

# Patterns and controlling factors of species diversity in the Arctic Ocean

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## ABSTRACT

**Aim** The Arctic Ocean is one of the last near-pristine regions on Earth, and, although human activities are expected to impact on Arctic ecosystems, we know very little about baseline patterns of Arctic Ocean biodiversity. This paper aims to describe Arctic Ocean-wide patterns of benthic biodiversity and to explore factors related to the large-scale species diversity patterns.

**Location** Arctic Ocean.

**Methods** We used large ostracode and foraminiferal datasets to describe the biodiversity patterns and applied comprehensive ecological modelling to test the degree to which these patterns are potentially governed by environmental factors, such as temperature, productivity, seasonality, ice cover and others. To test environmental control of the observed diversity patterns, subsets of samples for which all environmental parameters were available were analysed with multiple regression and model averaging.

**Results** Well-known negative latitudinal species diversity gradients (LSDGs) were found in metazoan Ostracoda, but the LSDGs were unimodal with an intermediate maximum with respect to latitude in protozoan foraminifera. Depth species diversity gradients were unimodal, with peaks in diversity shallower than those in other oceans. Our modelling results showed that several factors are significant predictors of diversity, but the significant predictors were different among shallow marine ostracodes, deep-sea ostracodes and deep-sea foraminifera.

**Main conclusions** On the basis of these Arctic Ocean-wide comprehensive datasets, we document large-scale diversity patterns with respect to latitude and depth. Our modelling results suggest that the underlying mechanisms causing these species diversity patterns are unexpectedly complex. The environmental parameters of temperature, surface productivity, seasonality of productivity, salinity and ice cover can all play a role in shaping large-scale diversity patterns, but their relative importance may depend on the ecological preferences of taxa and the oceanographic context of regions. These results suggest that a multiplicity of variables appear to be related to community structure in this system.

## Keywords

Arctic Ocean, biodiversity, deep sea, depth diversity gradients, ecosystem, latitudinal diversity gradients, macroecology, meiobenthos, shallow marine.

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## INTRODUCTION

Large-scale marine species diversity patterns reflect fundamental features of the world's biota (Willig *et al.*, 2003; Rex &

Etter, 2010; Tittensor *et al.*, 2010), and latitudinal species diversity gradients (LSDGs) have been detected in most taxonomic groups, although exceptions exist (Willig *et al.*, 2003; Rex & Etter, 2010; Tittensor *et al.*, 2010). Similarly,

widespread evidence suggests a hump-shaped relationship between benthic species diversity and water depth, with the highest diversity seen at mid-depths (Rex, 1981; Rex & Etter, 2010). However, the factors that control these large-scale species diversity patterns are still the subject of debate (Willig *et al.*, 2003; Hunt *et al.*, 2005; Corliss *et al.*, 2009; Yasuhara *et al.*, 2009, 2012; Rex & Etter, 2010; Tittensor *et al.*, 2011). Furthermore, comprehensive marine ecological and palaeo-ecological modelling studies are still largely restricted to the Atlantic Ocean, especially the North Atlantic (Rutherford *et al.*, 1999; Ellingsen & Gray, 2002; Corliss *et al.*, 2009; Renaud *et al.*, 2009; Yasuhara *et al.*, 2009; Tittensor *et al.*, 2011), with a few exceptions (Hunt *et al.*, 2005; Tittensor *et al.*, 2010; Yasuhara *et al.*, 2012).

