



Deep-sea ostracode species diversity: response to late Quaternary climate change

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Abstract

Late Quaternary ostracode assemblages from the North Atlantic Ocean were studied to establish the effect of climatic changes of the past 210,000 yr (marine oxygen isotope stages 7–1) on deep-sea benthic biodiversity and faunal composition. Two-hundred and twenty five samples from the *Chain* 82-24 Core 4PC (41°43'N, 32°51'W, 3427 m water depth) on the western Mid-Atlantic Ridge revealed high amplitude fluctuations in ostracode abundance and diversity coincident with orbital and suborbital scale climate oscillations measured by several paleoceanographic proxy records. During the past 210,000 yr, ostracode biodiversity as measured by species number (S) and the Shannon–Weaver index, $H(S)$, oscillated from $H(S) = 0.4$ during glacial periods (marine isotope stages 6, 5d, 5b, 4, and 2) to $H(S) = 1.1$ during interglacial and interstadial periods (stages 7, 5e, 5c, 5a, 3 and 1). A total of 23 diversity peaks could be recognized. Eleven of these signify major periods of high diversity [$H(S) > 0.8$, $S = 10–21$] occurring every 15–20 ka. Twelve were minor peaks which may represent millennial-scale diversity oscillations. The composition of ostracode assemblages varies with *Kriathe*-dominated assemblages characterizing glacial intervals, and *Argilloecia–Cytheropteron* characterizing deglacials, and trachyleberid genera (*Poseidonamicus*, *Echinocythereis*, *Henryhowella*, *Oxycythereis*) abundant during interglacials. Diversity and faunal composition changes can be matched to independent deep-sea paleoceanographic tracers such as benthic foraminiferal carbon isotopes, *Kriathe* trace elements (Mg/Ca ratios), and to North Atlantic region climate records such as Greenland ice cores. When interpreted in light of ostracode species' ecology, these faunal and diversity patterns provide evidence that deep-sea benthic ecosystems experience significant reorganization in response to climate changes over orbital to millennial timescales. Published by Elsevier Science B.V.

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1. Introduction

The response of the world's ecosystems to climate change has emerged as a major environmental issue as concern increases about the potential im-

pact of future human-induced climate changes on the world's biotas (e.g., Peters and Lovejoy, 1992). Although the deep-sea had been considered a fairly stable environment, fostering relatively high benthic species diversity (Hessler and Sanders, 1967; see Rex et al., 1993), paleoceanographers have shown that deep-sea circulation responds dynamically to

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global climate changes (e.g. Boyle and Keigwin, 1982, 1987; Broecker et al., 1985; Raymo et al., 1989, 1992) and that deep-sea benthic faunas respond to glacial–interglacial climate changes in general (Schnitker, 1979) and specifically in response to climate-induced variability in food resources (Goody, 1988; Thomas et al., 1995). Recently, Cronin and Raymo (1997) showed that orbital-scale climate change such as 41,000-yr obliquity cycles have a major impact on deep-sea benthic communities in the North Atlantic Ocean.

In addition to orbital scale climate change and diversity variability at orbital timescales, recent studies of high-sedimentation regions of the North Atlantic Ocean (Keigwin and Jones, 1994; Keigwin, 1995) demonstrate that past deep-ocean circulation changes occurred over centennial to millennial timescales as well. Do these shorter-term Quaternary climate changes cause deep-sea diversity changes? And, if so, what factors influence diversity most? These questions are especially pertinent because coupled atmosphere–ocean climate models predict major changes in North Atlantic thermohaline circulation over the course of the next few centuries (Manabe and Stauffer, 1995).

In this study we examined the response of deep-sea ostracode biodiversity to changes in benthic environments related to climate changes over the past 210,000 years in the North Atlantic Ocean. Our goal was to specifically address the question as to whether shorter-term climate changes (2 to 20 kyr) lead to diversity changes. Moreover, recent field studies of terrestrial diversity have shown that diversity itself is not the major attribute to maintain a functioning ecosystem, but rather it is the species composition as well (e.g. Tilman et al., 1997; Hooper and Vitousek, 1997). Therefore, in addition to obtaining secular trends in diversity, we also examined how benthic assemblage composition changes at these timescales by examining trends in key ostracode taxa indicative of climatically driven ecosystem dynamics.

2. Core site and material

The *Chain* Core 82-24 4PC site (Fig. 1) is situated on the western flank of the Mid-Atlantic Ridge in a region dominated during the current interglacial by North Atlantic Deep Water (NADW) (Boyle and Keigwin, 1985; Raymo et al., 1989, 1992). We chose

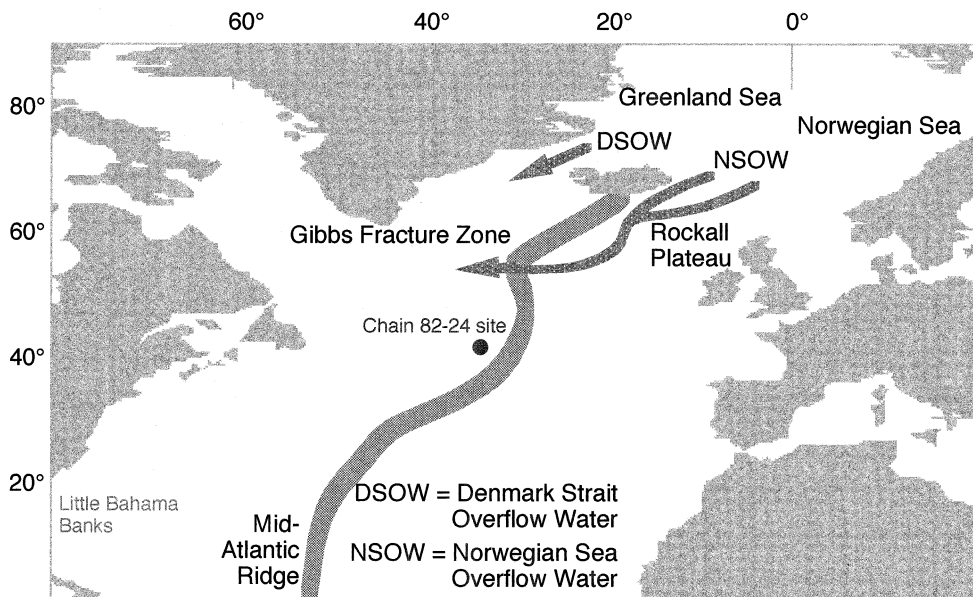


Fig. 1. Map showing location of Chain 82-24 core 4PC site in relation to sources of North Atlantic deep water originating in Nordic Seas.

this site to investigate ostracode diversity during climate change for several reasons. First, this region has a well-established late Neogene paleoceanographic history based on multiple proxy faunal and stable isotopic records from the *Chain* 82-24 core (Boyle and Keigwin, 1985) and Deep Sea Drilling Program (DSDP) Site 607 (Ruddiman et al., 1986; Raymo et al., 1989). These records include planktic and benthic foraminiferal abundances and shell $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, and cadmium/calcium (Cd/Ca) ratios (Boyle and Keigwin, 1985), and ostracode shell magnesium:calcium (Mg/Ca) ratios (Dwyer et al., 1995; Cronin et al., 1999). In brief, these studies show that over at least the last 3 million years, the site is influenced by NADW during interglacials and more so by Antarctic Bottom Water (AABW) during glacials (Raymo et al., 1992). The ostracodes studied here were obtained from the same samples used by Boyle and Keigwin (1985) in their original study of isotopic and trace element variability in the *Chain* 82-24 core and those used by Dwyer et al. (1995) and Cronin et al. (1999) to study Mg/Ca ratios in *Krithe* shells.

