Temporal latitudinal-gradient dynamics and tropical instability of deep-sea species diversity

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A benthic microfaunal record from the equatorial Atlantic Ocean over the past four glacial-interglacial cycles was investigated to understand temporal dynamics of deep-sea latitudinal species diversity gradients (LSDGs). The results demonstrate unexpected instability and high amplitude fluctuations of species diversity in the tropical deep ocean that are correlated with orbital-scale oscillations in global climate: Species diversity is low during glacial and high during interglacial periods. This implies that climate severely influences deep-sea diversity, even at tropical latitudes, and that deep-sea LSDGs, while generally present for the last 36 million years, were weakened or absent during glacial periods. Temporally dynamic LSDGs and unstable tropical diversity require reconsideration of current ecological hypotheses about the generation and maintenance of biodiversity as they apply to the deep sea, and underscore the potential vulnerability and conservation importance of tropical deep-sea ecosystems.

deep-sea Ostracoda | global climate change | latitudinal species diversity gradients | macroecology | Quaternary paleoceanography

Latitudinal species diversity gradients (LSDGs), the patterns in which tropical regions contain more species than high latitudes, are one of the most basic ecological patterns on the earth (1). In the modern ocean, deep-sea bivalves, gastropods, isopods, cumaceans, and foraminifera all show strong LSDGs (2–6), and studies of benthic foraminifera assemblages indicate that the deep-sea gradients were established ≈36 million years ago (7). The environmental stability hypothesis holds that stability in tropical (1, 8), and deep-sea (9, 10) environments might enhance species diversity, but there is now evidence for highly fluctuating high-latitude deep-sea diversity during Quaternary climatic cycles (11–16). Surprisingly little attention has been given to understanding low-latitude deep-sea diversity and the temporal dynamics of the LSDGs. Although pollen records suggest a persistent latitudinal diversity gradient existed in terrestrial ecosystems over the last 13,000 years (17, 18), we know of no studies of species-level temporal dynamics of LSDGs based on fossil assemblages from marine environments, despite the sensitivity of marine ecosystems to climatic change (12, 13, 19–24).

The Ostracoda (Crustacea) are an important component of the deep-sea benthos (25–27), and the only commonly fossilized metazoan group in deep-sea sediments (12, 13, 28). Their various habitats and ecological preferences represent a wide range of deep-sea benthic niches, and their fossil record is considered representative of the benthic community (12, 13, 28). Furthermore, large (≈130 m) glacial-interglacial sea-level changes (29), which drastically altered shallow-marine environments, had negligible effects on deep-sea habitats (e.g., >1,000 m water depth). Here, we examine low-latitude Quaternary records of deep-sea ostracods and temporal changes in LSDGs in the North Atlantic Ocean during the last four glacial-interglacial climatic cycles.

Ocean Drilling Program (ODP) Site 925 was cored at the Ceara Rise in the western equatorial Atlantic (4° 12.2′ N, 43° 29.3′ W; 3040 m water depth; Fig. 1) (30, 31). The Ceara Rise is an intensively researched tropical region for Cenozoic paleoceanography (32–34). Continuous sedimentation, excellent chronology, and availability of climatic proxy records make Site 925 an ideal sediment core for Quaternary biodiversity research in the low latitude ocean. Although postmortem dissolution can affect fossil ostracod preservation below lysocline and carbonate compensation depth (35), Site 925 is located well above these depths (31, 36) and so this record is not seriously influenced by carbonate dissolution. This high-quality record of the tropical deep ocean shows that ostracod species diversity exhibits large amplitude fluctuations during the last 500 ka (thousands of years ago), and that the LSDGs in the deep ocean seem to have weakened or even collapsed during glacial periods.