Our knowledge of the Arctic Ocean ecosystems is limited, and even large-scale species diversity patterns are relatively poorly known (Svavarsson, 1997; Clarke, 2003; Piepenburg, 2005; Renaud *et al.*, 2006; Cusson *et al.*, 2007; Fonseca & Soltwedel, 2009; Bluhm *et al.*, 2011a,b). In the Arctic Ocean, unimodal depth species diversity gradients (DSDGs) are known with a peak at *c.* 100–200 m in, for example, echinoderms (Anisimova, 1989; Clarke, 2003), but at *c.* 500–1000 m in isopods and foraminifera (Svavarsson, 1997; Wollenburg & Kuhnt, 2000). These diversity peaks are shallower than the *c.* 1000–2000 m peaks in other oceans (Rex & Etter, 2010). In contrast, LSDGs are much less pronounced in the Arctic Ocean (Fonseca & Soltwedel, 2009), although this may reflect this ocean's limited latitudinal range. Many environmental factors, including temperature and organic carbon flux, a primary determinant of food availability for benthic organisms, can change with depth or latitude. Sea ice is known to influence polar marine benthic communities, but little is known about its impact on species diversity (Gradinger, 1995; Gutt, 2001; Piepenburg, 2005; Tamelander *et al.*, 2006; Hoste *et al.*, 2007; Soltwedel *et al.*, 2009). Thus, it is still uncertain which factors govern diversity patterns.

Crustacean Ostracoda and unicellular foraminifera are the only deep-sea benthic groups abundant in both modern and fossil records (Wollenburg & Mackensen, 1998; Wollenburg & Kuhnt, 2000; Cronin *et al.*, 2010). Generally, *c.* 100–200 specimens, sufficient for quantitative biodiversity analyses, are easily available from small volumes (e.g. 20 mL) of sediment. Robust species-level taxonomy is available for these taxa, in contrast to the situation for other meiobenthic groups such as nematodes and copepods, for which most species are undescribed. Undertaking a comparison of patterns in ostracodes and foraminifera is useful because these two groups differ in several ecological respects, perhaps most importantly in their dispersal ability. Benthic ostracodes lack a dispersal stage and most do not swim, whereas benthic foraminifera are known to disperse widely (see Yasuhara *et al.*, 2012). Here we use large meiobenthic datasets to document Arctic Ocean-wide patterns of biodiversity, and apply comprehensive ecological modelling to test the degree to which these patterns are potentially governed by environmental factors such as temperature, productivity, seasonality, ice cover and others. These

and similar analyses can help to provide a robust baseline for understanding the impact on biodiversity of future climate change in the Arctic.

## MATERIALS AND METHODS

### Ostracode and foraminiferal data

The remote nature and extreme environments of the Arctic Ocean mean that there is limited human access. Despite this difficulty, extensive marine sediment sampling expeditions have been conducted because of this region's geological and palaeoclimatological importance (Stein *et al.*, 1994; Cronin *et al.*, 1995; Wollenburg & Kuhnt, 2000; Spielhagen *et al.*, 2004; Moran *et al.*, 2006). The Modern Arctic Ostracode Database (MAOD) 2010 (<http://www.ncdc.noaa.gov/paleo/metadata/noaa-ocean-10479.html>; Cronin *et al.*, 2010) is a comprehensive compilation of ostracode census data of modern surface sediments taken by multiple, box, and other corers and grab samplers during such expeditions. Ostracodes are small, bivalved crustaceans, and their dead shells are regularly preserved in marine sediments. The MAOD is based on the 'total assemblage', including both living specimens and dead shells. However, because living specimens are usually rare, the total assemblage represents a sample averaged over the period of time during which those sediments accumulated, from tens to thousands of years depending on local rates of sediment accumulation. Taxonomic control is good for this dataset: species identifications were carefully evaluated by multiple experienced ostracode taxonomists, including T. M. Cronin. This unique database is composed of 99 species and 680 samples, making it one of the largest taxonomically standardized datasets for marine benthic biodiversity. One species (*Acetabulastoma arcticum*) was omitted because it is not benthic (Cronin *et al.*, 2010). Among the 680 samples, 284 samples included a sufficient number of specimens (> 100) for our species diversity research. Foraminiferal data were drawn from 90 death-assemblage samples with consistent taxonomy by a single author group (Wollenburg & Mackensen, 1998; Wollenburg & Kuhnt, 2000). Locality maps are shown in Appendix S1 in the Supporting Information.