Another advantage of the *Chain* core is that it is located at the site of Deep Sea Drilling Project Site 607 where extensive Plio-Pleistocene ostracode-based biostratigraphic (Whatley and Coles, 1987), biodiversity (Cronin and Raymo, 1997), and paleoceanographic reconstructions (Dwyer et al., 1995; Cronin, 1996; Cronin et al., 1996) have been carried out. Thus, these data provide a comparative data base on pre-late Quaternary, low-frequency benthic faunal trends to which we can compare those that occurred during the last 210,000 years.

Adequate taxonomy is a prerequisite for investigating the impact of climate change on diversity. The taxonomy of deep-sea North Atlantic ostracodes is reasonably well known (Whatley and Coles, 1987) and species-level taxonomic identification was possible for most groups. One difference between the present study and the previous study of DSDP Site 607 ostracode diversity by Cronin and Raymo (1997), is that in the present study, we followed the taxonomy of Coles et al. (1994) for identifying species of the dominant deep-sea genus *Krithe*.

The *Chain* core also has an excellent age model (Boyle and Keigwin, 1985) based primarily on oxygen isotope stratigraphy. Boyle and Keigwin noted a gap in coring between about 350 and 380 cm,

which they corrected by subtracting 30 cm from the core depth below 380 cm to obtain a continuous paleoceanographic sequence. We provide the original sample core depths in Table 1; Fig. 2 plots abundance and diversity against corrected core depth.

We analyzed 266 total samples of which 258 samples were included in the plots of species diversity and ostracode assemblages. The ostracode species census data are given in Table 1. We picked all adult and juvenile (molt) ostracodes contained in the >150 μm size fraction. This method assured that all adults and, depending on the species, usually two to three prior molt stages were obtained.

3. Ostracode abundance and diversity

Fig. 2 plots ostracode total abundance in each sample (N , >150 μm) and diversity as measured by both number of species (S) and by the Shannon–Weaver information function, $H(S)$ [$H(S) = -\sum_1^n p_i \ln(p_i)$ where p_i is the proportion of the i th species, \ln is the natural log, n is the total number of species]. $H(S)$ is one of many available indices to measure diversity; it has the advantage that it takes into account both the number of species and their relative proportions. A maximum value of $H(S)$ would occur when all species are equally distributed in a sample.

As shown in Fig. 2, the number of individuals in any sample varies greatly from 0 to almost 150; the mean was about 40 for all samples (Table 1). S varies from 1–2 species to as many as 20 species in a single sample; $H(S)$ varies from about 0.4 to almost 1.2.

It is well known that the fewer individuals in a sample, the greater the chance that rare species are missed. In such cases, an ecosystem's true diversity would be underestimated. Consequently, it would be preferable to have 200–300 individual specimens per sample to analyze trends in diversity. There are not, however, enough ostracode specimens in each sampled 2 to 4 cm interval to do this. One way to overcome the problem of small sample size would be to group assemblages from several samples from a 10–20-cm interval and thereby obtain a greater sample size. This solution has several drawbacks. First, it sacrifices the temporal resolution from using 2–4 cm

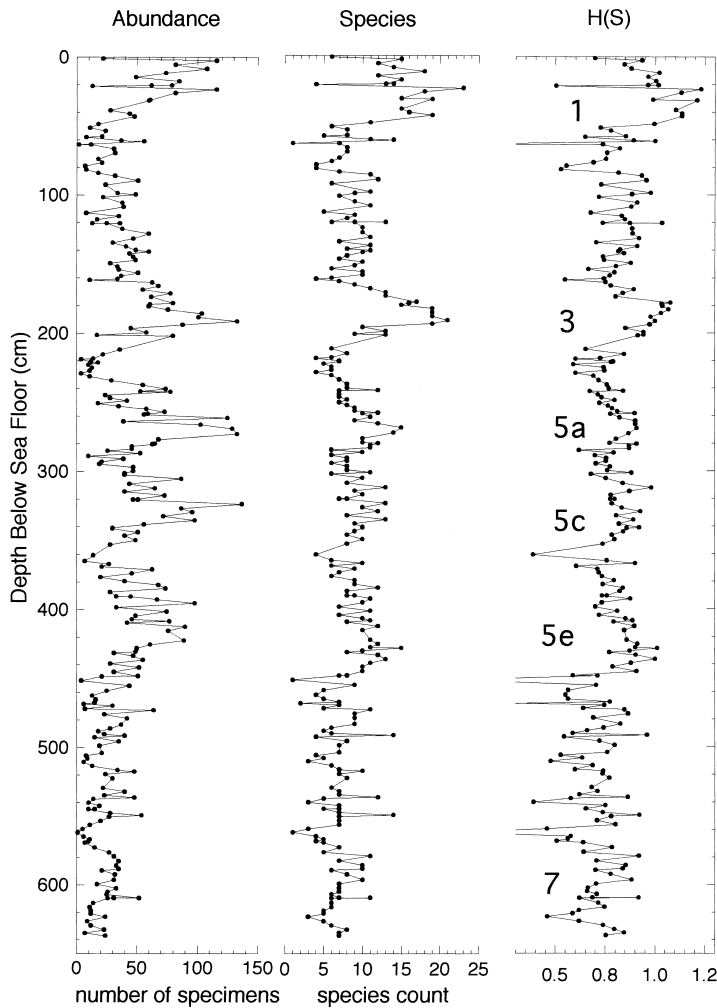


Fig. 2. Plot of ostracode abundance, species number and species diversity measured by $H(S)$ (Shannon Weaver Index) for the *Chain* 82-24 core 4PC, western mid-Atlantic Ridge, North Atlantic Ocean. Original core depths below 347 cm have been corrected by subtracting 32 cm from core depth per Boyle and Keigwin (1985) to account for a gap in the coring. Odd-numbered oxygen isotope stages (1, 3, 5a, 5c, 5e, and 7) are labeled for reference to later figures.

sampling intervals and might obscure rapid changes in ostracode faunas. Second, it makes direct comparison between ostracode trends and paleoceanographic isotopic and trace element indicators obtained from the same sample splits more difficult. Third, the changes in ostracode abundance may in fact reflect environmentally influenced biotic factors, such as changes in standing stock of ostracodes, as well as sedimentological and post-mortem taphonomic processes. A fourth reason is that the $H(S)$ index is not as sensitive to total abundance as is simple species

number, S , and using $H(S)$ to measure diversity overcomes the low abundances to a certain degree. This is illustrated in Fig. 3 which plots N versus both S and $H(S)$ for our data set and illustrates the common relationship between abundance and diversity. Diversity as measured by $H(S)$ increases with abundance asymptotically such that obtaining greater numbers of specimens may lead to the discovery of only rare species. The curve of N versus $H(S)$ tends to level out with increasing abundance and thus is less likely to be biased by low num-