Results and Discussion

The ODP 925 record for the past four glacial-interglacial cycles shows diversities measured as the expected number of species in a sample of 50 individuals, E(50), that are high (up to ≈25) during interglacial and low (≈5 at minimum) during glacial periods (Fig. 2*A*). Diversity increases during glacial to interglacial transitions (Terminations 1–4) range from 2-fold to nearly 4-fold (Fig. 2*A*). These substantial oscillations span the present-day pole-to-equator diversity gradient in deep-sea ostracods (Figs. 2*A* and 3*A*). Data from ODP 925 produce a near-recent equatorial diversity estimate of E(50) approximately 25, whereas diversity in the Arctic Ocean is E(50) approximately 5, and values for midlatitude sites are intermediate (Fig. 3*A* and Table S1). During glacial intervals, tropical diversity is greatly depressed, but diversities at middle and high latitudes are much less affected (Fig. 3*A*). Consequently, the deep-sea LSDGs are weakened during glacial times, so much so that they appear to be completely absent, at least during the Last Glacial Maximum (≈20 ka).

Spectral analysis shows that ODP 925 ostracod diversity fluctuated with periodicities that match those of 100 ka (eccentricity) and 41 ka (obliquity) Milankovitch climatic forcing (Fig. 2*B*). There is also a correlation between ODP 925 diversity and the deep-sea benthic foraminiferal oxygen isotope record (37), a proxy for global changes in temperature and ice volume (Figs. 2 and 4*A*). Diversity peaks correspond with the negative oxygen isotope excursions during interglacial and interstadial maxima (Fig. 2*A*). This pattern shows that global climate changes have strongly influenced tropical deep-sea diversity, similar to previously reported effects at mid to high latitudes (11, 13, 28). This result, coupled with the extremely dynamic diversity trajectory of the tropical ODP 925, suggests that the LSDGs in the deep ocean are not driven by a gradient of increasing environmental stability from poles to tropics.

Both temperature and productivity have been considered important factors controlling deep-sea species diversity but their relative importance is uncertain (4, 13, 28, 38–41). Species diversity

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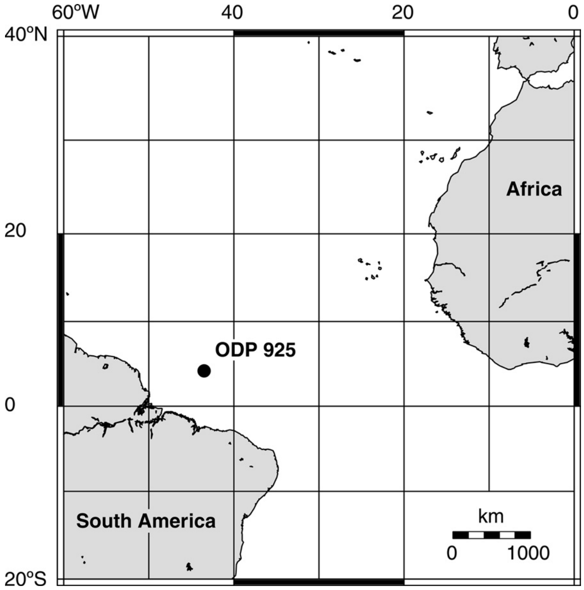

Fig. 1. Location of OSP site 925. This map was created using the Online Map Creation web site (www.aquarius.ifm-geomar.de).

at ODP 925 is positively correlated with both bottom water temperature (P = 0.0003) and surface productivity oscillations (P = 0.003) (Fig. 4 *B* and *C*). However, temperature and surface productivity are themselves correlated at this site. When we perform