Ostracode and foraminiferal diversities were measured as raw species richness for samples with large enough sample size (> 100 specimens for ostracodes and > 200 specimens for foraminifera; i.e. asymptotic species richness). The sufficiency of 200 specimens as a cut-off is confirmed by previous foraminiferal studies (Thomas *et al.*, 1995; Hunt *et al.*, 2005). Arctic ostracode diversity is low, however, and so a 100 specimen cut-off is sufficient: species accumulation curves in our dataset generally flattened strongly between 50 and 100 specimens. Expected species richness rarefied to 100 individuals [ $E(S_{100})$ ], a commonly used diversity index in deep-sea ecology, was also calculated for ostracodes, but not for foraminifera because the available foraminiferal data do not permit rarefaction calculations. Because asymptotic species richness results are similar to rarefied species results, we

present only the asymptotic species richness results. The rarefied species results can be found in Appendix S2. Detrended correspondence analysis (DCA) was performed on the square-root-transformed relative abundances of ostracode and foraminiferal species. Rare taxa were not excluded, because repeating the analyses using a range of abundance thresholds produced quite similar results. The DCA was performed for sample subsets of shallow-marine ostracodes, deep-sea ostracodes, and deep-sea foraminifera separately (see below). We interpret the first and second DCA axes (DCA1 and DCA2) as capturing variation in faunal composition among samples.

### Environmental parameters

Particulate organic carbon (POC) flux to ocean floor ( $\text{g C m}^{-2} \text{ yr}^{-1}$ ) was calculated based on surface productivity, which was estimated from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellite ocean colour data for 1998–2007 using a regional net primary production algorithm (Pabi *et al.*, 2008) and the seasonal variation index (SVI) of a production export flux algorithm (Lutz *et al.*, 2007), by assuming that the local export depth is 400 m (Lutz *et al.*, 2007) and that production is zero during ice-covered periods (Pabi *et al.*, 2008). We considered continuous missing values, including winter data, to be the result of ice cover, while other sporadic missing production estimates, presumably resulting from cloud cover, were substituted using the linear interpolation of adjacent values. There are some uncertainties in this approach because the primary production algorithm does not account for production by phytoplankton growing under sea ice and by sea-ice algae, although these contributions are likely to represent only a small fraction of total Arctic primary production (Pabi *et al.*, 2008). Nonetheless, this is currently the best estimate of Arctic production, and further details on the uncertainties are available (Pabi *et al.*, 2008; Arrigo & van

Dijken, 2011). We used the SVI of Lutz *et al.* (2007) as the index of seasonality of productivity, which is statistically similar to other seasonality indices (Berger & Wefer, 1990; Lampitt & Antia, 1997; see Lutz *et al.*, 2007). We omitted samples with permanent ice cover from our multiple regression and model averaging analyses because surface production and its seasonality cannot be estimated reliably in this case. The number of ice-free days per year, as described above, is used as the index of ice cover.

Bottom water temperature and salinity are from the *World Ocean Atlas 2001* (1/4 degree version; Boyer *et al.*, 2002; Stephens *et al.*, 2002). Geographic regions are based on those in the MAOD 2010 (Cronin *et al.*, 2010). Each geographic region is coded (e.g. Amundsen Basin as 1, Beaufort Sea as 2, Canada Basin as 3, etc., as listed in Appendix S1) and included as a factor in our regression analyses.

### Testing controlling factors

We used regression models to test factors that might control species diversity and faunal patterns, including temperature, POC flux (surface productivity), seasonality of productivity, ice cover, salinity, water depth and geographic region (Table 1). Because hump-shaped relationships between diversity and productivity have been reported frequently in previous studies (Tittensor *et al.*, 2011; Yasuhara *et al.*, 2012), we included a quadratic term for POC flux (surface productivity) in the models. Regression models were run separately for ostracodes and foraminifera, for shallow-marine (< 200 m) and deep-sea samples (> 400 m), and for species diversity and DCA axes 1 and 2; however, the shallow-marine analysis was not conducted for foraminifera because of the small number of samples. The samples taken from 200 to 400 m water depth were omitted from the deep-sea analyses because reliable POC flux estimation is impossible in areas shallower than the

**Table 1** Best three regression models of deep-sea ostracode, shallow-marine ostracode and deep-sea foraminiferal diversities in the Arctic Ocean.