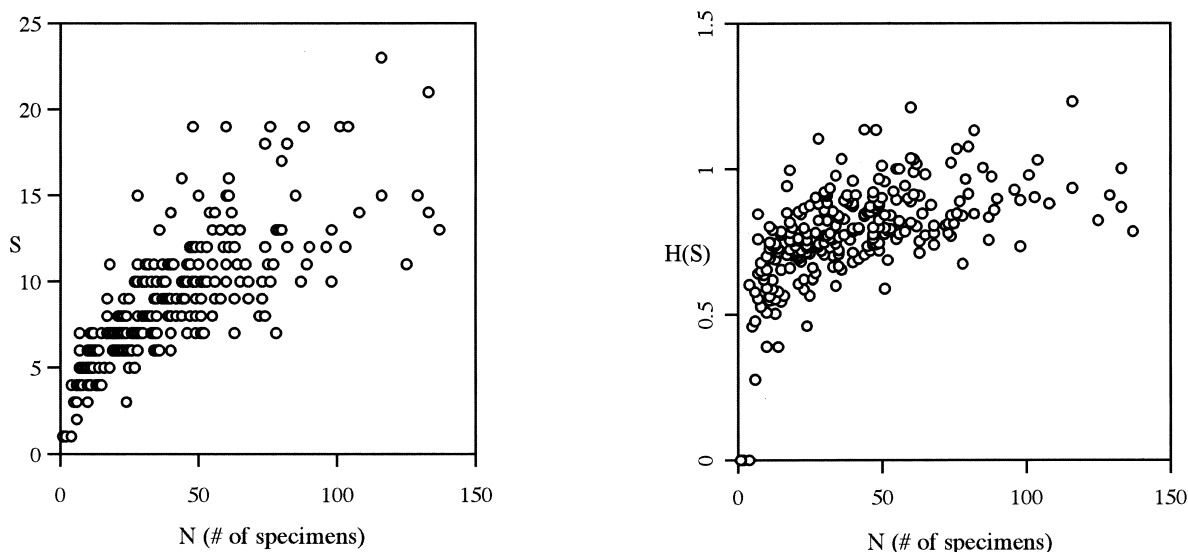


Fig. 3. Plot showing relationship between number of ostracode species (S) and diversity [$H(S)$] and number of specimens. Using $H(S)$ as an index of diversity lessens the effects of low abundance on estimating real species diversity.

bers of individuals. For example, the most diverse samples [$H(S) > 1$] are not those with the greatest abundance, but those that have <50 to about 100 individuals, whereas samples with the greatest abundance (>100 specimens) have moderate diversity [$H(S) = 0.75$ – 1.0]. Samples with <20 individuals clearly must be suspected of missing certain taxa. We compared diversity trends using all 256 samples with trends obtained using only a subset consisting only of samples with >20 specimens with little apparent differences in the major trends.

In sum, the strategy to investigate diversity trends represents a tradeoff between maintaining the temporal resolution and paleoenvironmental context necessary to test ideas about climate and benthic communities and the desired adequate representation of rare taxa. We consider the diversity trends to represent a first order benthic signal, though certainly less common species are underrepresented in some samples, and the abundance trends themselves may also signify ecological changes over millennial timescales. We hope our preliminary results lead to additional research using cores in which more sediment can be sacrificed to obtain larger numbers of individual ostracode specimens and provide a stronger statistical basis for inferring diversity trends.

4. Diversity, climate and deep-sea environmental change

4.1. Diversity and paleoceanographic changes in the deep North Atlantic

We first compared $H(S)$, using a three-point moving average to Mg/Ca ostracode shell ratios and the benthic foraminiferal carbon and oxygen isotopic curves from Boyle and Keigwin (1985) for the last 210 ka to examine the diversity/climate linkage at this site (Fig. 4; Table 2). We identified 23 total excursions in diversity, labeled 1–23 in Fig. 4 (see Table 2). Eleven of these diversity peaks (DPs) are periods when $H(S)$ exceeded 0.8 and S ranged from 10 to 21 species (DPs 1, 4/5, 6/7, 8/9, 11, 12/13, 15, 17, 20, 21, 23). Most of these peaks correspond to periods of global climatic warmth defined by odd-numbered marine isotope stages (MIS) as follows: MIS 1 = DP 1; MIS 3 = DP 8; MIS 5a = DP 11; MIS 5c = DP 13; MIS 5e = DP 15; MIS 7 = DP 21/23. Other notable features of the smoothed $H(S)$ curve are that the highest $H(S)$ values correspond to the early Holocene hypsithermal and isotope stage 3, and that there are multiple periods of high diversity during isotope stage 6 (DPs 17–20).

