Reports

Paleoceanographic Events and Deep-Sea Ostracodes

Abstract. *Eight recognized or theorized paleoceanographic events during the past 70 million years were tested against changes in the global deep-sea benthic ostracode fauna. Two events, the sudden Cretaceous-Tertiary boundary event at 66 million years ago and the more gradual 40-million-year event (formation of the psychrosphere), show up most dramatically. Before the 40-million-year event, ostracodes freely radiated into the deeper water regions but were provincial. The development of thermal stratification isolated these deep-water taxa, mostly the survivors of the Cretaceous-Tertiary boundary event, which adapted to a new, free-flowing but more frigid ecosystem and spread rapidly throughout the world.*

Benthic ostracodes are the only group of complex metazoans providing a detailed fossil record of environmental changes in the deep sea. The overlying water column acts as a buffer to shield the fauna from climatic fluctuations that may strongly affect shallow marine or terrestrial habitats. Consequently, the fossil remains of the benthic deep-sea ostracodes contain a modulated record of paleoceanographic history emphasizing major global events.

We compared changes in the fossil record of the deep-sea benthic ostracode fauna with recognized or theorized paleoceanographic events of global proportions during the past 70 million years. We made this comparison by integrating techniques from quantitative ecology (the use of community or assemblage parameters such as diversity indices), evolutionary analyses (standing diversity and taxonomic turnover), and morphometrics (shape analysis).

Events of particular interest include the Cretaceous-Tertiary boundary event 66 to 65 million years ago (Ma) (*1*, *2*), the early Eocene event (52 Ma) (*3*), the 40-million-year event (43 to 39 Ma) (*4*, *5*) that we believe is the precursor to the terminal Eocene event (37 to 34 Ma) (*3*, *6*), the terminal Oligocene event (25 to 22 Ma) (*3*, *7*), the middle Miocene event (15 to 14 Ma) (*8*), the terminal Miocene event (6 to 5 Ma) (*9*), and the Pliocene event (3.5 Ma) (*3*). Reactions of the deep-sea benthic ostracodes ranged from insignificant (the terminal Oligocene event), to predicted but earlier (the 40-million-year event), to unexpectedly catastrophic (the Cretaceous-Tertiary boundary event). The measurement of taxonomic change and assemblage similarity reveals, indirectly, changes in energy transfer and structural differences in the world ocean before and after the origin of the present thermally dominated system.

Data having a global distribution were obtained through the analysis of more than 1600 core samples ($50\ cm^3$) from 156 sites and more than 50 legs of the Deep-Sea Drilling Project (DSDP). Of these, 1044 samples yielded ostracodes (approximately 30,000 specimens were identified). Only genera are considered for the present census, which includes every major stratigraphic subdivision for almost every site of the first 50 DSDP legs plus legs 72 through 75. To reduce error in taxonomic judgment, all identifications were made or reconfirmed by one of us (R.H.B.) during a 6-week period. Sample ages were estimated to the nearest million-year interval. Community or assemblage parameters were calculated for each sample, including the number of taxa, the number of specimens, and diversity and equitability coefficients (*10*). The stratigraphic range of each genus was also considered.

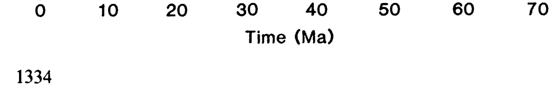


Fig. 1. Global parameters through time: (A) standing diversity at the generic level and (B) the percentage of the DSDP samples obtained that contained ostracodes. Abbreviations: *P-P*, Plio-Pleistocene; *M*, Miocene; *O*, Oligocene; *E*, Eocene; *P*, Paleocene; and *K*, Cretaceous.

Global time-series plots for the last 70 million years (Figs. 1 through 3) are shown; analyses of subsets of the sample data for different geographic regions were also used (*11*).

Global generic diversity (Fig. 1A) shows remarkably little change through time, reflecting the presence of very long-lived genera. Longer-term trends show a gradual increase from 65 to 40 Ma, a plateau between 40 and 25 Ma, and a gradual decline thereafter. Important and abrupt decreases occurred at 66 to 65 and 3 to 2 Ma with a moderate increase between 7 and 4 Ma.