Model	D	I	P	P <sup>2</sup>	SP	T	S	R <sup>2</sup>	AIC <sub>c</sub>	AW
Deep-sea ostracode species richness models										
1	<b>-15.51</b>	<b>4.83</b>	<b>-4.96</b>	-1.05	-	-	-	0.44	250.0	0.113
2	<b>-15.31</b>	<b>4.99</b>	<b>-5.20</b>	-	-	-	-	0.40	250.6	0.087
3	<b>-18.46</b>	<b>4.31</b>	<b>-5.03</b>	-	-	-2.27	-	0.43	250.7	0.083
Shallow-marine ostracode species richness models										
1	-	-	<b>-0.04</b>	-	<b>-24.42</b>	<b>-1.67</b>	<b>1.33</b>	0.31	813.7	0.230
2	2.24	-	<b>-0.04</b>	-	<b>-25.02</b>	<b>-1.70</b>	0.83	0.31	814.6	0.146
3	<b>4.88</b>	-	<b>-0.05</b>	-	<b>-25.97</b>	<b>-1.64</b>	-	0.30	815.0	0.121
Deep-sea foraminiferal species richness models										
1	<b>-52.10</b>	-	<b>-9.51</b>	-	-	-	-	0.57	228.1	0.142
2	<b>-31.24</b>	-	-	-	-	-	-	0.68	229.3	0.081
3	<b>-55.17</b>	-	<b>-9.20</b>	-	-	-	63.42	0.58	230.4	0.045

D, water depth; I, ice covering (number of ice-free days per year); P, surface productivity or POC flux; P<sup>2</sup>, quadratic term of surface productivity or POC flux; SP, seasonality of productivity; T, temperature; S, salinity.

The table shows the coefficient of each term, R<sup>2</sup>, the Akaike information criterion corrected for small sample size (AIC<sub>c</sub>), and the Akaike weight (AW). Bold denotes significance at  $P < 0.05$ . Overall  $P$  is  $< 0.05$  in all models.

export-zone depth (*c.* 400 m at high latitudes; Lutz *et al.*, 2007). We used annual surface production instead of POC flux for our shallow-marine modelling for the same reason, assuming that annual surface production generally reflects POC flux at shallow-water depths. Salinity outliers (salinity < 25) in the shallow-marine ostracode subset were omitted from the multiple regression in order to remove brackish sites. All environmental parameters, except geographic region, were zero-centred. The log transformation was used for water depth in all subsets, for seasonality of productivity in the shallow-marine ostracode subset, and for ice cover and POC flux in the deep-sea ostracode and foraminiferal subsets, respectively, to make their distributions more symmetric.

The Akaike information criterion corrected for small sample size ( $AIC_c$ ) 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; Table 1). We also considered parameter estimates averaged over models with  $\Delta AIC_c < 4$ , proportional to the support that each model receives (Table 2; Appendix S2). This approach accounts for uncertainty in model selection and thus leads to appropriately broader confidence intervals than would be obtained by relying only on the single, best-supported model. The influences of the various predictor variables were measured as relative importance, which is the sum of the Akaike weights of models that include the variable in question (Burnham & Anderson, 2002).