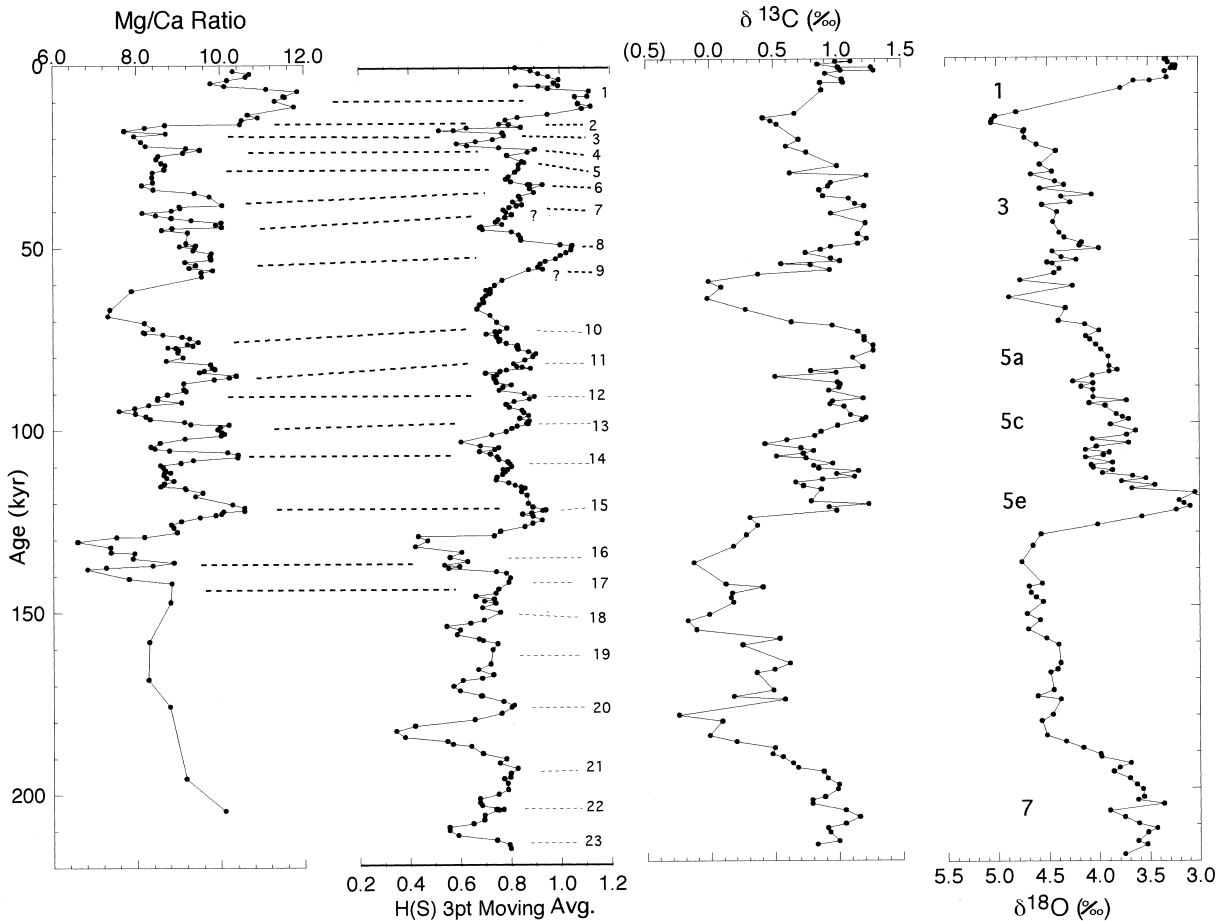


Fig. 4. Comparison of ostracode diversity [three-point moving average of $H(S)$] and Mg/Ca ratio of *Krithe* shells, $\delta^{13}C$ and $\delta^{18}O$ of *C. wuellerstorfi*. Twenty-three diversity peaks (DPs) are labeled in the second column; tentative correlation to spikes in Mg/Ca values signifying relatively warm bottom water temperatures are shown with dotted lines. Odd-numbered marine oxygen isotope stages signifying interglacial climates are labeled at right. Age model is that of Boyle and Keigwin (1985). Not all samples yielded both adult *Krithe* for Mg/Ca measurements and adequate specimens for diversity measure. These sampling biases, plus the effects of smoothing, bioturbation and a possible lagged response of diversity, mean that the ages of peaks in Mg/Ca and $H(S)$ do not always match exactly. Resolution of these fine-scale differences between $H(S)$ and Mg/Ca requires studies of higher sedimentation rate situations.

Periods of high diversity also correspond to relatively warm bottom water temperatures (BWT) indicated by high Mg/Ca ratios. Mg/Ca ratios ranging from 10 to 12 mmol/mol suggest BWT from 3 to 3.5°C using the Mg/Ca temperature calibration of Dwyer et al. (1995). Modern BWT at the Chain core sites is about 2.3°C. In contrast, periods of lowest diversity had estimated BWT equal to 0–1°C. In general, the record of first-order diversity variability suggests that it is related to deep-sea environmental changes occurring at orbital timescales of 20–100

ka which dominate many climate records of the past 200 kyr.

Millennial-scale changes in diversity are also evident from the data in Figs. 2 and 4. Although the sedimentation rate was too slow to determine the exact frequency and duration of each event, minor diversity excursions appear to correspond to excursions in Mg/Ca ratios (Fig. 4). For example, during the past 150 kyr, an interval for which Mg/Ca data are available at a sampling resolution comparable to that for diversity, 15 of 17 DPs have a correspond-

Table 2

Ostracode diversity peaks, Dansgaard–Oeschger events, Mg/Ca peaks

Diversity peak	Dansgaard–Oeschger Event	Mg/Ca peak	Comments
1	hypsothermal	yes	double peak
2	1?	yes	
3	1?	yes	
4	2	yes	
5	3	?	
6	8	yes	DP and Mg/Ca peaks not coincident
7	12	yes	weak DP peak
8	14	yes	strong DP peak
9	15	yes	weak DP peak
10	19/20	yes	
11	21	yes	double peak
12	22	?	
13	23	yes	
14	24	yes	
15		yes	double peak
16		yes	
17		yes	
18–23	no data	no data	

ing excursion in Mg/Ca; the two exceptions are DP 12 and DP 5 (Table 2). We caution that the effects of small sample size, curve-smoothing in Figs. 4 and 5, and sedimentation can obscure fine details of the actual diversity history of this region. This is especially pertinent as the net diversity change during rapid excursions is only 0.2 to 0.5 [e.g., $H(S)$ changes from 0.5 to 0.8]. Even with this limitation, the apparent correspondence of even minor changes in BWT with ostracode diversity suggests the trends are not a sampling or preservation artifact but rather that $H(S)$ successfully captures real high-frequency diversity variability that is somehow linked to the same environmental changes that caused the temperature variability. To cite one example, the drop in diversity between DP 2 and DP 1 occurs during the well-known 1000-year climate reversal Younger Dryas (Broecker et al., 1985; Lehman and Keigwin, 1992). Two major diversity peaks, DP 1 and DP 11, have double peaks that correspond to double peaks in Mg/Ca ratios.

4.2. Comparison with other climatic records

Because deep-sea diversity appears to be linked to deep- and surface-water paleoceanographic variability in the North Atlantic region, it is instructive

to compare diversity to other records of climate change in the North Atlantic region. The GISP 2 and GRIP Greenland ice cores provide a detailed climate records of the past 110 kyr (Dansgaard et al., 1993; Johnsen et al., 1992; Stuiver et al., 1995; Brook et al., 1996; Alley et al., 1997). Fig. 5 compares the smoothed diversity record against the GISP2 oxygen isotope curve for $\delta^{18}\text{O}$ of Greenland ice, considered mainly a record of atmospheric temperatures of the source of precipitation over Greenland, secondarily influenced by atmospheric circulation (Stuiver et al., 1995). Although the ice core sampling exceeds that of the Chain core and the age models are somewhat different, several first-order similarities and differences are apparent. During the latter part of marine isotope stage 5 (110–80 ka), four DPs [$H(S) > 0.8$] are tentatively correlated with light isotope excursions in the Greenland record centered at approximately 110, 95–98, 90 and about 80 kyr. These are the equivalent of Dansgaard–Oeschger (D–O) interstadial events #24, 23, 22, and 21, respectively, recognized in the GRIP ice core (Johnsen et al., 1992; Dansgaard et al., 1993). There are no diversity excursions during the brief but strong D–O events #19 and 20 about 68 and 72 kyr. The major DP centered on 50 kyr (= DP #8, Fig. 4) corresponds to Dansgaard–Oeschger event #14; the interval of

