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.

Results and Discussion

The ODP 925 record for the past four glacial-interglacial cycles shows diversity measured as the expected number of species in a sample of 50 individuals, E(50), that are high (up to \( \approx 25 \)) during interglacial and low (\( \approx 5 \)) at minimum) during glacial periods (Fig. 2A). Diversity increases during glacial to interglacial transitions (Terminations 1–4) range from 2-fold to nearly 4-fold (Fig. 2A). These substantial oscillations span the present-day pole-to-equator diversity gradient in deep-sea ostracods (Figs. 2A and 3A). 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. 3A and Table S1). During glacial intervals, tropical diversity is greatly depressed, but diversities at middle and high latitudes are much less affected (Fig. 3A). 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 (\( \approx 20 \) 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. 2B). 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 4A). Diversity peaks correspond with the negative oxygen isotope excursions during interglacial and stadial maxima (Fig. 2A). 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...
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 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 \([\sim 25–60 \text{ gC m}^{-2} \text{ yr}^{-1}]\) (44), much smaller than the current range across the modern North Atlantic, \([\sim 50–450 \text{ gC m}^{-2} \text{ yr}^{-1}]\) (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 research has 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 productivity prevailed (Fig. 4D) 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...
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., Chejudocorythere spp., Ruggieriella spp., and Swainocorythere spp.) show low diversity and abundances, even when finer size fractions are used (55–57). Further-

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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 (E50) were calculated based on the well-established carbonate accumulation based method that 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 based on this updated carbonate accumulation 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).

In computing the relative abundance of slope species from Site 925, the following genera were considered typical slope inhabitants (56, 64): Bythocyrpus, Aratrocypris, Cytherella, Cytheropteron, Polycystotheutus, Eucytherura, Paracytherois, Paradoxostoma, Argillocerca, Zabthocythere, Ruggieriella, and Pedicythere. Thus, our results...