For each dataset, we computed variance inflation factors and pairwise correlations between predictor variables to assess whether multicollinearity was likely to influence the regression results. In all datasets, seasonality of productivity and the number of ice-free days were strongly and negatively correlated (all  $r < -0.85$ ), and variance inflation factors above 20 indicate that these correlations may be influencing the regressions (temperature and depth were also strongly correlated in the foraminiferal dataset,  $r = -0.89$ ). Although multicollinearity increases the standard error of regression coefficients, it does not bias their estimation. Moreover, our strategy of basing inference on multiple models limits the effects of individual models with spurious coefficients. As a result, we did not omit variables or otherwise alter the analyses, but we do note that it may be difficult to separately estimate the effects of seasonality of productivity and ice cover in these data.

We measured the degree of spatial autocorrelation in model residuals for the five best models for each dataset by computing the Moran's  $I$  statistic for neighbourhood sizes of 100, 500 and 1000 km. The only evidence for significant spatial autocorrelation in model residuals was found in the shallow-water ostracode dataset. For these data, we re-ran the analysis, forcing the geographic region variable to be included in all models in order better to account for spatial autocorrelation. These modified analyses resulted in residuals with little spatial correlation (except for DCA2, which retained some at the 100-km scale), and their coefficients were qualitatively similar to the original regressions. Accordingly, we present only the original results.

**Table 2** Model-averaged parameter estimates and CIs of deep-sea ostracode, shallow-marine ostracode and deep-sea foraminiferal diversities in the Arctic Ocean.

Term	RI	Coefficient	Lower CI	Upper CI
Deep-sea ostracode species richness (sample size = 45)				
<b>D</b>	<b>1.00</b>	<b>-16.32</b>	<b>-26.06</b>	<b>-6.58</b>
P	0.92	-4.48	-9.02	0.06
<b>I</b>	<b>0.73</b>	<b>4.81</b>	<b>0.10</b>	<b>9.52</b>
T	0.53	-2.61	-6.13	0.91
P <sup>2</sup>	0.51	-1.08	-2.39	0.23
SP	0.26	-0.31	-2.19	1.57
S	0.18	20.09	-52.19	92.38
Shallow-marine ostracode species richness (sample size = 129)				
<b>P</b>	<b>1.00</b>	<b>-0.04</b>	<b>-0.08</b>	<b>-0.01</b>
<b>SP</b>	<b>1.00</b>	<b>-27.19</b>	<b>-44.79</b>	<b>-9.59</b>
<b>T</b>	<b>1.00</b>	<b>-1.61</b>	<b>-2.32</b>	<b>-0.90</b>
<b>S</b>	<b>0.77</b>	<b>1.16</b>	<b>0.24</b>	<b>2.08</b>
D	0.51	3.43	-0.76	7.63
I	0.27	-0.03	-0.13	0.06
P <sup>2</sup>	0.23	0.00005	-0.0003	0.0004
Deep-sea foraminiferal species richness (sample size = 29)				
<b>D</b>	<b>0.81</b>	<b>-46.23</b>	<b>-72.07</b>	<b>-20.39</b>
P	0.63	-11.38	-27.59	4.84
R	0.33	7.82	-12.69	28.33
T	0.24	13.80	-8.73	36.34
I	0.20	14.32	-44.02	72.67
SP	0.15	6.64	-6.36	19.64
S	0.13	-26.26	-281.78	229.27
P <sup>2</sup>	0.06	1.64	-4.18	7.45