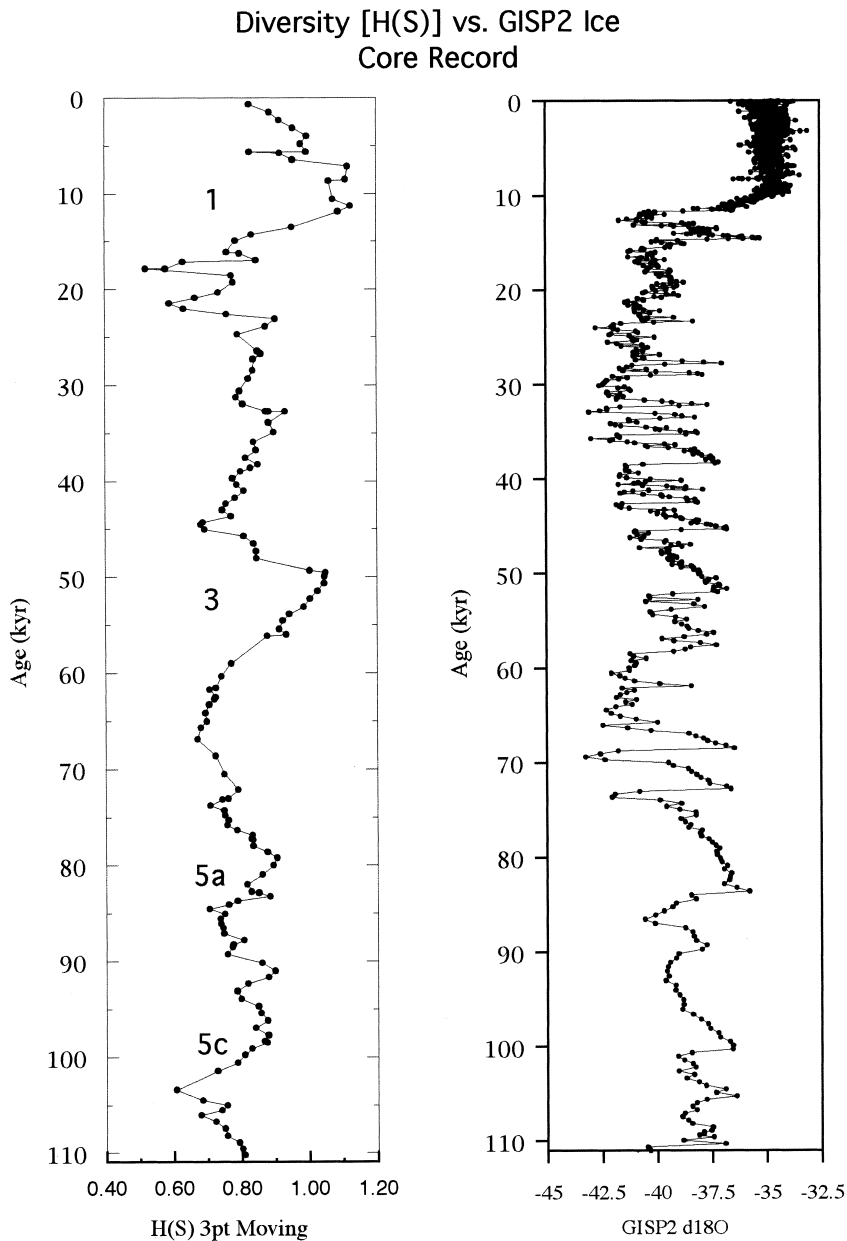


Fig. 5. Comparison of smoothed *Chain* core ostracode $H(S)$ with unsmoothed Greenland GISP2 ice core oxygen isotope record for past 110 kyr. High species diversity generally corresponds to light isotope values and warm climate.

moderately high diversity about 37–33 kyr corresponds to D–O events 8–5 but the details of the two records cannot be discerned. About 16 kyr (near 60 cm core depth, Fig. 2). *Chain* core diversity rises at a time that is tentatively correlated with D–O event #1. Finally, the increase in diversity during the last

deglaciation (Termination 1) and the early Holocene hypsithermal corresponds to the GISP2 isotopic shift to light values. While diversity decreases during the latter part of the Holocene, GISP2 isotopic record remains steady except for an important negative excursion at 8 kyr, which may correspond to the brief

drop in diversity at 7–8 kyr in the Fig. 5 smoothed record, which is due mainly to a sharp drop from early Holocene levels near 20 cm core depth (Fig. 2). More detailed Holocene records are needed to confirm this relationship.

Another paleoceanographic record providing independent evidence for millennial-scale climate impacts in the deep North Atlantic Ocean is that of Rasmussen et al. (1996). Rasmussen et al. found that significant changes in surface and deep-water conditions occurred during fifteen Dansgaard–Oeschger events of the past 150 ka in the Faeroe–Shetland Channel at water depth of 1020 m. They also documented major oscillations in the benthic foraminiferal assemblages during short-term climate events when changes in North Atlantic Deep Water occurred. Such a pattern is entirely consistent with the Chain core variability in ostracode diversity and assemblage structure discussed below.

5. Comparison to other deep-sea ostracode records

5.1. Pliocene versus late Quaternary diversity

We compared the Chain core diversity trends for late Quaternary climate oscillations with those obtained for Pliocene 41-kyr obliquity cycles from DSDP Site 607 at the Chain core site. Cronin and Raymo (1997) described a pattern of oscillating ostracode diversity during eleven 41-kyr cycles that was probably linked to variability in food resources stemming from surface ocean productivity changes described by Thomas et al. (1995) and Versteeg et al. (1996). They also documented comparable diversity instability at DSDP Site 610 in the northeastern North Atlantic Ocean on the Rockall Plateau during the Late Pliocene. At both DSDP sites, ostracode diversity oscillated from $H(S)$ values of 0.2–0.6 during glacials and 1.2–1.6 during interglacials. This range of $H(S)$ values is quite similar to the range obtained for the late Quaternary ostracode record from the Chain core. As with the Chain core record, DSDP Site 607 was also characterized by oscillating deep-sea bottom water temperatures (Dwyer et al., 1995). Thus, it appears that late Quaternary 100-kyr and Pliocene 41-kyr glacial–interglacial climatic

cycles had similar impacts on deep-sea ostracode diversity in these parts of the North Atlantic Ocean, even though the amplitude of the Pliocene obliquity cycles as measured by isotopic and trace element proxies is 1/2 to 1/3 the amplitude of late Quaternary climatic extremes.

5.2. Ocean margin refuges for ostracode species

The quasi-cyclic nature of deep sea ostracode diversity means that some species inhabit deep-sea habitats intermittently, disappearing for periods of thousands to tens of thousands of years when glacial conditions exist. The question then arises as to what regions do species that are typically abundant in deep (>2500 m water depth) North Atlantic environments during interglacial periods inhabit during glacial periods? One logical place to search is shallower depths along North Atlantic continental margins. Extensive data on last glacial–Holocene interglacial ostracode faunas obtained from mid-depth (500–1500 m water depth) regions off the Little Bahama Banks provide a preliminary answer.

Slowey and Curry (1992, 1995) documented significant paleoceanographic changes during the last glacial at water depths just below the thermocline in the Little Bahama Banks region. Preliminary results on ostracode $H(S)$, S , and N from some of these sites (Fig. 6) show that upper slope habitats had greater species diversity as measured by $H(S)$ and by S than do deep-sea regions like the Chain core site during both the Holocene interglacial and, on the basis of more limited data, during the last glacial (Rodriguez and Cronin, in press). Within the Little Bahama Banks region, $H(S)$ values for core 117 JPC (1535 m) were consistently lower [$H(S)$ about 2.0] than those for cores 7 JPC (1320 m) and 103 GGC (965 m) [$H(S)$ about 2.5–2.8], suggesting some type of depth-related diversity gradient. Finally, the data from core 103 GGC suggest that ostracode diversity may have been lower in this region during the last glacial compared to the Holocene, although additional margins must be studied to confirm this.

