.817	0.040
7	BFAR ~ T + P + P <sup>2</sup>	564.0	<b>-1253.8</b>	<b>485.9</b>	-1.7	—	<b>0.000</b>	0.842	0.026
8	BFAR ~ P + P <sup>2</sup>	566.0	—	<b>414.5</b>	-0.4	—	<b>0.000</b>	0.817	0.011
9	BFAR ~ 1	614.0	—	—	—	—	—	—	0.000
10	BFAR ~ T	615.0	1327.0	—	—	—	0.320	0.034	0.000
11	BFAR ~ SP	616.0	—	—	—	-11.5	0.803	0.002	0.000
12	BFAR ~ T + SP	618.0	1593.0	—	—	17.3	0.584	0.038	0.000

TABLE 7. Ostracod model-averaged parameter estimates and confidence intervals (CI). Bold: CIs that exclude zero.

	Coefficient	Lower CI	Upper CI
Ostracod diversity $E(S_{100})$			
$P^2$	-0.00583	-0.0147	0.003
$P$	0.153	-0.0824	0.388
$SP$	-0.00651	-0.0266	0.0136
$T$	0.116	-0.288	0.521
Ostracod abundance BOAR			
$P^2$	-0.0265	<b>-0.0472</b>	<b>-0.00593</b>
$P$	1.09	<b>0.433</b>	<b>1.75</b>
$SP$	0.0126	-0.0402	0.0654
$T$	0.56	-1.29	2.41
Ostracod faunal composition MDS1			
$P^2$	-0.000598	-0.00172	0.000525
$P$	0.0171	-0.0169	0.051
$SP$	0.000778	-0.00213	0.00368
$T$	-0.0736	-0.199	0.052

that the climatically driven interglacial-high and glacial-low diversity pattern is largely global. A few exceptions to this pattern have been reported from the subpolar North Atlantic (Thomas et al. 1995; Didié et al. 2002; Yasuhara and Cronin 2008), but these patterns may be related to Heinrich ice-rafting events during glacial periods (see Yasuhara and Cronin 2008 for details).

This interglacial-high and glacial-low biodiversity pattern is not a preservational artifact of glacial-interglacial scale shifts in lysocline depth. Carbonate dissolution, as measured by the fragmentation rate of planktic foraminifera (see Ohkushi et al. 2000), clearly shows increased dissolution during interglacial periods, when species diversity is

TABLE 8. Foraminiferal model-averaged parameter estimates and confidence intervals (CI). Bold: CIs that exclude zero.

	Coefficient	Lower CI	Upper CI
Foraminiferal diversity $E(S_{200})$			
$P^2$	0.004	-0.009	0.017
$P$	-0.143	-0.618	0.331
$T$	1.620	-2.210	5.450
Foraminiferal abundance BFAR			
$P^2$	-0.2	-1.8	1.4
$P$	434.0	<b>332.0</b>	<b>535.0</b>
$SP$	40.5	-8.4	89.4
$T$	-274.0	-1210.0	660.0
Foraminiferal faunal composition MDS 1			
$P^2$	0.0000	-0.0001	0.0002
$P$	0.0029	-0.0069	0.0127
$T$	-0.1950	<b>-0.3180</b>	<b>-0.0720</b>

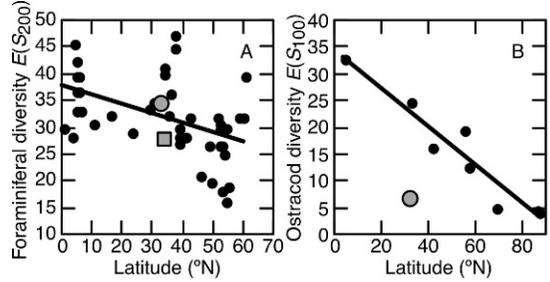


FIGURE 3. Comparison between modern coretop (= Holocene) North Atlantic and Shatsky Rise species diversities. A, Foraminiferal diversity. B, Ostracod diversity. Solid circle, North Atlantic diversity; gray circle, Shatsky Rise diversity; gray square, Hess Rise foraminiferal diversity, which is calculated from Ujiie (2003) census data. Regression lines for North Atlantic diversity ( $p = 0.0002$ ,  $r^2 = 0.9135$  for ostracods;  $p = 0.0009$ ,  $r^2 = 0.2327$  for foraminifera). North Atlantic foraminiferal diversities  $E(S_{200})$  are calculated from Sun et al. (2006) census data (see Corliss et al. 2009). See Supplement Table S9 for North Atlantic ostracod  $E(S_{100})$ .

elevated (Fig. 4). Thus, depressed species diversity in glacial intervals cannot be the result of selective dissolution and removal of thin-shelled species during these intervals.

*Faunal Composition and Abundance.*—The ostracod ordination first axis shows systematic glacial-interglacial variation. In particular, interglacial peaks in the global oxygen isotope stack record correspond well with negative peaks in MDS1 (Fig. 5). MDS1 scores track temporal trends of the two dominant genera, *Krithe* and *Henryhowella*, and are especially tightly correlated with the latter (Fig. 5; MDS1 versus *Henryhowella*:  $r^2 = 0.651$ ; MDS1 versus *Krithe*:  $r^2 = 0.267$ ). The foraminiferal MDS first axis also shows similar glacial-interglacial variation, although the correspondence is perhaps noisier than for the ostracods. MDS1 is highly correlated with the relative abundance of two of the three dominant foraminifera species, *Alabaminella weddellensis* and *Uvigerina peregrina* (Fig. 6; MDS1 versus *Alabaminella weddellensis*:  $r^2 = 0.415$ ; MDS1 versus *Epistominella exigua*:  $r^2 = 0.015$ ; MDS1 versus *Uvigerina peregrina*:  $r^2 = 0.722$ ).

Both benthic foraminiferal (BFAR) and ostracod accumulation rates (BOAR) are generally higher during peak glacial and stadial periods represented by the global  $\delta^{18}\text{O}$  stack (Fig. 7). These systematic glacial-interglacial