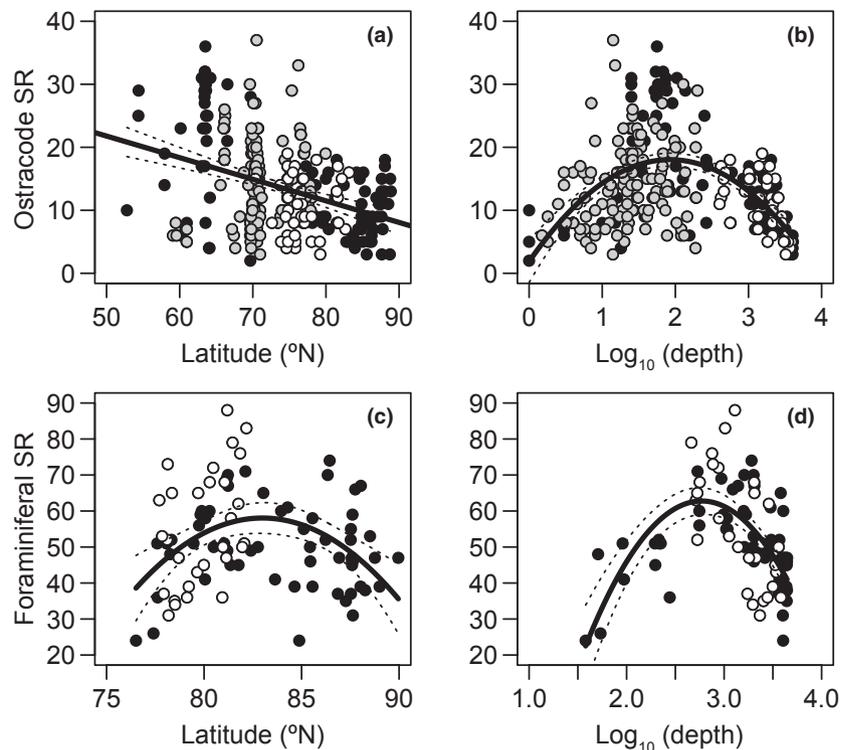
CIs, confidence intervals; RI, relative importance (the sum of the Akaike weights of models that include the variable in question; see Materials and Methods); R, region. Other abbreviations are as in Table 1.

Bold denotes CIs that exclude zero. For R, the coefficient, lower CI and upper CI values shown are averages of those for geographic regions.

Analyses reported here were implemented in the R programming language (R Development Core Team, 2011), using functions from the R packages: *VEGAN* (Oksanen *et al.*, 2010) for diversity and DCAs; *MUMIN* (Bartoń, 2009) to perform the model averaging; and *SPDEP* to measure spatial autocorrelation (Bivand, 2011). Datasets used for this paper are deposited at Dryad (<http://dx.doi.org/10.5061/dryad.9gc21>).

## RESULTS

Benthic Arctic ostracode species diversity showed a noisy but significant negative LSDG ( $R^2 = 0.13$ ,  $P < 0.0001$ ;  $n = 284$ ) and a unimodal DSDG (in log scale:  $R^2 = 0.32$ ,  $P < 0.0001$ ;  $n = 280$ ; Fig. 1). The LSDG was also significant for the shallow-marine ( $R^2 = 0.03$ ,  $P = 0.03$ ;  $n = 173$ ) and deep-sea ( $R^2 = 0.05$ ,  $P = 0.03$ ;  $n = 107$ ) samples separately, although very noisy. The deep-sea samples were concentrated at higher latitudes and showed lower species diversity than shallow-marine samples, making the whole-dataset LSDG clearer (Fig. 1). Ostracode diversity showed a peak at *c.* 100 m water



**Figure 1** Large-scale benthic species diversity patterns in the Arctic Ocean showing the relationships between ostracode species richness (SR) and (a) latitude ( $^{\circ}\text{N}$ ;  $R^2 = 0.13$ ,  $P < 0.0001$ ;  $n = 284$ ), and (b) water depth (m) in log scale ( $R^2 = 0.32$ ,  $P < 0.0001$ ;  $n = 280$ ); and between foraminiferal species richness (SR) and (c) latitude ( $^{\circ}\text{N}$ ;  $R^2 = 0.14$ ,  $P = 0.001$ ;  $n = 90$ ), and (d) water depth (m) in log scale ( $R^2 = 0.42$ ,  $P < 0.0001$ ;  $n = 90$ ). Grey circles: shallow-marine subset; white circles: deep-sea subset for the multiple regression and model averaging analyses; black circles: sites not used for statistical modelling. Regression lines are for whole datasets (dashed lines: 95% confidence intervals).

depth (Fig. 1). In foraminifera, both latitude–diversity and depth–diversity relationships were unimodal ( $R^2 = 0.14$ ,  $P = 0.001$  for LSDGs;  $R^2 = 0.42$ ,  $P < 0.0001$  for DSDGs in log scale;  $n = 90$ ), although the relationships were rather noisy. The foraminiferal DSDG showed an intermediate peak at *c.* 1000 m (Wollenburg & Kuhnt, 2000; Fig. 1).