The composition of the glacial-age ostracode faunal assemblages from the Little Bahama Banks suggests that there was an ‘upslope migration’ of certain ostracode species typically found at greater

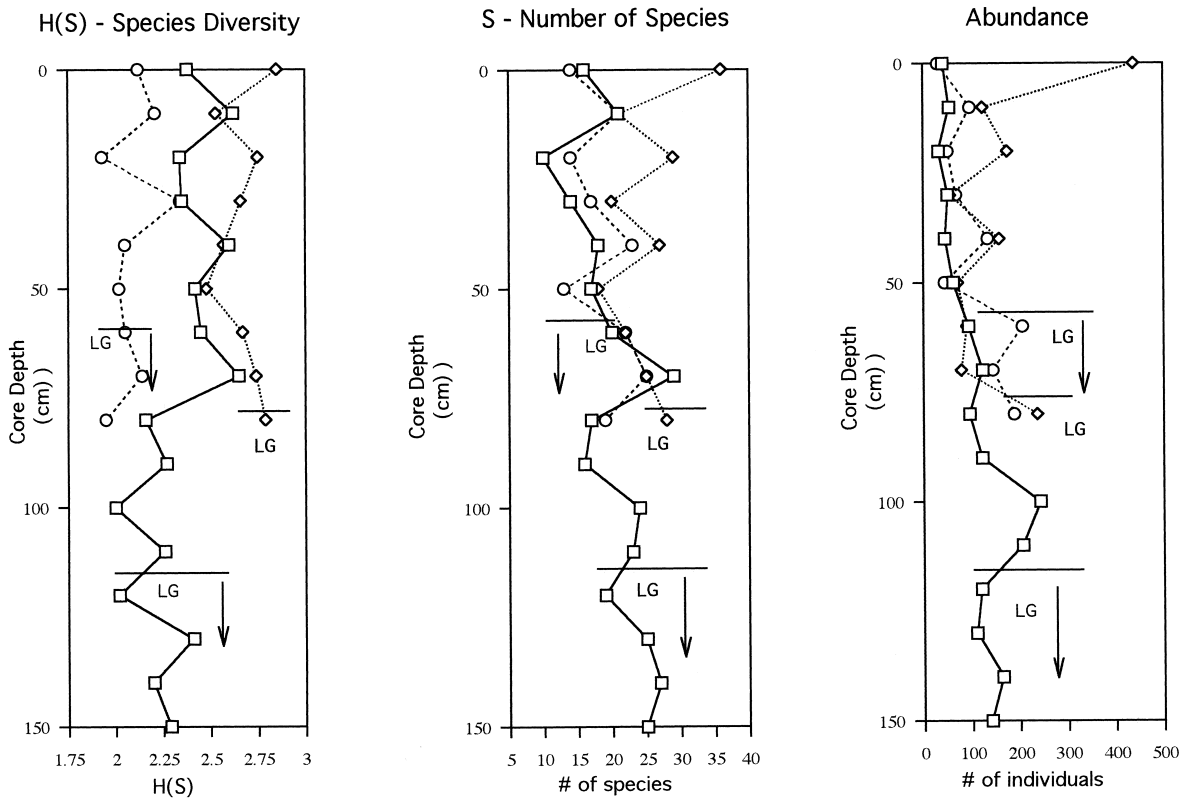


Fig. 6. Ostracode species diversity measured by $H(S)$ and S and abundance for three cores from Little Bahama Bank region. Stratigraphy and paleoceanography from Slowey and Curry (1992, 1995). LG signifies samples believed to represent last glacial. Samples above the horizontal lines represent the deglacial and Holocene intervals.

depths. Among the more obvious examples of altered bathymetric ranges were several species of *Krithe*, *Bradleya dictyon*, and *Poseidonamicus*. Rodriguez and Cronin postulate that changes in bottom water conditions and food resources led to more suitable habitats in mid-depth regions during glacials, providing a temporary refuge for deep-sea species. The upslope migration hypothesis of ostracode species' paleobiogeography needs to be confirmed with additional ocean margin faunal studies in other parts of the North Atlantic. Nonetheless, it is consistent with late Quaternary changes in high-latitude ostracode species paleobathymetric distributions in response to glacial climates in several parts of the Arctic Ocean (Cronin et al., 1994, 1995) and with inferred glacial age bottom water changes based on isotopic and other proxy data. Upslope migration may be hypothesized to be a common ecological response among

deep-sea species stressed by glacial oceanographic conditions.

6. Variability in ostracode functional groups during climatic change

Recent experimental field studies of plant diversity have shown that changes in plant species assemblage composition better explain variation in primary production and nutrient dynamics than does simple diversity of functional ecological groups (e.g., Hooper and Vitousek, 1997; Tilman et al., 1997). These studies suggest that diversity per se is not the critical factor in the functioning of an ecosystem responding to disturbance, especially in situations when the ecology of one or several key species dominate ecosystem functioning. We investi-

gated the question of assemblage composition on the timescales of thousands to tens of thousands of years by examining variability in key functional ostracode groups in the *Chain* core record.

Four key ostracode assemblages were recognized in the *Chain* core record of the past 210 kyr: *Argilloecia/Cytheropteron*, PEHO (abbreviation for a group comprised mostly of *Poseidonamicus major*, *Echinocythereis echinata*, *Henryhowella asperima*, and *Oxycythereis dorsoserrata*), *Krithe*, and *Pelecocythere* (mainly *P. foramena*). Each group is dominated by a few species that possess generally similar ecological requirements and/or similar modern geographic and bathymetric distributions in the North Atlantic and adjacent seas. The species comprising each group are associated with distinct water depths, water mass characteristics, nutrient and/or food resources. Details of many species' ecology, bathymetry, and zoogeography can be found in Whatley and Coles (1987), Dingle et al. (1990), Van Harten (1990), Coles et al. (1994), Cronin et al. (1995), and Rodriguez-Lazaro and Cronin (in press).

In addition to their modern distributions, these four groups of ostracodes also characterize distinct oceanographic stages of Pliocene 41-kyr obliquity climate cycles that can be identified based on isotopic and trace element data (Cronin et al., 1996). *Krithe* predominates during glacial periods, *Argilloecia/Cytheropteron* typically inhabit the deep North Atlantic during deglacial environments, the PEHO assemblage during peak interglacial periods, and *Pelecocythere* occurs almost exclusively during interglacial/deglacial transitions.

We discovered secular patterns of ostracode assemblages in the *Chain* core late Quaternary record that were quite similar to those occurring during Pliocene climatic cycles in several important respects. Fig. 7 shows the unsmoothed trends in the proportions of these four assemblages; Fig. 8 shows a three-point moving average of the same data, excluding *Pelecocythere* which does not occur in enough late Quaternary assemblages to offer meaningful results. The dominant ostracode genus is *Krithe*; at least 10 species are found at various depths throughout the North Atlantic region (Coles et al., 1994).