Global abundance (Fig. 1B) shows major drops at 66 to 60, 55 to 53, 43 to 40, and 25 to 20 Ma. Major increases occurred at 58 to 55 Ma, 50 to 48 Ma, and 36 to 34 Ma. In general, abundance was highest in the Cretaceous, Oligocene, and Plio-Pleistocene and lowest in the Paleocene, Eocene, and Miocene.

Major faunal turnover (Fig. 2) occurs at 66 to 65 Ma (mostly extinctions) and 6 to 2 Ma (extinctions and originations). Turnover of intermediate importance occurred at 40 to 36 Ma (originations), 25 to 20 Ma (extinctions), and 60 to 50 Ma (originations).

Sample diversity and abundance patterns (Fig. 3) suggest three major times of change: 66 to 60 and 36 to 35 Ma (decreasing) and 44 to 36 Ma (increasing), with an additional and gradual negative trend from 7 to 0 Ma. Secondary periods of change are seen at 17 to 13 and 4 to 3 Ma, both decreasing.

Two very different temporal groupings are revealed by a Rho-groups analysis (*12*) of faunal similarity (Fig. 4) across the South Atlantic (*13*), an important area where several world-ocean water-mass systems converge. Before 40 Ma similarities were low, on the average, with major connections occurring through time at or near the same site. This reflects the observed provinciality of faunas of this age and suggests the presence of localized isotropic ecosystems with little geographic interchange. After 40 Ma, however, the pattern changes. Similarity values become consistently higher, and isochronous connections between stations are much more common. This reflects the presence of stratified, anisotropic, global ecosystems with accelerating interchange across geographic regions.

Two major events appear to have occurred during the last 70 million years. The first occurred at the Cretaceous-Tertiary boundary (66 to 65 Ma). The initial effect was sudden, and the results continued to accelerate for 4 to 5 million years. Global diversity, turnover, and abundance were affected first, followed by an increasingly severe drop in local abundance and diversity, responses that could be related to an external cause such as an extraterrestrial agent (*2*).

The second major event, called here the 40-million-year event, was positive and diachronous, apparently starting slowly in deeper waters and having the most abrupt effect in shallower depths. The change may start as early as 45 to 43 Ma, but a preferred datum is 40 Ma, when the effect is first global in extent. The effects of this event were felt mostly at the assemblage level as mean sample abundance and diversity increased sharply. The global effects of the 40-million-year event intensified as the taxa of the current world deep-sea benthic ostracode fauna evolved locally and spread laterally with increased thermal stratification of the water column.

From these changes in the ostracode fauna, we maintain that the 40-million-year event marks the time of the origin of the psychrosphere and the modern two-layered ocean (*4*), and that the diachronous pattern is to be expected from threshold effects found in a sharply stratified water-mass structure. This period marks a change in energy flow in the deep sea from a warm, sluggish, saline-driven water-mass system (the prepsychrospheric thermosphere) to a cold, strongly stratified, psychrospheric water-mass system with higher velocity and nutrient content. The high mean sample diversity and abundance values are viewed as localized responses to a mixing of the waters of the two systems. The marked decrease back to pre-event levels at 36 to 35 Ma (Fig. 3) indicates a cessation of this mixing. Consequently, the terminal Eocene event is viewed as the shallow-water stage of the ongoing 40-million-year event, not as a separate and catastrophic event in itself.

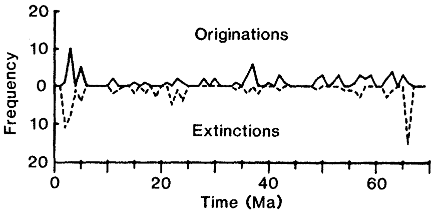
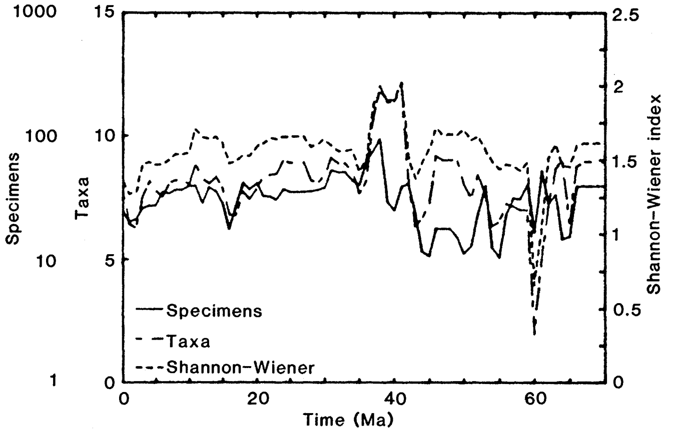


Fig. 2. Plots of the number of originations (solid line) and number of extinctions (dashed line) through time.