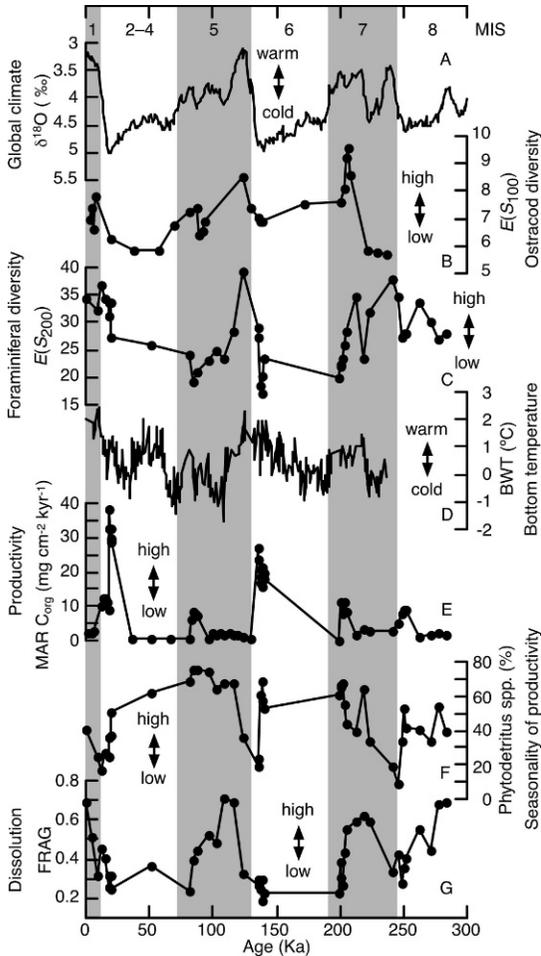


FIGURE 4. Relationship between North Pacific deep-sea species diversity and paleoclimatic and paleoceanographic proxy records. A, Deep-sea oxygen isotope curve (LR04 global stack [Lisiecki and Raymo 2005]). B, Ostracod species diversity  $E(S_{100})$ . C, Foraminiferal species diversity  $E(S_{200})$ . D, Benthic foraminiferal Mg/Ca-based bottom-water temperature (BWT) (Martin et al. 2002). E, Productivity proxy of mass accumulation rate of organic carbon (MAR  $C_{org}$ ). F, Relative abundance of phytodetritus species (*Epistominella exigua* and *Alabaminella weddellensis*), proxy of seasonality of productivity. G, Carbonate dissolution index, planktic foraminiferal fragmentation (FRAG) (see Ohkushi et al. 2000). The oxygen isotope curve represents global climate changes, and the lower isotope values indicate warmer, interglacial intervals. Marine isotope stages (MIS) are labeled and interglacial periods are shaded.

faunal and abundance changes further support a global nature of ecosystem response to orbital-scale climate changes. However, it is also true that the time series of these environmental and faunal parameters differ from each other, and thus it may be possible to disentangle possible causal relationships between

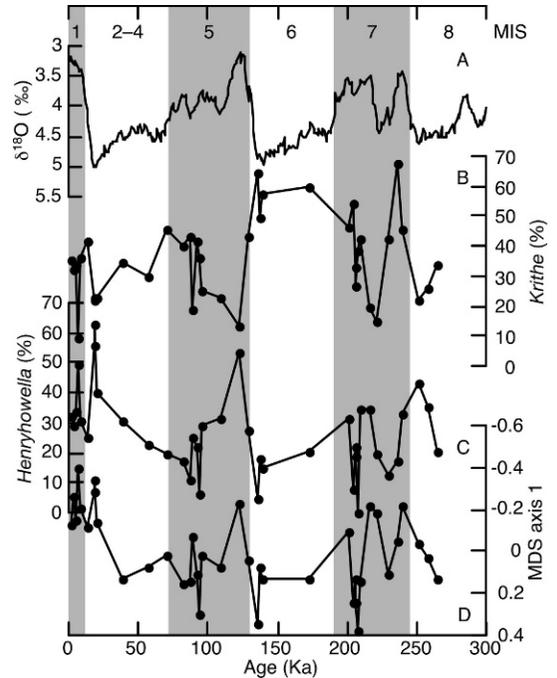


FIGURE 5. Relationship between climate change and ostracod faunal composition, showing deep-sea oxygen isotope curve (Lisiecki and Raymo 2005) (A), relative abundance of *Kriithe* (B) and *Henryhowella* (C), and MDS first axis (D).

them. The next section presents one approach, multiple regression, for doing so.

#### Regression Models to Evaluate Potential Drivers of Deep-Sea Ecological Change

*Species Diversity.*—Ostracod diversity is most strongly predicted as a quadratic function of productivity (Table 1, Fig. 8). The three models that receive more support than the null (intercept only) model all include a squared productivity term, and in all of these models, this term is significant (Table 1). The coefficient for the squared productivity term is negative, indicating an intermediate maximum with respect to productivity, i.e., a hump-shaped relationship (although the confidence interval slightly overlaps with zero; Table 7). All other models receive minimal support, and in particular there is little evidence for relationships between diversity and either temperature or seasonality of productivity (Table 1, Fig. 8).

For foraminiferal diversity, there is weak indication that diversity increases linearly with

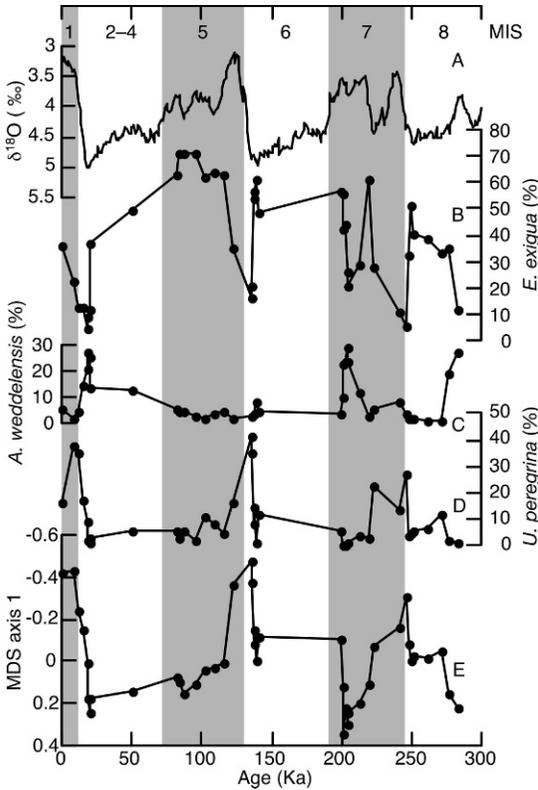


FIGURE 6. Relationship between climate change and foraminiferal faunal composition, showing deep-sea oxygen isotope curve (Lisiecki and Raymo 2005) (A); relative abundance of *Epistominella exigua* (B), *Alabaminella weddellensis* (C), and *Uvigerina peregrina* (D); and MDS first axis (E).

temperature (models 2 and 3 in Table 2; Fig. 8). However, environmental proxies have low predictive power for foraminiferal diversity; the best-supported causal model receives slightly less support than the null model (Table 2), and no model-averaged coefficients are significantly different from zero (Table 8). Seasonality of productivity, which was not included in our models for foraminifera, may play a role here, because seasonality has been shown to be an important determinant of modern deep-sea benthic foraminiferal diversity in the North Atlantic Ocean (Corliss et al. 2009). Although foraminiferal diversity and seasonality have a significant and negative relationship in our data set (Ohkushi et al. 2000), it is difficult to rule out mathematical artifact as a cause (see “Materials and Methods”).