We refer to the first stage of the secular pattern as the period of maximum glacial climate when the genus *Krithe* dominates ostracode assemblages. In

deep-sea North Atlantic glacial-age sediments at water depths below about 2000 m, *Krithe* is almost always the most common genus, and sometimes the sole genus present, in both Pliocene and late Quaternary sediments. Cronin et al. (1996) showed through spectral analyses that the *Krithe* assemblage varied at a 41-kyr frequency over 10 Pliocene climatic cycles (marine isotope stages 111–95) and its variation was coherent at the 95% confidence level and in phase with minimum $\delta^{13}\text{C}$ (AABW formation), maximum $\delta^{18}\text{O}$ (maximum continental ice volume), and low Mg/Ca ratios (minimum bottom water temperature). In the *Chain* core record, *Krithe* occurs in maximum percentages (80 to >90%) during relatively cold periods corresponding to marine isotope stages 6, 5d, 5b, 4, and 2 (Fig. 8).

The second stage is defined as a period when the *Argilloecia/Cytheropteron* assemblage appears immediately following the peak glacial interval. Nine Quaternary *Argilloecia/Cytheropteron* events are labeled AC1 through AC9 in Fig. 8 when these genera reach >7–8% of an assemblage (maximum >30% during late marine isotope 8 and the early Holocene stage 1). The species-level taxonomy of the former genus is not well known but most of the *Chain* core *Argilloecia* represent a single species or two or three closely related species. *Cytheropteron* is usually represented by between 2 to 4 species. It is well established that many species of *Argilloecia* and *Cytheropteron* typically inhabit mid-depth high-latitude Arctic and subarctic seas during the Holocene interglacial (Cronin et al., 1995; Whatley et al., 1996). The periodic occurrence of short-term increases in *Argilloecia/Cytheropteron* above background level of 0–3% supports the idea that during times of deglaciation, a strong pulse of North Atlantic Deep Water overflow from Nordic Seas brings a spike in the genera *Argilloecia* and *Cytheropteron* in both Pliocene and late Quaternary sequences (Cronin et al., 1996).

Following this brief peak in *Argilloecia/Cytheropteron*, a third stage of a cycle corresponds to peak interglacial climates. Interglacial climates are characterized by increased proportions of the PEHO group, usually 20 to >40% and decreased proportions of *Krithe*, to 40–70%. To illustrate the temporal relationship between the *Argilloecia/Cytheropteron* and PEHO assemblages, dashed lines are drawn in

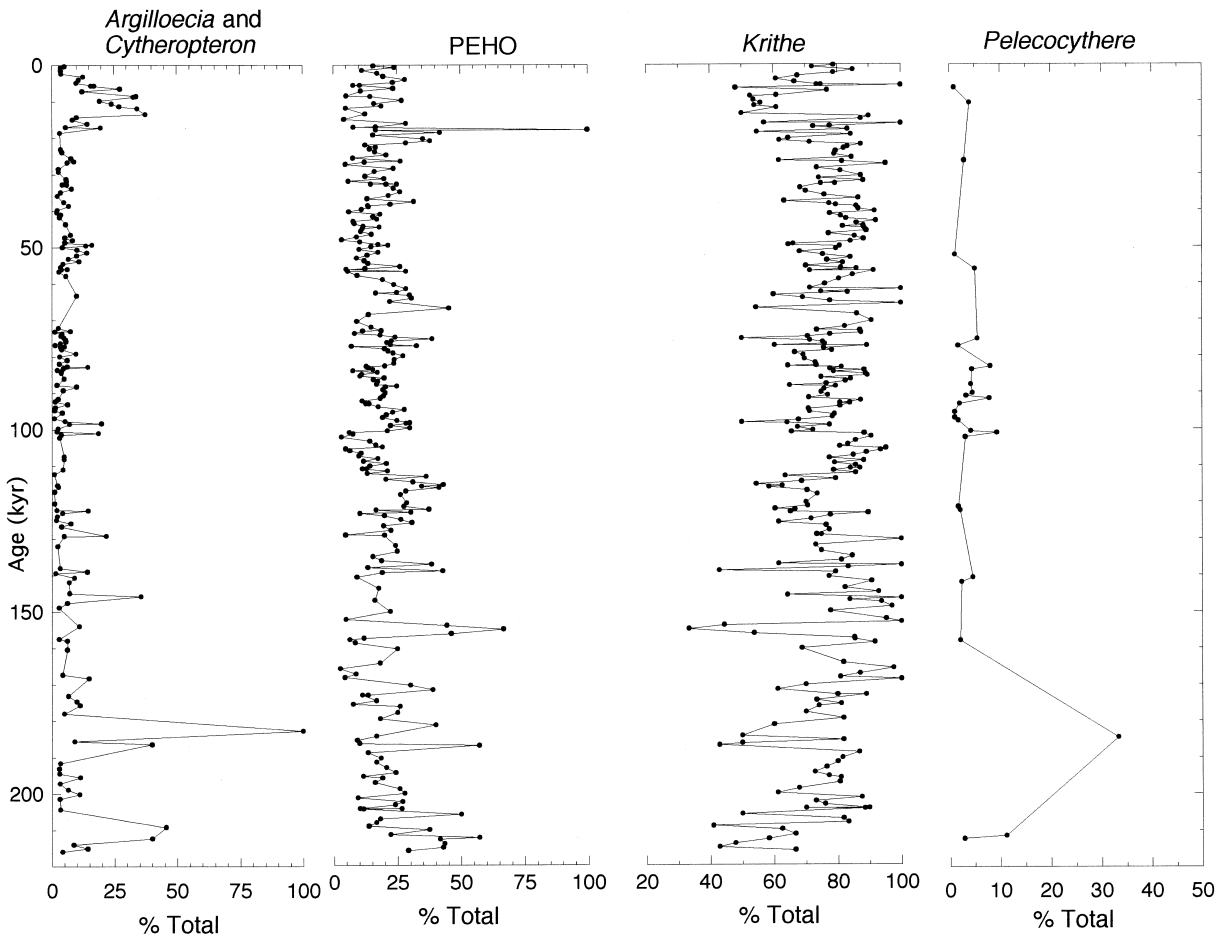


Fig. 7. Percentages of four key ostracode groups in the *Chain* core for the past 210 kyr. PEHO = *Posidonamicus*, *Echinocythereis*, *Henryhowella*, and *Oxycythereis*.

Fig. 8 showing a tentative correlation between each AC event and a succeeding rise in PEHO. In contrast to assemblage patterns during the Pliocene 41-kyr climatic cycles, the match between *Argilloecia/Cytheropteron* and succeeding PEHO events in the late Quaternary is not so clearcut and additional cores will be required to sort out the succession of faunal assemblages during these suborbital climatic events.

Although occasional specimens of *Pelecocythere* occur in the *Chain* core, additional studies are needed with greater abundance to establish late Quaternary trends in *Pelecocythere* in the North Atlantic.

In sum, the ostracode assemblage trends shown in Figs. 7 and 8 suggest that the main features of the

faunal sequences that characterized 41-kyr Pliocene climatic cycles are also typical of suborbital-scale climate oscillations of the past 210 kyr. Although it is tempting to speculate on the periodicity of ostracode assemblages and the phase relationships among them and geochemical proxy indicators, additional high sedimentation rate cores will be needed to justify spectral analyses.