A third period of extensive flux is a composite of two events, the terminal Miocene event (6 Ma) and a Pliocene event (3.5 to 1.8 Ma). Causal agents include the closure of the Iberian Portal (6 Ma) and the cessation of Tethyan thermospheric inflow, the closure of the Isthmus of Panama (3.5 Ma), and glaciation in the Northern Hemisphere (3.5 to 1.8 Ma). Throughout, mean sample diversity and the number of ostracodes per sample decreased. Global diversity first increased, then decreased, reflecting either high environmental variability or limitations in our sampling of that interval. As with the 40-million-year event, the full effect developed gradually and was not as abrupt as at the Cretaceous-Tertiary boundary.

The three remaining events do not approach those just described in importance, so far as the ostracodes are concerned; the ostracode data fail to support anything but minor, localized events. The early Eocene (52 Ma) ostracode data are variable and contradictory, with high

Fig. 3. Sample parameters for the global data set through time. Plotted are mean values for each million-year interval of the number of taxa (genera), the number of specimens, and the Shannon-Wiener index.



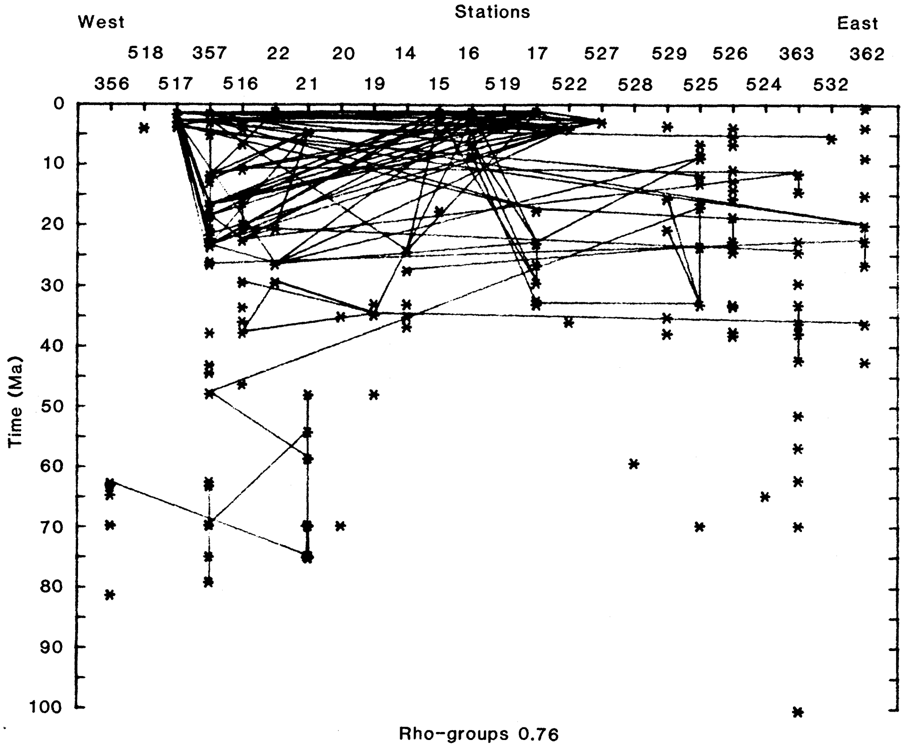


Fig. 4. Rho-groups analysis at the 0.76 level for DSDP stations containing abundant ostracodes along a west-east transect in the South Atlantic. Asterisks represent one or more samples at the indicated age and site. Lines indicate connections between two samples at or above the indicated level of similarity. Vertical lines are within site connections, horizontal ones between sites. This figure is best interpreted by noting patterns of concatenation in much the same way as a nearest-neighbor analysis.

mean sample diversity and abundance values in the Indo-Pacific and low ones in the South Atlantic. The terminal Oligocene event (25 to 22 Ma) is indicated only by an increase in mean sample diversity in the North Atlantic. The trends of the middle Miocene (15 to 14 Ma) data are mixed, with increasing mean sample diversity restricted to the South Atlantic. A major speciation event in *Poseidonamicus* accompanied the circulation pattern changes of this key region (*14*).