Other published case studies report different correlates of diversity from those found

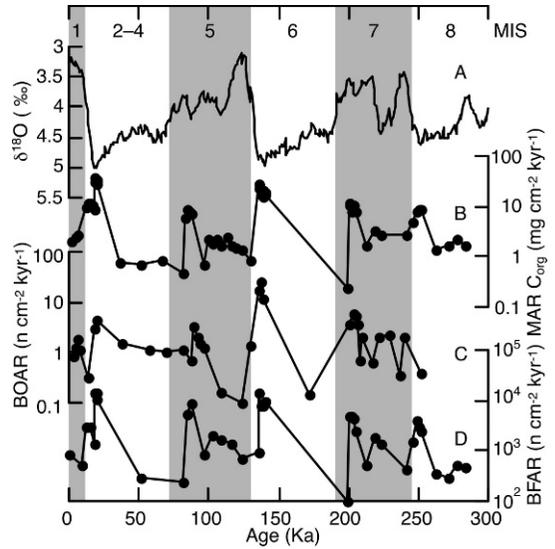


FIGURE 7. Relationship among climate change, surface productivity and abundance. A, Deep-sea oxygen isotope curve (Lisiecki and Raymo 2005). B, MAR  $C_{org}$ . C, Benthic ostracod accumulation rate (BOAR). D, Benthic foraminiferal accumulation rate (BFAR). MAR  $C_{org}$  is a proxy for particulate organic carbon flux to the ocean floor, i.e., food supply. BFAR was calculated from the new age model.

here: diversities often show significant positive relationship with temperature both in ostracods (Cronin and Raymo 1997; Cronin et al. 1999; Yasuhara and Cronin 2008; Yasuhara et al. 2009b) and foraminifera (Hunt et al. 2005), and foraminiferal diversity can have a hump-shaped relationship with productivity (Wollenburg and Kuhnt 2000; Gooday 2003a). We found no significant correlation between seasonality of productivity and ostracod diversity in any models, but a recent study of modern deep-sea foraminifera found a negative effect of seasonality on diversity (Corliss et al. 2009). Different factors may therefore dominate in different regions and/or taxonomic groups.

*Faunal Composition.*—The regressions of ostracod faunal composition (MDS1) parallel the ostracod diversity result, which suggest faunal composition as a quadratic function of productivity (Table 3, Fig. 9). Four of the five best-supported models include a significant squared productivity term (Table 3). This hump-shaped relationship implies that faunas at low and high levels of productivity are more similar to each other than either is to faunas

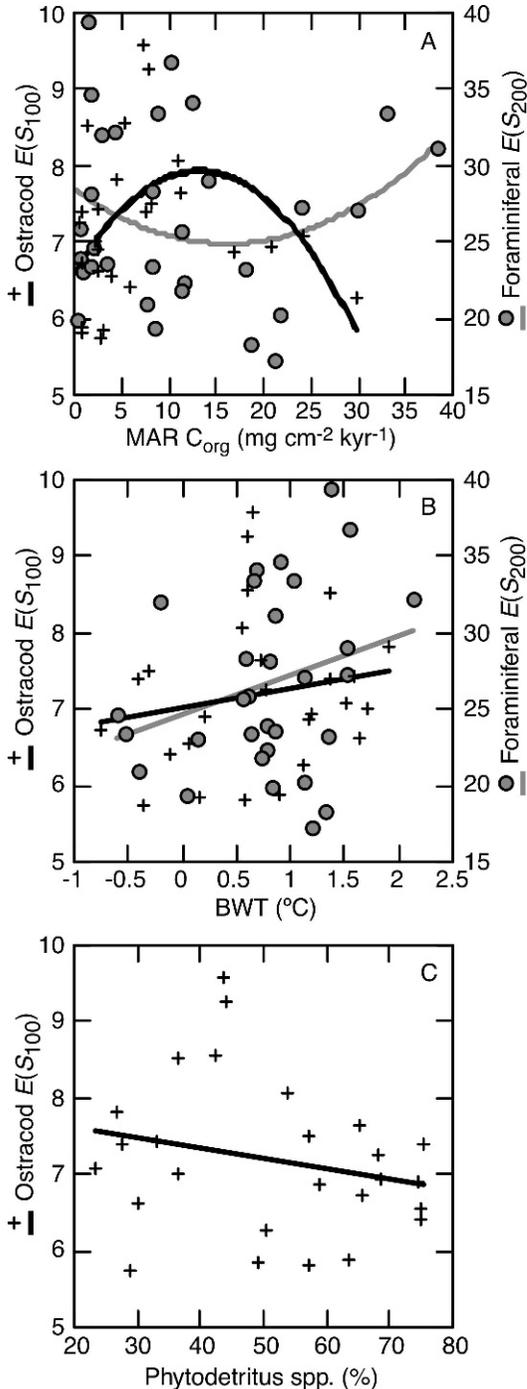


FIGURE 8. Species diversity as a function of productivity (A), temperature (B), and seasonality of productivity (C). Linear and/or second-order polynomial regression lines are shown, but these may not correspond to the best-fitting model (see Tables 1, 2, 7, and 8 for detailed statistical results).

during intervals of intermediate productivity. The two dominant genera may be driving this pattern: *Krithe* is most abundant at intermediate levels of food availability, and *Henryhowella* shows the opposite pattern (Fig. 10). Didié et al. (2002) suggested that another ostracod taxon, *Eucythere*, peaks in abundance at intermediate levels of productivity. Although this genus is too rare in our study to evaluate this claim in detail, such patterns may be fairly common. If so, this would require reconsideration of the practice of assuming linear relationships between the relative abundance of productivity-indicator taxa and surface productivity (Cronin et al. 1995; Yasuhara et al. 2008b; Alvarez Zarikian et al. 2009). Instead, approaches that consider the niche position of taxa along gradients (Holland 2003) may be more informative.

The quadratic relationships between productivity and relative abundances of these taxa are somewhat at odds with recent suggestions that *Krithe* is an indicator of low-food conditions and *Henryhowella* indicates ample food supply (Didié et al. 2002). We must therefore regard the environmental preferences of even these very common genera as still uncertain. Nonlinear patterns between productivity and relative abundance may complicate attempts to infer general relationships because the form of the relationship will change depending on the productivity range of a particular locality.

In addition to productivity, several models support a significant relationship between ostracod MDS1 and temperature (models 1, 2, and 8 in Table 3; Fig. 9), a result consistent with previous suggestions (Cronin et al. 1996, 2002; Didié and Bauch 2000; Didié et al. 2002; Alvarez Zarikian et al. 2009).