To test environmental control of these diversity patterns, subsets of samples for which all environmental parameters were available were analysed with multiple regression and model averaging. The three best regressions indicated that, for each dataset, several factors were significant predictors of species diversity (Table 1). The significant terms were not always consistent across models, however, and the model-averaged coefficients revealed a much smaller list of covariates that had consistent enough effects across models to differ significantly from zero when model uncertainty was taken into account. These results suggest that deep-sea ostracode diversity has a significant relationship with water depth (negative) and ice cover (positive), that shallow-marine ostracode diversity has a significant relationship with surface productivity (negative), seasonality of productivity (negative), temperature (negative) and salinity (positive), and that deep-sea foraminiferal diversity has a significant negative relationship with water depth (Table 2). Deep-sea faunal composition (DCA axes 1 and 2) was strongly related to water depth, salinity, and seasonality of productivity in ostracodes, and to water depth, temperature, ice cover and POC flux in foraminifera (Appendix S2), suggesting inter-taxa differences of response to environmental parameters. Shallow-marine faunal composition is related to geographic region, ice cover, salinity, surface productivity, seasonality of productivity and temperature

(Appendix S2), suggesting local differentiation of shallow-marine ostracode assemblages. A data overview showing relationships between species richness and environmental parameters is found in Appendix S3.

## DISCUSSION

The comprehensive ostracode and foraminiferal datasets enabled us to show clear large-scale species diversity patterns in the Arctic Ocean. The negative LSDG in ostracodes in the Arctic Ocean is consistent with typical large-scale diversity patterns known in other regions and taxa (Willig *et al.*, 2003; Rex & Etter, 2010; Tittensor *et al.*, 2010), but the unimodal gradient in foraminifera is unexpected. The peak in ostracode diversity at a depth of *c.* 100 m is consistent with previous Arctic studies (Anisimova, 1989; Clarke, 2003) and much shallower than the diversity peak in other oceans (Rex, 1981; Rex & Etter, 2010). Although the weak plateau at *c.* 2000 m (Fig. 1) is consistent with the peak depth of standard DSDGs in other oceans (Rex, 1981; Rex & Etter, 2010), the data are noisy and a depth-related trend is not clear. The *c.* 1000-m peak in foraminifera is still shallower than the peak in the typical DSDGs in other oceans (Rex, 1981; Rex & Etter, 2010).

In the shallow-marine environments, species diversity usually increases with temperature (Roy *et al.*, 1998; Tittensor *et al.*, 2010), at least when temperatures are not overly high [mean annual sea-surface temperature  $< c.$  25  $^{\circ}\text{C}$  (Rutherford *et al.*, 1999)]. The model averaging results for shallow-marine ostracodes show a significant relationship between species diversity and temperature, but the relationship is negative (Table 2). Other controlling factors for shallow-marine ostracode

diversity are surface productivity, seasonality of productivity and salinity (Table 2); the model-averaging results for all of these point to a significant relationship with species diversity (Table 2).

The negative relationship between diversity and temperature in the shallow ostracode fauna is opposite in direction to that in most previous reports. This effect might be related to the relatively restricted range of temperatures in the Arctic; the relatively low species richness in the Arctic suggests that a positive relationship might be found over a broader latitudinal range. Or, the reason might be related to the evolutionary or ecological characteristics of the Arctic fauna, which may be the product of the diversification of cryophilic species (Jones *et al.*, 1998). A negative relationship is also known from relatively warm bathyal environments in the Mediterranean (nematodes: Danovaro *et al.*, 2004) and South Pacific (ophiuroids: O'Hara & Tittensor, 2010). The negative deep-sea diversity–temperature relationship observed in these relatively warm temperature ranges may reflect the descending rim of a unimodal diversity–temperature relationship over a wide temperature range (Rutherford *et al.*, 1999; Tittensor *et al.*, 2010). Thus, the mechanism of the negative diversity–temperature relationship may be different between relatively warm bathyal environments and very cold, shallow Arctic Ocean environments.