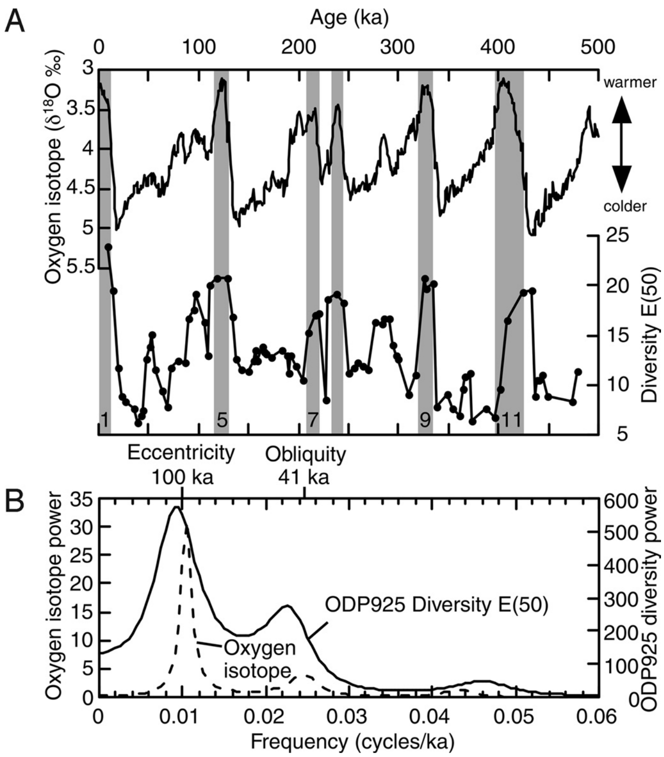

Fig. 2. Late Quaternary tropical deep-sea diversity changes. (*A*) Comparison between deep-sea oxygen isotope curve [LR04 global stack (37)] and ODP 925 ostracod species diversity E (50). The oxygen isotope curve represents global climate changes, and the lower isotope values indicate warmer (interglacial and interstadial) intervals. Major interglacial and interstadial peaks are highlighted by gray bars. Peak interglacial marine isotope stages are labeled. (*B*) Result of spectral analysis.

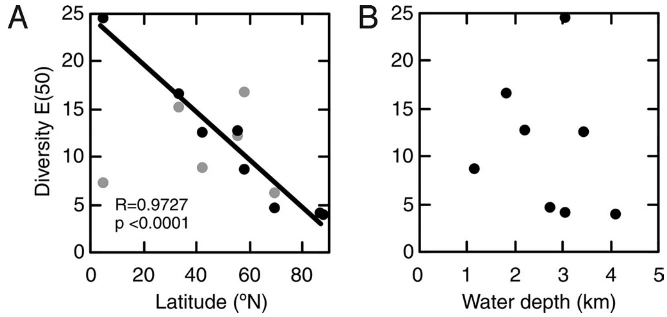

Fig. 3. Modern and Last Glacial Maximum (≈20 ka) deep-sea diversity patterns. (*A*) Latitudinal patterns of modern coretop (black circles) and Last Glacial Maximum (gray circles) ostracod diversity. Regression line and *r* and *P* values for modern E(50). (*B*) Comparison between modern E(50) and water depth.

a multiple regression to tease apart these relationships, we find that diversity is significantly and positively associated with temperature (P = 0.02) but not with productivity (P = 0.24). A positive correlation between temperature and species diversity has been reported before for deep-sea ostracods and foraminifera using late Quaternary and mid-Pliocene core records (11, 28, 38), and may reflect available energy (42) or perhaps physiological limits in which few taxa can tolerate very cold temperatures.

Although total productivity has been invoked as a determinant of deep-sea diversity (28, 40, 43), these analyses suggest a minor role, at least in this region and in this time scale. This result may partly reflect the lack of strong oscillations in productivity in this region during the late Quaternary [≈25–60 gC m^{-2} yr^{-1} (44), much smaller than the current range across the modern North Atlantic, ≈50–450 gC m^{-2} yr^{-1} (45)]. Nevertheless, although productivity was apparently not strongly seasonal at the Ceara Rise (36), no quantitative proxy for seasonality is currently available for ODP 925. Given that such seasonality has been shown to be an important determinant of modern deep-sea benthic foraminifera diversity (46), it is possible that this factor also plays a role here (3, 4, 28).

The multiple regression results indicate that downcore variations in species diversity at ODP 925 are predicted by temperature but not total productivity. While this temperature-diversity relationship may be causal, it is also possible that diversity is instead driven by some other environmental driver that, like temperature, tracks glacial-interglacial cycles. Such factors might be mediated by latitudinal shifts in the Intertropical Convergence Zone (ITCZ) and changes in North Brazil Current (33, 47), or changes in deep water characteristics reflecting the relative influence of North Atlantic Deep Water (NADW) versus Antarctic Bottom Water (AABW) (48, 49). NADW and AABW differ in temperature, nutrients contents, and salinity, although at present there is not much evidence that nutrients and salinity have much influence on deep-sea diversity.