All foraminiferal faunal composition (MDS1) models including the temperature term receive moderate and similar amounts of model support, and this term is significant in all of these models. No other models receive more than minimal support (Table 4), and only the coefficient for the temperature term is significantly different from zero when averaged across models (Table 8, Fig. 9). This result suggests that foraminiferal composition can be strongly modulated by temperature, even though this factor is often emphasized

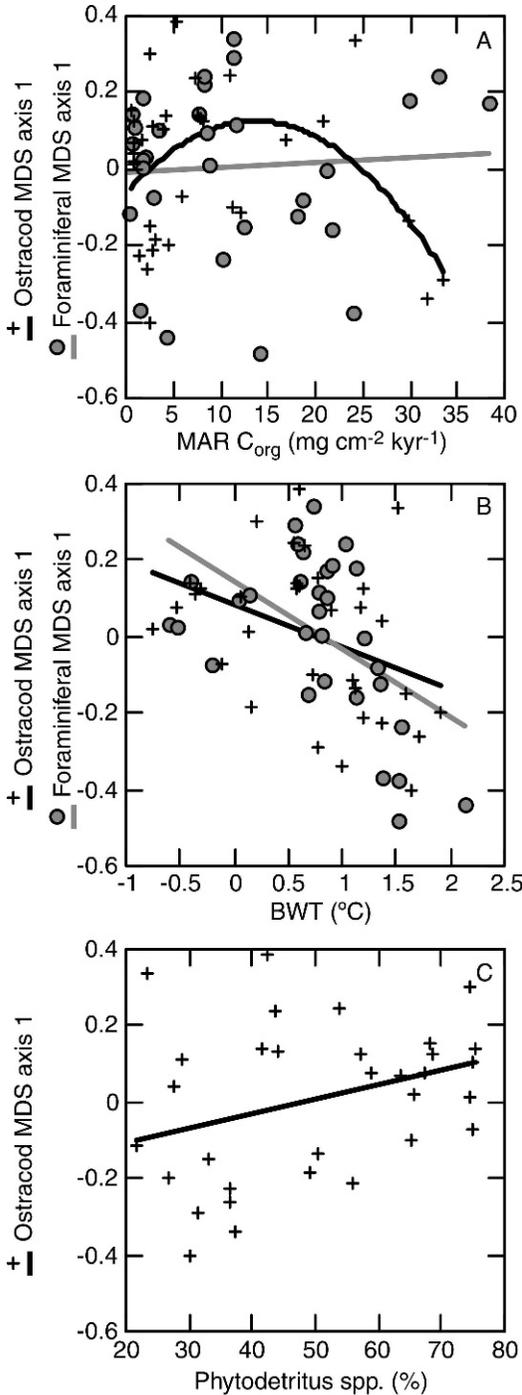


FIGURE 9. Faunal composition (MDS1) as a function of productivity (A), temperature (B), and seasonality of productivity (C). Linear and/or second-order polynomial regression lines are shown, but these may not correspond to the best-fitting model (see Tables 3, 4, 7, and 8 for detailed statistical results).

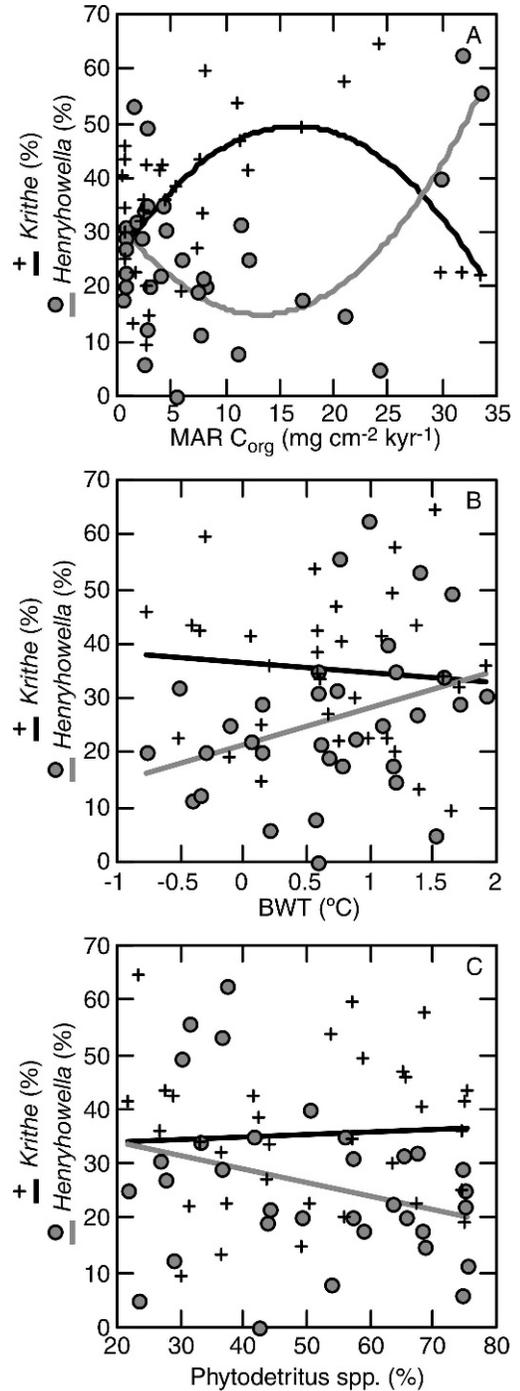


FIGURE 10. Relative abundance of dominant ostracod genera *Krithe* and *Henryhowella* as a function of productivity (A), temperature (B), and seasonality of productivity (C). Linear and/or second-order polynomial regression lines are shown.

less than food-related parameters by researchers (Hayward et al. 2002; Gooday 2003a). However, we note that two of three dominant foraminiferal species, *Alabaminella weddellensis* and *Epistominella exigua*, are known as indicator species for seasonal productivity (Sun et al. 2006), but we cannot evaluate seasonality in these analysis.

**Abundance.**—Accumulation rates for ostracods (BOAR) and foraminifera (BFAR) differ in their relationship to environmental factors. For ostracods, all models that receive more than negligible support indicate a hump-shaped relationship between abundance and productivity (Table 5). Only the coefficient for the squared productivity term is significantly different from zero, and its negative value indicates an intermediate maximum with respect to productivity (Table 7, Fig. 11). In contrast, model fits suggest that BFAR increases linearly with productivity (Tables 6, 8, Fig. 11). In addition to productivity, several models support a significant positive relationship between BFAR and seasonality of productivity (models 1 and 3 in Table 6; note that a slightly negative regression line is shown in Figure 11 based on simple linear regression [= model 11 in Table 6, insignificant], but the multiple regression results revealed the positive relationship, i.e., the coefficient for the seasonality term is positive in models 1 and 3), although the confidence interval slightly overlaps with zero (Table 8). These results indicate benthic-pelagic coupling (close link between benthic and planktic ecosystems) for the last 300 Kyr and support studies showing that deep-sea ecosystems are sensitive to changes in flux of organic matter (Gooday 1988; Kitazato et al. 2000). In foraminifera, pulsed organic matter input (i.e., high seasonality of productivity) should strongly enhance reproduction of opportunistic species (= “phytodetritus species”) and, consequently, may positively affect total foraminiferal abundance, suggesting higher sensitivity of foraminifera to seasonality of productivity than ostracods. Moreover, the linear relationship between BFAR and productivity supports the widespread use of BFAR as a proxy for surface paleoproductivity (e.g., Nees et al. 1999; Herguera 2000;