In the deep sea, Arctic ostracode diversity shows a negative relationship with water depth and a positive relationship with ice cover, and foraminiferal diversity shows a negative relationship with water depth (Table 2). Strong water-depth controls of deep-sea ostracode and foraminiferal diversities are difficult to interpret. Deep-sea ostracode and foraminiferal diversities may be controlled by environmental parameters that change with water depth but are not included in the present study (see Levin *et al.*, 2001), or this negative diversity–depth relationship may be related to evolutionary dynamics such as the deep-sea source–sink hypothesis (Rex *et al.*, 2005). In this hypothesis, low population sizes make abyssal populations demographic sinks, which are maintained by immigration from shallower bathyal sources. As a result, diversity decreases with increasing distance from the bathyal source population.

The Arctic-wide marine biodiversity patterns suggest that Arctic LSDGs are less obvious than those in the adjacent North Atlantic Ocean. The ostracode LSDGs are relatively noisy, and foraminifera exhibit unimodal latitudinal gradients typically not seen in other deep-sea regions. These noisier latitudinal gradients are probably a consequence of the limited latitudinal range of the Arctic Ocean compared with that of the North Atlantic Ocean. Unimodal Arctic depth gradients with diversity peaks shallower than those known in other oceans (Rex & Etter, 2010) are consistent with those for other taxonomic groups of, for example, isopods and echinoderms (Svavarsson, 1997; Clarke, 2003).

Our results suggest that the underlying mechanisms causing these species diversity patterns are unexpectedly complex, with contributions from multiple environmental factors. In the Arctic Ocean, water depth, bottom water temperature, POC

flux (surface productivity), seasonality of productivity, salinity and/or ice cover are the important factors related to marine benthic species diversity, depending on taxonomic groups and water depth categories (i.e. deep sea or shallow marine). Although our ostracode and foraminiferal results consistently show negative diversity–productivity relationships (Table 1), the relationship is not always significant after accounting for model uncertainty, and other parameters are often more dominant (Table 2). These results strongly suggest that consideration of all of these factors in order to evaluate the fundamental controlling factor(s) of, especially deep-sea, biodiversity is important in marine ecological research on various geographic scales from local to global. Deep-sea ostracode diversity is predominantly controlled by water depth and ice cover in the Arctic (Table 2), but by temperature in the North Atlantic (Yasuhara *et al.*, 2009) and by POC flux in the North Pacific (Yasuhara *et al.*, 2012). In contrast, foraminiferal diversity is predominantly controlled by water depth in the Arctic (Table 2), by seasonality of productivity in the North Atlantic (Corliss *et al.*, 2009), and by temperature in the North Pacific (Yasuhara *et al.*, 2012). These environmental parameters are not necessarily mutually exclusive, and their relative importance may depend on the ecological preferences of taxa and the oceanographic context of regions. In other words, a multiplicity of variables appears to be related to deep-sea biodiversity. These results suggest that the traditional and widely held perspective that POC flux is a dominant controlling factor for most community-level phenomena in this food-limited deep ocean floor environment is oversimplified, although balanced approaches are increasing (Hunt *et al.*, 2005; Yasuhara *et al.*, 2009, 2012; Tittensor *et al.*, 2011).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

- Appendix S1** Locality maps and geographic region codes.
- Appendix S2** Arctic ostracode and foraminiferal model averaging results.
- Appendix S3** Data overview showing relationships between species richness and environmental parameters for ostracode and foraminiferal subsets.

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## BIOSKETCH

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