7. Discussion

The study of biological diversity has in recent years come to the forefront as humans influence the numbers and types of species (Peters and Love-

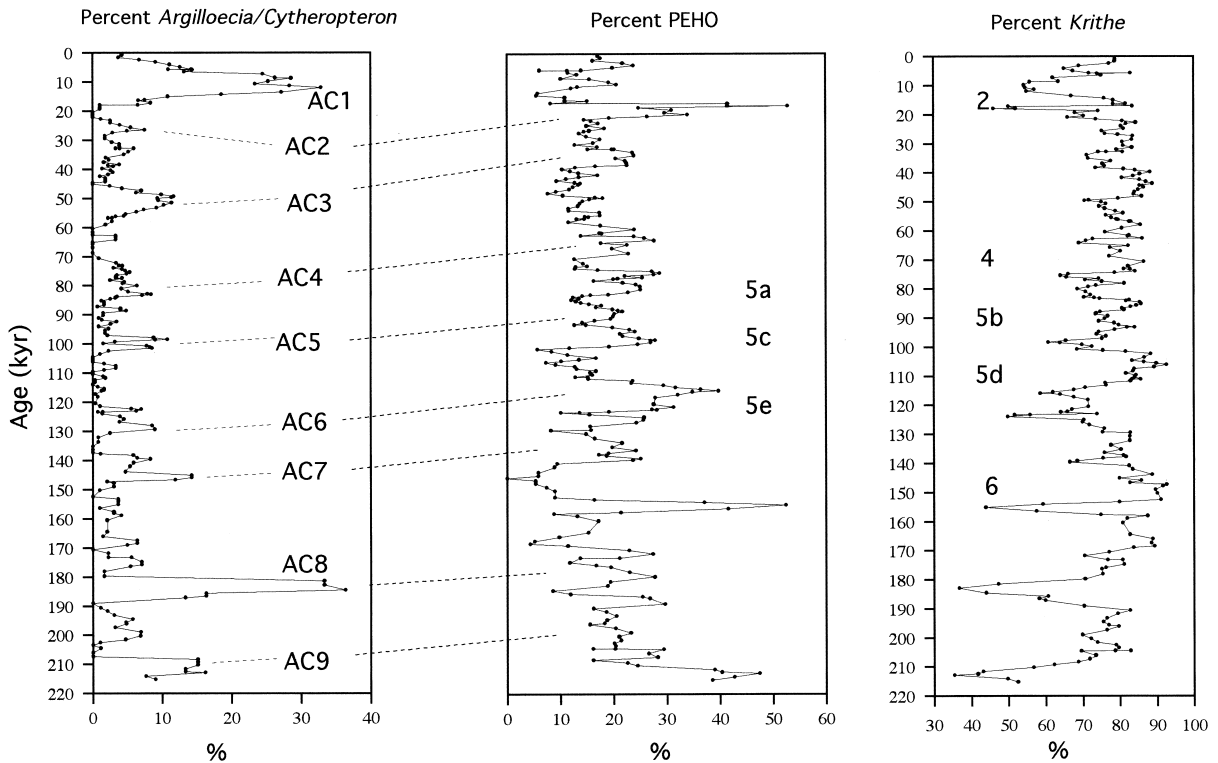


Fig. 8. Three-point moving averages of proportions of three common ostracode groups plotted in Fig. 7. *AC1–AC9* are nine distinct spikes in the genera *Argilloecia/Cytheropteron* which signifies strong deep-water overflow probably from the Nordic Seas during deglaciation. *PEHO* is most abundant during warm periods, substages *5a*, *5c*, *5e*; there is not a simple one-to-one correspondence of *AC* to *PEHO* peaks. *Kriithe* is dominant during glacials and cool stadials, marine isotope stages *2*, *4*, *5b*, *5d*, and *6*.

joy, 1992; Huston, 1994). Whereas many studies of species diversity have traditionally focused on small spatial and short temporal scales, some ecologists have called for a 'scaling up' of both spatial and temporal scales in studies designed to understand patterns of species diversity in general (e.g., Ricklefs, 1987; Levin, 1992; Brown, 1995) and in the deep sea in particular (Rex et al., 1993). Our results have bearing on several aspects of the relationship between environmental disturbance of deep-sea habitats due to climate changes over timescales of thousands of years and accompanying deep-sea benthic biodiversity variability.

First, as evidence mounts that deep-sea environments and deep-oceanic circulation have varied during the late Quaternary at millennial timescales (Keigwin et al., 1991; Keigwin and Jones, 1994; Oppo and Lehman, 1996), our evidence indicates that ostracode biodiversity and assemblage compo-

sition also vary and that climate change plays a significant role in altering these deep-sea ecosystems. In essence, our new results extend the idea that climate exerts a primary influence on deep-sea diversity over orbital timescales (Cronin and Raymo, 1997) to suborbital timescales. The amplitude of suborbital climate events was not as great as most orbitally induced climatic cycles, but our results nevertheless indicate significant short-term modification of deep-sea benthic ecosystems.

One obvious implication of these data in terms of future climate change is the potential sensitivity of deep-sea ecosystems to relatively small changes in deep-ocean circulation changes. If the ostracode assemblage is assumed to be a relatively accurate proxy for the entire benthic community of a region, then it appears that the deep sea ecosystem is not immune to climate perturbations experienced in surface waters and terrestrial environments. Although the

fine spatial fabric of biodiversity cannot be inferred from one or two cores from a site, the hypothesis that observed diversity variability characterizes a large region of the deep North Atlantic and perhaps other ocean basins can be tested.

More generally, our results support the ideas of Rex et al. (1993) that different mechanisms control diversity trends at different spatial and temporal scales. While it may be true, as argued by Etter and Grassle (1992), that at small spatial scales, sediment composition correlates most strongly with diversity in deep-sea soft sediment communities, climate changes may ultimately be a major influence on surface water productivity and seasonal and interannual phytodetrital fluxes to the bottom (Gooday, 1988; Thomas et al., 1995; Versteeg et al., 1996).

Finally, large-scale spatial and temporal patterns of deep-sea biodiversity are still poorly understood. Although we have not yet studied ostracodes from sedimentary sequences in the North Atlantic having a sub-millennial scale resolution, we suspect on the basis of our observations of Quaternary assemblages from the Nordic Seas that ostracode assemblage response to even shorter-scale perturbations will be pronounced. Consequently, one ultimate goal might be to obtain decadal and centennial scale diversity records which would provide at least a preliminary means of understanding natural levels of diversity variability prior to and since humans have begun to modify climate. Moreover, as improved paleoclimate and biodiversity records at centennial timescales become available from deep-sea sites (Keigwin, 1995), it is not inconceivable that temporal resolution approaching that of experimental diversity data sets (Tilman et al., 1997) might be achieved. Such a marriage between experimental field studies and retrospective analyses of diversity would be unprecedented and provide valuable data on how ecosystems respond to perturbation and how human activities might be altering diversity in the oceans.

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