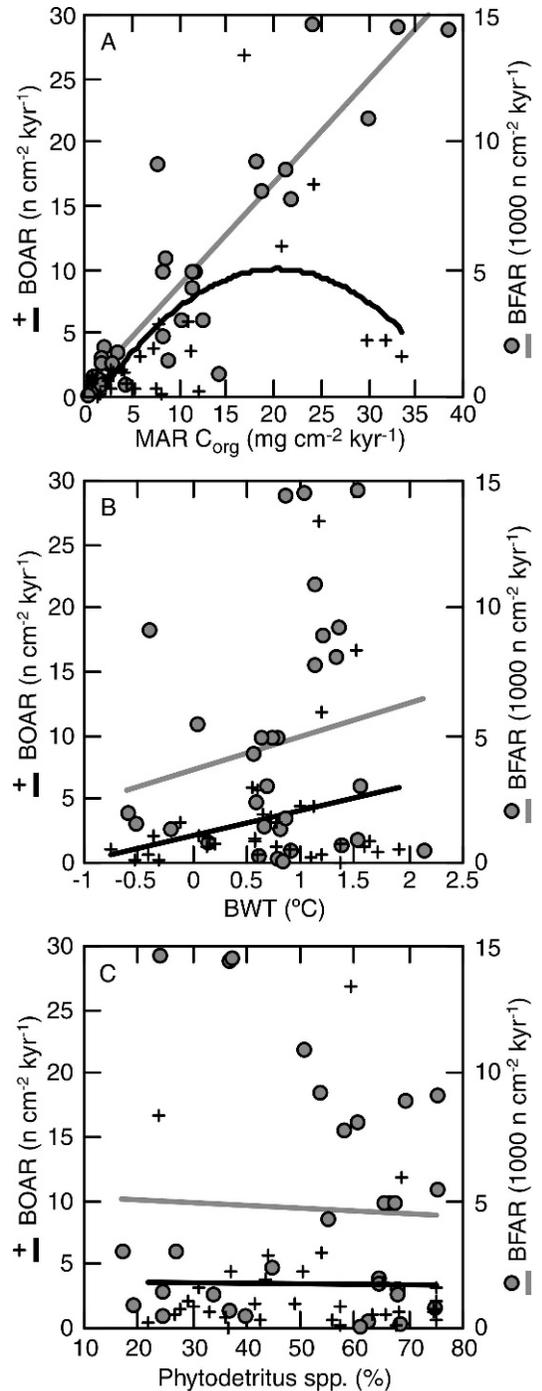


FIGURE 11. Abundance (BOAR and BFAR) as a function of productivity (A), temperature (B), and seasonality of productivity (C). Linear and/or second-order polynomial regression lines are shown, but these may not correspond to the best-fitting model (see Tables 5–8 for detailed statistical results).

Rasmussen et al. 2002; Gooday 2003a), but taking into account seasonality of productivity may be important for development of better paleoproductivity proxy using foraminiferal abundance. Because greater surface productivity translates into more food for benthic organisms, the decrease in ostracod abundances at very high productivity values may be somewhat surprising. It remains to be seen if this pattern is general, but if so, it might relate to niche differences between ostracods and foraminifera in their preference for habitats with relatively abundant food and possibly lower oxygen concentrations.

### Conclusions

Climatically driven deep-sea biodiversity and ecosystem changes occur not only in the North Atlantic but also in the North Pacific Ocean during late Quaternary glacial-interglacial cycles. Ostracod and foraminiferal species diversities, faunal compositions, and abundance are all sensitive to late Quaternary climate change. Diversity in both taxa is systematically lower during glacial periods and higher during interglacials on Shatsky Rise, which is similar to patterns from the North Atlantic Ocean. These Shatsky Rise microfossils also provided insights into unique characteristics of remote oceanic plateau ecosystems. In modern Shatsky Rise, ostracod diversity is depressed but foraminiferal diversity is comparable to that of similar latitude North Atlantic sites. These differences, along with the much greater endemism of the ostracod fauna, are likely explained by the isolation of this oceanic plateau and the poor dispersal ability of ostracods compared to foraminifera.

At Shatsky Rise, ostracod diversity is a hump-shaped function of surface productivity, whereas there is a weak tendency for foraminiferal diversity to increase linearly with bottom-water temperature. Relative abundance of dominant ostracod species and MDS first axis showed systematic glacial-interglacial changes, suggesting response of faunal composition to orbital climate changes. The multiple regression results suggested that these faunal composition patterns are explained as a quadratic function of productivity and a linear function of temperature in

ostracods and foraminifera, respectively. BFAR and BOAR were higher during glacials and lower during interglacials, but BFAR is a linear function of productivity and seasonality of productivity, whereas BOAR declines at very high productivity values.

These findings underscore the global-scale link between deep-sea ecosystems and climate change, and highlight differences in biotic response across different taxonomic groups and different regions of the ocean. More broadly, these analyses support the utility of combining biological and macroecological perspectives (Brown and Maurer 1989; Jablonski et al. 2003; McClain et al. 2009a) with paleoceanographic data to better understand the history of the biosphere.

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### Literature Cited

- Alvarez Zarikian, C. A., A. Y. Stepanova, and J. Grützner. 2009. Glacial-interglacial variability in deep sea ostracod assemblage composition at IODP Site U1314 in the subpolar North Atlantic. *Marine Geology* 258:69–87.
- Alve, E., and S. T. Goldstein. 2003. Propagule transport as a key method of dispersal in benthic foraminifera (Protista). *Limnology and Oceanography* 48:2163–2170.
- . 2010. Dispersal, survival and delayed growth of benthic foraminiferal propagules. *Journal of Sea Research* 63:36–51.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912–923.
- Bartoń, K. 2009. MuMIn: Multi-model inference. R package version 0.12.2/r18. <http://R-Forge.R-project.org/projects/mumin/>.
- Berger, W. H., C. G. Adelseck, and L. A. Mayer. 1976. Distribution of carbonate in surface sediments of the Pacific Ocean. *Journal of Geophysical Research* 81:2617–2627.
- Boomer, I., and R. C. Whitley. 1995. Cenozoic Ostracoda from guyots in the western Pacific: Holes 865B and 866B (Leg 143). *Proceedings of the Ocean Drilling Program, Scientific Results* 143:75–86.