Whatever the driver, these diversity fluctuations are not determined by species' originations or extinctions because the period covered in this study is much shorter than the durations of ostracod species, and few, if any, species originate or go extinct during this late Quaternary period. Instead, glacial-interglacial scale diversity changes must result from the shifting of species' distributions, either bathymetrically or laterally. Previous researches have hypothesized that the deep-sea diversity fluctuations involve the depth migrations of fauna during glacial-interglacial cycles (11, 28, 50). At ODP 925, the greater abundance of slope species during warmer periods when higher diversity prevailed (Fig. 4*D*) suggests the downward migration of slope species during these intervals. The rarity of slope taxa during glacial and stadial periods is consistent with shallowing of

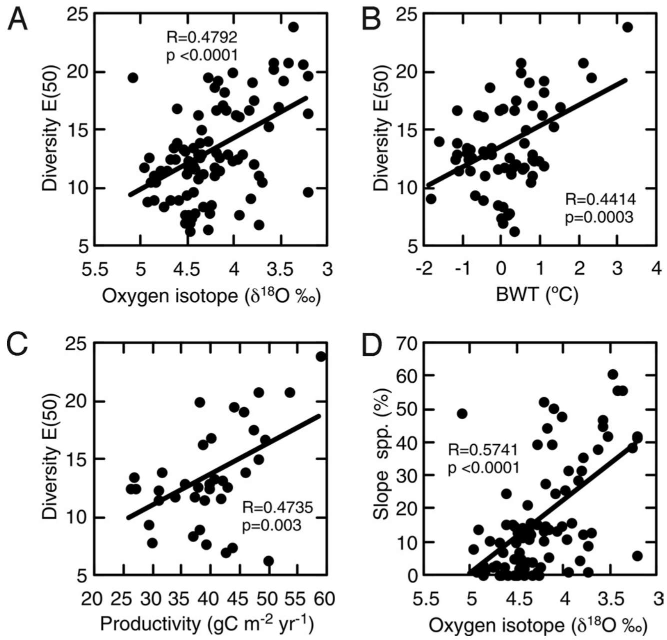

Fig. 4. Tropical deep-sea benthic species diversity and climatic and paleoecological factors. Relationships between ODP 925 diversity [E(50)] and (*A*) deep-sea oxygen isotope (37), (*B*) bottom-water temperature (BWT) (60), and (*C*) surface productivity (44). (*D*) Comparison between relative abundance of slope species and deep-sea oxygen isotope (37).

their ranges during these colder intervals. These range shifts might track temperature tolerances, or possibly some other aspect of the environment changing on Milankovitch time scales. Because slope species are much more diverse in tropical deep sea than in higher latitude oceans (Table S1), bathymetric shifts have greater diversity consequences at low latitudes, and thus modulate the deep-sea LSDGs. This idea is consistent with the deep-sea source-sink hypothesis suggesting that abyssal diversity of taxa having good dispersal ability is maintained by immigration from bathyal sources (51), a mechanism that may be applicable to organisms such as ostracods that lack swimming or dispersal larval stages (25).

Our results underscore the vulnerability and conservation importance of tropical deep-sea ecosystems, which may be an engine of global deep-sea biodiversity (52) and ecosystem functioning (53). Dramatic changes in the deep-sea LSDGs demonstrated here require reconsideration of view of persistent LSDGs in the deep sea, at least in the glacial-interglacial or shorter time scales. This dynamic nature seems to be consistent with recent discoveries of high ecosystem sensitivity to short time-scale climate changes (12, 20–22, 24).