To conclude, benthic deep-sea ostracode data support the presence of three major periods of flux during the past 70 million years. The Cretaceous-Tertiary boundary event is more sudden than the others. No satisfactory paleoceanographic mechanism thus far proposed can explain this event. Two other global and strong faunal changes are in agreement with known or hypothesized paleoceanographic events. Finally, three additional intervals, suggested as times of important changes, are not supported as events of global significance by our ostracode data, which suggest only localized and weak effects.

The benthic deep-sea ostracodes represent a conservative animal group living in a conservative environment. They tend to show fewer major reactions to minor paleoceanographic events of localized importance. They have persisted through critical changes in the development of the floor of the world ocean from times of parochial invasions of the depths, through the abrupt punctuation of the Cretaceous-Tertiary boundary event, into a period of confinement to these depths but with increased cosmopolitanism after the development of the psychrosphere.

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14. R. H. Benson, *Paleobiology*, in press. Studied using resistant-fit theta-rho analysis, a form of transformational analysis [R. H. Benson *et al.*, *Paleobiology* **8**, 328 (1982)].
15. We gratefully acknowledge the comments of S. Lidgard, M. Buzas, N. Sohl, and R. Grant. This study was sponsored by the Scholarly Research Program of the Smithsonian Institution.

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Community Recovery After Storm Damage: A Case of Facilitation in Primary Succession

Abstract. *Manipulations of early arriving, fast-growing algal stands, which appeared soon after a severe storm denuded a Southern California marine reef habitat, indicated that the dense cover protected newly settled kelp plants from excessive damage by grazing fishes. This is an example of refuge facilitation in primary succession after a major natural disturbance, a mechanism that may contribute substantially to the regeneration of a kelp forest.*

The process of community succession has been well documented (*1*), and three mechanisms have been proposed for the sequential replacement of species: facilitation, inhibition, and neutral effect (*2*). These mechanisms may work by competitive interactions between species that arrive earlier or later during the process. They may be activated by major disturbances, whether biological (predation) or physical (weather). For example, predation of sea urchins by sea otters, mediated by human exploitation, can initiate a change in the structure of coastal kelp bed communities from an open, cleared state (barren grounds) overgrazed by urchins to a densely vegetated state (kelp forest) dominated by macroalgae (*3*). Severe storm damage to subtidal reefs may start the successional process as well (*4*). At our study site in a kelp bed off the coast of Southern California, two major storms occurring 3 years apart perturbed the reef community in opposite directions. The first storm started degenerative changes from a lush kelp forest dominated by large kelps (*Macrocystis pyrifera* and *Pterygophora californica*) to a barren grounds overgrazed by sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*), and the second storm initiated regenerative changes culminating once again in the kelp forest (*5*). This gave us the opportunity to collect the first experimental evidence that facilitation—whereby an early successional dominant provides a refuge for establishment of a later one—is an important mechanism of community succession in kelp forests. We now show that early arriving, fast-growing algae enhanced the survival of young kelp plants by sheltering them from herbivorous fish.

Table 1. Survival of kelp sporophytes in treatment (filamentous algae removal) and control (unmanipulated) plots. Each plot (covering 0.1 m^2) of a treatment-control pair was located within 0.5 m of the other. The first and second trials of five replicates each were observed after 5 and 2 days, respectively. Tabulated are counts of sporophytes (plants with more than half their blade intact) and stipes (plants with little or no blade remaining). Abbreviations: MB, many bitten plants (> 50 percent); FB, few bitten plants (< 25 percent); and NB, no bitten plants. No change in number or condition of sporophytes in control plots was observed at the end of the two trials.

Beginning of trial		End of trial	
Sporophytes (number) and condition		Sporophytes (number)	Stipes (number)
Treatment	Control		
First trial (12 to 17 May 1983)			
77 MB	100 FB	0	15
35 FB	40 FB	0	21
30 FB	40 FB	0	17
77 NB	100 FB	0	55
26 FB	30 FB	No change	
Second trial (17 to 19 May 1983)			
29 FB	30 FB	2	21
39 FB	50 FB	20	10
37 FB	100 FB	4	20
56 FB	40 FB	40	8
55 FB	100 FB	14	18

In early March 1983, the second storm ravaged the area (*6*). At Naples Reef near Santa Barbara (34°25′N, 119°57′W),