- Brandão, S. N., J. Sauer, and I. Schön. 2010. Circumantarctic distribution in Southern Ocean benthos? A genetic test using the genus *Macroscapia* (Crustacea, Ostracoda) as a model. *Molecular Phylogenetics and Evolution* 55:1055–1069.
- Brandt, A., A. J. Gooday, S. N. Brandão, S. Brix, W. Brökeland, T. Cedhagen, M. Choudhury, N. Cornelius, B. Danis, I. De Mesel, R. J. Diaz, D. C. Gillan, B. Ebbe, J. A. Howe, D. Janussen, S. Kaiser, K. Linse, M. Maljutina, J. Pawlowski, M. Raupach, and A. Vanreusel. 2007. First insights into the biodiversity and biogeography of the Southern Ocean deep sea. *Nature* 447:307–311.
- Brown, J. H., and B. A. Maurer. 1989. Macroecology: the division of food and space among species on continents. *Science* 243:1145–1150.
- Butlin, R., I. Schön, and K. Martins. 1998. Asexual reproduction in nonmarine ostracods. *Heredity* 81:473–480.
- Carney, R. S. 2005. Zonation of deep biota on continental margins. *Oceanography and Marine Biology: An Annual Review* 43:211–278.
- Chaplin, J. A., J. E. Havel, and P. D. N. Hebert. 1994. Sex and ostracodes. *Trends in Ecology and Evolution* 9:435–439.
- Corliss, B. H., C. W. Brown, X. Sun, and W. J. Showers. 2009. Deep-sea benthic diversity linked to seasonality of pelagic productivity. *Deep-Sea Research I* 56:835–841.
- Cronin, T. M., and G. S. Dwyer. 2003. Deep sea ostracodes and climatic change. *Paleontological Society Papers* 9:247–263.
- Cronin, T. M., and M. E. Raymo. 1997. Orbital forcing of deep-sea benthic species diversity. *Nature* 385:624–627.
- Cronin, T. M., T. R. Holtz Jr., R. Stein, R. Spielhagen, D. Futterer, and J. Wollenburg. 1995. Late Quaternary paleoceanography of the Eurasian Basin, Arctic Ocean. *Paleoceanography* 10:259–281.
- Cronin, T. M., M. E. Raymo, and K. P. Kyle. 1996. Pliocene (3.2–2.4 Ma) ostracode faunal cycles and deep ocean circulation, North Atlantic Ocean. *Geology* 24:695–698.
- Cronin, T. M., D. M. DeMartino, G. S. Dwyer, and J. Rodriguez-Lazaro. 1999. Deep-sea ostracode species diversity: response to late Quaternary climate change. *Marine Micropaleontology* 37:231–249.
- Cronin, T. M., I. Boomer, G. S. Dwyer, and J. Rodriguez-Lazaro. 2002. Ostracoda and paleoceanography. Pp. 99–119 in *Holmes and Chivas 2002*.
- Culver, S. J., and M. A. Buzas. 2000. Global latitudinal species diversity gradient in deep-sea benthic foraminifera. *Deep-Sea Research I* 47:259–275.
- Danovaro, R., A. Dell'Anno, and A. Pusceddu. 2004. Biodiversity response to climate change in a warm deep sea. *Ecology Letters* 7:821–828.
- Diaz, R. J., and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321:926–929.
- Didié, C., and H. A. Bauch. 2000. Species composition and glacial-interglacial variations in the ostracode fauna of the northeast Atlantic during the past 200,000 years. *Marine Micropaleontology* 40:105–129.
- . 2002. Implications of upper Quaternary stable isotope records of marine ostracodes and benthic foraminifers for paleoecological and paleoceanographical reconstructions. Pp. 279–299 in *Holmes and Chivas 2002*.
- Didié, C., H. A. Bauch, and J. P. Helmke. 2002. Late Quaternary deep-sea ostracodes in the polar and subpolar North Atlantic: paleoecological and paleoenvironmental implications. *Paleoceanography, Palaeoclimatology, Palaeoecology* 184:195–212.
- Elderfield, H., M. Greaves, S. Barker, I. R. Hall, A. Tripathi, P. Ferretti, S. Crowhurst, L. Booth, and C. Daunt. 2010. A record of bottom-water temperature and seawater  $\delta^{18}\text{O}$  for the Southern Ocean over the past 440 kyr based on Mg/Ca of benthic foraminiferal *Uvigerina* spp. *Quaternary Science Reviews* 29:160–169.
- Garcia, H. E., R. A. Locarnini, T. P. Boyer, and J. I. Antonov. 2006. *World Ocean Atlas 2005*, Vol. 3. Dissolved oxygen, apparent oxygen utilization, and oxygen saturation. U.S. Government Printing Office, Washington, D.C.
- Glover, A. G., A. J. Gooday, D. M. Bailey, D. S. M. Billett, P. Chevaldonne, A. Colaco, J. Copley, D. Cuvelier, D. Desbruyeres, V. Kalogeropoulou, M. Klages, N. Lampadariou, C. Lejeusne, N. C. Mestre, G. L. J. Paterson, T. Perez, H. Ruhl, J. Sarrazin, T. Soltwedel, E. H. Soto, S. Thatje, A. Tselepidis, S. Van Gaever, and A. Vanreusel. 2010. Temporal change in deep-sea benthic ecosystems: a review of the evidence from recent time-series studies. *Advances in Marine Biology* 58:1–95.
- Goldstein, S. T. 1999. Foraminifera: a biological overview. Pp. 37–55 in B. K. Sen Gupta, ed. *Modern Foraminifera*. Kluwer Academic, Dordrecht.
- Gooday, A. J. 1988. A response by benthic foraminifera to the deposition of phytodetritus in the deep sea. *Nature* 332:70–73.
- . 1994. The biology of deep-sea foraminifera: a review of some advances and their applications in paleoceanography. *Palaios* 9:14–31.
- . 2003a. Benthic foraminifera (Protista) as tools in deep-water paleoceanography: environmental influences on faunal characteristics. *Advances in Marine Biology* 46:1–90.
- . 2003b. Benthic foraminifera. Pp. 274–286 in J. Steele et al., eds. *Encyclopedia of ocean sciences*. Elsevier, Amsterdam.
- Gooday, A. J., L. A. Levin, P. Linke, and H. Heeger. 1992. The role of benthic Foraminifera in deep-sea food webs and carbon cycling. Pp. 63–91 in G. T. Rowe and V. Pariente, eds. *Deep-sea food chains and the global carbon cycle*. Kluwer Academic, Rotterdam.
- Hayward, B. W., H. Neil, R. Carter, H. R. Grenfell, and J. J. Hayward. 2002. Factors influencing the distribution patterns of recent deep-sea benthic foraminifera, east of New Zealand, Southwest Pacific Ocean. *Marine Micropaleontology* 46:139–176.
- Herguera, J. C. 2000. Last glacial paleoproductivity patterns in the eastern equatorial Pacific: benthic foraminifera records. *Marine Micropaleontology* 40:259–275.
- Hessler, R. R., and H. L. Sanders. 1967. Faunal diversity in the deep-sea. *Deep-Sea Research* 14:65–78.
- Holland, S. M. 2003. Confidence limits on fossil ranges that account for facies changes. *Paleobiology* 29:468–479.
- Holmes, J. A., and A. R. Chivas, eds. 2002. *The Ostracoda: applications in Quaternary research*. American Geophysical Union, Washington, D.C.
- Horne, D. J., A. Cohen, and K. Martens. 2002. Taxonomy, morphology and biology of Quaternary and living Ostracoda. Pp. 5–36 in *Holmes and Chivas 2002*.
- Hunt, G., T. M. Cronin, and K. Roy. 2005. Species-energy relationship in the deep sea: a test using the Quaternary fossil record. *Ecology Letters* 8:739–747.
- Ikeya, N., and M. Kato. 2000. The life history and culturing of *Xestoleberis hanaui* (Crustacea, Ostracoda). *Hydrobiologia* 419:149–159.
- Jablonski, D., K. Roy, and J. W. Valentine. 2003. Evolutionary macroecology and the fossil record. Pp. 368–390 in T. M. Blackburn and K. J. Gaston, eds. *Macroecology: concepts and consequences*. Blackwell, Oxford.
- . 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102–106.
- Jellinek, T., and K. M. Swanson. 2003. Report on the taxonomy, biogeography and phylogeny of mostly living benthic Ostracoda (Crustacea) from deep-sea samples (Intermediate Water depths) from the Challenger Plateau (Tasman Sea) and Campbell Plateau (Southern Ocean), New Zealand. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 558:1–329.