Materials and Methods

The composite section of ODP Site 925 (30, 31) was sampled at approximately 20-cm intervals on average, yielding a sampling resolution of approximately 5 ka. The >150-μm-size fraction was examined for ostracod diversity. This size fraction is a standard for recent deep-sea ostracod research (54) and allows us to obtain all adults and juveniles of late molt stages from most deep-sea species. Although finer size fractions (63, 100, or 125 μm) are occasionally used in ostracod research, small ostracod species (e.g., *Eucytherura* spp., *Pedicythere* spp., *Aratrocypris* spp., *Chejudocythere* spp., *Ruggieriella* spp., and *Swainocythere* spp.) show low diversity and abundances, even when finer size fractions are used (55–57). Furthermore, even these small species mostly have >150-μm minor axis (i.e., height) of adult valve, and therefore will be recovered on a 150-μm sieve. Thus, our results are unlikely to be influenced by sieve mesh size. Body size does evolve, and ostracods tend to be larger during colder intervals (58). However, these evolutionary changes are much smaller than the differences between taxa, especially on these relatively short, glacial-interglacial time scales. Moreover, larger sizes during glacial periods would tend to increase observed diversity if the few smallest species became more likely to be retained on a sieve, and this effect therefore cannot explain low glacial diversity. The number of specimens refers to valves. More than 79 species were identified in total. The species identifications were initially conducted by M.Y. and H.O., but all were then confirmed by M.Y. This procedure assured consistent species concepts were applied to all samples. Ostracod carapaces have many morphological characters useful for species identification (59). Although juvenile valves in genera with smooth carapaces such as *Krithe* can be difficult, they still have characteristic morphological features (e.g., size and outline) specific to each species. We used $E(S_n)$, the expected number of species in n individuals, for species diversity because it is widely used in deep-sea ecology. Other representative diversity measures show similar trends (Fig. S1). The ostracod species diversity calculation is based on three-point moving sums of the census dataset because of relatively small sample size (≈50 specimens per sample on average), but the trend is unchanged if the raw census dataset is used. Age control was established with correlation of the ODP 925 benthic foraminiferal $\delta^{18}O$ record (31) to the LR04 global stack (37).

Published bottom-water temperature curve based on well-established Mg/Ca paleothermometry was available from tropical Atlantic deep-sea core M16772 (60), which was cored at similar latitude and water depth to Site 925 and so is ideal for comparison with the ODP 925 ostracod data. Published surface productivity curve estimated by the well established carbonate accumulation based method was available from the core GeoB 1523–1 (44), which was cored at almost the same location as ODP 925. It is known that carbonate accumulation can be affected by other factors than productivity (e.g., carbonate dissolution) as well as other productivity proxies (36). However, GeoB 1523–1 is located well above the lysocline and carbonate accumulation in this core is not seriously influenced by dissolution (36, 44). Furthermore, in oligotrophic regions dominated by calcite-secreting organisms (e.g., Ceara Rise), carbonate accumulation is known to be more reliable measure of productivity than organic carbon accumulation (36, 44). Oxygen isotope chronologies for these curves were updated using new global stack of the LR04 (37). The productivity values were recalculated based on this updated chronology because sedimentation rate enters into the productivity calculation. We smoothed temperature, LR04, and productivity curves using a cubic spline and used them to estimate the value for each of these variables for each faunal sample (Fig. 4) as described in Hunt et al. (38).

A maximum entropy spectral analysis was performed by using the software AnalySeries version 2.0.4.2 (61). ODP 925 diversity data were resampled every 1 ka before the analysis, which is equivalent to LR04 time resolution.

Modern coretop and Last Glacial Maximum ostracod diversities [E(50)] were calculated based on the census data of North Atlantic and Arctic deep-sea cores (11, 12, 62, 63) as shown in Table S1. All included data have robust chronology and similar taxonomy (i.e., most abundant genus *Krithe* and most of other major ostracod genera are identified to species level). A few samples were lumped for E(50) calculation if single samples included <50 specimens. Modern E(50) has no clear relationship with water depth for this selection of data (Fig. 3*B*).

In computing the relative abundance of slope species from Site 925, the following genera were considered typical slope inhabitants (56, 64): *Bythocypris*, *Aratrocypris*, *Cytherella*, *Cytheropteron*, *Polycope*, *Pseudocythere*, *Eucytherura*, *Paracytherois*, *Paradoxostoma*, *Argilloecia*, *Zabythocypris*, *Ruggieriella*, and *Pedicythere*.

Analyses other than spectral analysis were performed by using the statistical programming environment R (65). Ostracod data are available at the National Oceanic and Atmospheric Administration World Data Center for Paleoclimatology, www.ngdc.noaa.gov/paleo/paleo.html.

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