- Kawabe, M., S. Fujio, D. Yanagimoto, and K. Tanaka. 2009. Water masses and currents of deep circulation southwest of the Shatsky Rise in the western North Pacific. *Deep-Sea Research I* 56:1675–1687.
- Kawagata, S. 2001. Tasman Front shifts and associated paleoceanographic changes during the last 250,000 years: foraminiferal evidence from the Lord Howe Rise. *Marine Micropaleontology* 41:167–191.
- Kawahata, H., K. Ohkushi, and Y. Hatakeyama. 1999. Comparative late Pleistocene paleoceanographic changes in the mid latitude boreal and austral western Pacific. *Journal of Oceanography* 55:747–761.
- Kitazato, H., Y. Shirayama, T. Nakatsuka, S. Fujiwara, M. Shimanaga, Y. Kato, Y. Okada, J. Kanda, A. Yamaoka, T. Masuzawa, and K. Suzuki. 2000. Seasonal phytodetritus deposition and responses of bathyal benthic foraminiferal populations in Sagami Bay, Japan: preliminary results from "Project Sagami 1996–1999." *Marine Micropaleontology* 40:135–149.
- Larwood, J., and R. C. Whatley. 1993. Tertiary to Recent evolution of Ostracoda in isolation on seamounts. Pp. 531–549 in K. G. McKenzie and P. J. Jones, eds. *Ostracoda in the earth and life sciences*. A. A. Balkema, Rotterdam.
- Lecroq, B., A. J. Gooday, and J. Pawlowski. 2009. Global genetic homogeneity in the deep-sea foraminiferan *Epistominella exigua* (Rotalida: Pseudoparrellidae). *Zootaxa* 2096:23–32.
- Levin, L. A. 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanography and Marine Biology* 41:1–45.
- Levin, L. A., R. J. Etter, M. A. Rex, A. J. Gooday, C. R. Smith, J. Pineda, C. T. Stuart, R. R. Hessler, and D. Pawson. 2001. Environmental influences on regional deep-sea species diversity. *Annual Review of Ecology and Systematics* 32:51–93.
- Levin, L. A., W. Ekau, A. J. Gooday, F. Jorissen, J. J. Middelburg, W. Naqvi, C. Neira, N. N. Rabalais, and J. Zhang. 2009. Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences* 6:2063–2098.
- Lisiecki, L. E., and M. E. Raymo. 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic  $\delta^{18}\text{O}$  records. *Paleoceanography* 20:PA1003. doi:10.1029/2004PA001071.
- Locarnini, R. A., A. V. Mishonov, J. I. Antonov, T. P. Boyer, and H. E. Garcia. 2006. *World Ocean Atlas 2005*, Vol. 1. Temperature. U.S. Government Printing Office, Washington, D.C.
- Loubere, P., and M. Fariduddin. 2003. Patterns of export production in the eastern equatorial Pacific over the past 130,000 years. *Paleoceanography* 18:1028. doi:10.1029/2001PA000658.
- Maeda, L., H. Kawahata, and M. Nohara. 2002. Fluctuation of biogenic and abiogenic sedimentation on the Shatsky Rise in the western North Pacific during the late Quaternary. *Marine Geology* 189:197–214.
- Martin, P. A., D. W. Lea, Y. Rosenthal, N. J. Shackleton, M. Sarnthein, and T. Papenfuss. 2002. Quaternary deep sea temperature histories derived from benthic foraminiferal Mg/Ca. *Earth and Planetary Science Letters* 198:193–209.
- McClain, C. R., and J. P. Barry. 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* 91:964–976.
- McClain, C. R., M. A. Rex, and R. J. Etter. 2009a. Patterns in deep-sea macroecology. Pp. 65–100 in J. D. Witman and K. Roy, eds. *Marine macroecology*. University of Chicago Press, Chicago.
- McClain, C. R., L. Lundsten, M. Ream, J. Barry, and A. DeVogelaere. 2009b. Endemicity, biogeography, composition, and community structure on a Northeast Pacific seamount. *PLoS ONE* 4:e4141. doi:10.1371/journal.pone.0004141.
- Nees, S., L. Armand, P. De Deckker, M. Labracherie, and V. Passlow. 1999. A diatom and benthic foraminiferal record from the South Tasman Rise (southeastern Indian Ocean): implications for palaeoceanographic changes for the last 200,000 years. *Marine Micropaleontology* 38:69–89.
- Ohkushi, K., E. Thomas, and H. Kawahata. 2000. Abyssal benthic foraminifera from the northwestern Pacific (Shatsky Rise) during the last 298 kyr. *Marine Micropaleontology* 38:119–147.
- Oksanen, J., G. B. Blanchet, R. Kindt, P. Legendre, B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and W. H. 2010. *vegan*: community ecology package. R package, Version 1.17-4. <http://CRAN.R-project.org/package=vegan>.
- Paillard, D., L. Labeyrie, and P. Yiou. 1996. Macintosh program performs time-series analysis. *EOS, Transactions, American Geophysical Union* 77:379.
- Pawlowski, J., J. Fahrni, B. Lecroq, D. Longet, N. Cornelius, L. Ecoffier, T. Cedhagen, and A. J. Gooday. 2007. Bipolar gene flow in deep-sea benthic foraminifera. *Molecular Ecology* 16:4089–4096.
- R Development Core Team. 2010. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>.
- Rasmussen, T. L., E. Thomsen, S. R. Troelstra, A. Kuijpers, and M. A. Prins. 2002. Millennial-scale glacial variability versus Holocene stability: changes in planktic and benthic foraminifera faunas and ocean circulation in the North Atlantic during the last 60,000 years. *Marine Micropaleontology* 47:143–176.
- Rex, M. A. 1973. Deep-sea species diversity: decreased gastropod diversity at abyssal depths. *Science* 181:1051–1053.
- . 1981. Community structure in the deep-sea benthos. *Annual Review of Ecology and Systematics* 12:331–353.
- Rex, M. A., and R. J. Etter. 2010. *Deep-sea biodiversity: pattern and scale*. Harvard University Press, Cambridge.
- Rex, M. A., C. T. Stuart, R. R. Hessler, J. A. Allen, H. L. Sanders, and G. D. F. Wilson. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365:636–639.
- Rex, M. A., C. T. Stuart, and G. Coyne. 2000. Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. *Proceedings of the National Academy of Sciences USA* 97:4082–4085.
- Rex, M. A., J. A. Crame, C. T. Stuart, and A. Clarke. 2005. Large-scale biogeographic patterns in marine mollusks: a confluence of history and productivity? *Ecology* 86:2288–2297.
- Rex, M. A., R. J. Etter, J. S. Morris, J. Crouse, C. R. McClain, N. A. Johnson, C. T. Stuart, J. W. Deming, R. Thies, and R. Avery. 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Marine Ecology Progress Series* 317:1–8.
- Ruhl, H. A., and K. L. Smith Jr. 2004. Shifts in deep-sea community structure linked to climate and food supply. *Science* 305:513–515.
- Ruhl, H. A., J. A. Ellena, and K. L. Smith Jr. 2008. Connections between climate, food limitation, and carbon cycling in abyssal sediment communities. *Proceedings of the National Academy of Sciences USA* 105:17006–17011.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist* 102:243–282.
- Sanders, H. L., and R. R. Hessler. 1969. Ecology of the deep-sea benthos. *Science* 163:1419–1424.
- Schellenberg, S. A. 2007. Marine ostracods. Pp. 2046–2062 in S. A. Elias, ed. *Encyclopedia of Quaternary science*. Elsevier, Amsterdam.
- Shimanaga, M., H. Kitazato, and Y. Shirayama. 2000. Seasonal patterns of vertical distribution between meiofaunal groups in relation to phytodetritus deposition in the bathyal Sagami Bay, central Japan. *Journal of Oceanography* 56:379–387.
- Smith, C. R., W. Berelson, D. J. Demaster, F. C. Dobbs, D. Hammond, D. J. Hoover, R. H. Pope, and M. Stephens. 1997. Latitudinal variations in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. *Deep-Sea Research II* 44:2295–2317.

- Smith, K. L. Jr, H. A. Ruhl, B. J. Bett, D. S. M. Billett, R. S. Lampitt, and R. S. Kaufmann. 2009. Climate, carbon cycling, and deep-ocean ecosystems. *Proceedings of the National Academy of Sciences U.S.A.* 106:19211–19218.
- Sosdian, S., and Y. Rosenthal. 2009. Deep-sea temperature and ice volume changes across the Pliocene-Pleistocene climate transitions. *Science* 325:306–310.
- Steineck, P. L., and E. Thomas. 1996. The latest Paleocene crisis in the deep sea: ostracode succession at Maud Rise, Southern Ocean. *Geology* 24:583–586.
- Stuart, C. T., M. A. Rex, and R. J. Etter. 2003. Large-scale spatial and temporal patterns of deep-sea benthic species diversity. Pp. 295–311 in P. A. Tyler, ed. *Ecosystems of the deep oceans*. Elsevier, Amsterdam.
- Sun, X., B. H. Corliss, C. W. Brown, and W. J. Showers. 2006. The effect of primary productivity and seasonality on the distribution of deep-sea benthic foraminifera in the North Atlantic. *Deep-Sea Research I* 53:28–47.
- Thomas, E., and A. J. Gooday. 1996. Cenozoic deep-sea benthic foraminifera: tracers for changes in oceanic productivity? *Geology* 24:355–358.
- Thomas, E., L. Booth, M. Maslin, and N. J. Shackleton. 1995. Northeastern Atlantic benthic foraminifera during the last 45,000 years: changes in productivity seen from the bottom up. *Paleoceanography* 10:545–562.
- Tittensor, D. P., M. A. Rex, C. T. Stuart, C. R. McClain, and C. R. Smith. 2011. Species-energy relationships in deep-sea molluscs. *Biology Letters*. doi:10.1098/rsbl.2010.1174.
- Ujiié, H. 2003. A 370-ka paleoceanographic record from the Hess Rise, central North Pacific Ocean, and an indistinct 'Kuroshio Extension.' *Marine Micropaleontology* 49:21–47.
- Webb, A. E., L. R. Leighton, S. A. Schellenberg, E. A. Landau, and E. Thomas. 2009. Impact of the Paleocene-Eocene thermal maximum on deep-ocean microbenthic community structure: using rank-abundance curves to quantify paleoecological response. *Geology* 37:783–786.
- Whatley, R. C., and M. A. Ayress. 1988. Pandemic and endemic distribution patterns in Quaternary deep-sea Ostracoda. Pp. 739–755 in T. Hanai et al., eds. *Evolutionary biology of Ostracoda: its fundamentals and applications*. Kodansha, Tokyo.
- Whatley, R. C., and I. Boomer. 1995. Upper Oligocene to Pleistocene Ostracoda from guyots in the western Pacific: Holes 871A, 872C, and 873B. *Proceedings of the Ocean Drilling Program, Scientific Results* 144:87–96.
- Wollenburg, J. E., and W. Kuhnt. 2000. The response of benthic foraminifera to carbon flux and primary production in the Arctic Ocean. *Marine Micropaleontology* 40:189–231.
- Wollenburg, J. E., A. Mackensen, and W. Kuhnt. 2007. Benthic foraminiferal biodiversity response to a changing Arctic palaeoclimate in the last 24,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* 255:195–222.
- Yamane, M. 2003. Late Quaternary variations in water mass in the Shatsky Rise area, northwest Pacific Ocean. *Marine Micropaleontology* 48:205–223.
- Yasuhara, M., and T. M. Cronin. 2008. Climatic influences on deep-sea ostracode (Crustacea) diversity for the last three million years. *Ecology* 89:552–565.
- Yasuhara, M., T. M. Cronin, and P. Martínez Arbizu. 2008a. Abyssal ostracods from the South and Equatorial Atlantic Ocean: Biological and paleoceanographic implications. *Deep-Sea Research I* 55:490–497.
- Yasuhara, M., T. M. Cronin, P. B. deMenocal, H. Okahashi, and B. K. Linsley. 2008b. Abrupt climate change and collapse of deep-sea ecosystems. *Proceedings of the National Academy of Sciences U.S.A.* 105:1556–1560.
- Yasuhara, M., H. Okahashi, and T. M. Cronin. 2009a. Taxonomy of Quaternary deep-sea ostracods from the western North Atlantic Ocean. *Paleontology* 52:879–931.
- Yasuhara, M., G. Hunt, T. M. Cronin, and H. Okahashi. 2009b. Temporal latitudinal-gradient dynamics and tropical instability of deep-sea species diversity. *Proceedings of the National Academy of Sciences U.S.A.* 106:21717–21720.
- Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–693.