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11. EOCENE-OLIGOCENE FAUNAL TURNOVER IN PLANKTIC FORAMINIFERA, AND ANTARCTIC GLACIATION

by Gerta Keller, Norman MacLeod and Enriqueta Barrera

ABSTRACT

Low-latitude planktic foraminiferal populations experienced a major faunal turnover between the late middle to early late Oligocene. This faunal turnover involved over 80% of planktic foraminiferal species and took place quasi-continuously over an interval of approximately 14 m.y. The overwhelming majority of species becoming extinct during this interval were surface-dwelling forms that were ecologically replaced by more cold-tolerant subsurface-dwelling species as the thermal contrast between surface and subsurface (> 400 m) marine pelagic habitats diminished. Within this 14 m.y. interval of widespread ecological reorganization of the planktic foraminiferal faunas, two subintervals stand out as being characterized by brief, but markedly intensified turnover; these are the middle/late Eocene and the early/late Oligocene. Contrary to previous reports, there was no major faunal change across the Eocene/Oligocene (E/O) boundary.

Stable isotope records and glacio-marine sediments from high latitude southern ocean ODP Legs 113 and 119 provide evidence of major glaciation on East Antarctica during the late middle to late Eocene and early Oligocene with glaciation persisting into the late Oligocene. Carbon and oxygen isotopic gradients for planktic and benthic foraminiferal species reflect decreasing surface productivity and thermal stratification during this time. The remarkably close correspondence between these stable isotope records and planktic foraminiferal turnovers strongly suggests that changes in climate and productivity were the primary driving forces behind the gradual decline and eventual extinction of the Eocene planktic foraminiferal fauna.

INTRODUCTION

Contrary to some previous reports, the so-called Eocene-Oligocene (E/O) mass extinction among planktic foraminifera was not centered at this boundary, but rather was part of a long-term trend that began during the middle Eocene and continued into the late Oligocene (Steineck, 1971; Keller, 1983a,b, 1985, 1986; Corliss et al., 1984; Molina et al., 1988), an interval spanning over 14 m.y. Within this interval, accelerated faunal turnovers can be recognized near the middle/late Eocene and early/late Oligocene boundaries. These faunal turnovers include the successive extinction of tropical and subtropical faunas and their replacement by cool and temperate assemblages of species (Kennett, 1977, 1978; McGowran, 1978; Keller, 1983a,b, 1985, 1986).

Correlated with these faunal changes was a major shift in the earth's climate. Stable isotopic records indicate a significant cooling (~1.0 per mil) beginning in the early middle Eocene (magnetochron C22 to C21; 52.6 to 49 Ma, Katz and Miller, 1991) and a major cooling (~2.0 per mil) near the middle/ late Eocene boundary (Oberhansli et al., 1984; Keigwin and Corliss, 1986; Miller et al., 1987; Prentice and Matthews, 1988; Kennett and Stott, 1990; Barrera and Huber, 1991). A further drop in temperature began near the E/O boundary and reached a global minimum at the base of Chron 13N (Keigwin and Keller, 1984; Oberhänsli et al., 1984; Keigwin and Corliss, 1986; Miller et al., 1987). Cooler surface and bottom water temperatures continued through most of the Oligocene reaching maximum low temperatures at about 29 Ma and followed by a short warming during the latest Oligocene (Keigwin and Keller, 1984).

The late Paleogene cooling trend has generally been interpreted to be a consequence of the development of circum-Antarctic circulation made possible by the northward movement of Tasmania and Australia by middle Eocene time (Kennett et al., 1975; Shackleton and Kennett, 1975). Until recently, the middle to late Eocene increases in $\delta^{18}O$ values have been attributed solely to high latitude cooling that was devoid of major Antarctic glaciation. In contrast, the early Oligocene isotopic shift has been interpreted as a combination of cooling and the first major glaciation on Antarctica (Matthews and Poore, 1980; Keigwin and Keller, 1984; Miller and Thomas, 1985; Keigwin and Corliss, 1986; Miller et al., 1987). However, evidence of extensive early to late Oligocene glaciation has recently been discovered in glacio-marine sediments in the Ross Sea, Antarctica (Barrett, 1989; Bartek et al., this volume), as well as in ice-rafted debris from early Oligocene sediments from the Kerguelen Plateau (Site 744, Barrera and Huber, 1991). Prentice and Matthews (1988) have used a composite low to mid-latitude planktic and benthic oxygen isotope record to argue that substantial ice volume (equal to the present) has existed since about 40 Ma. These observations are consistent with major Antarctic glaciation as early as 42 Ma; this in turn suggests the possibility of a causal link between changes in marine planktic habitats brought about by substantial global cooling and planktic foraminiferal faunal turnovers.

In this paper we examine the middle Eocene to Oligocene record of planktic foraminiferal faunal turnover beginning with the source of the common misconception of a mass extinction at the E/O boundary. After using taxic and morphotypic data to describe the major outlines of this faunal turnover, we then turn to a more detailed consideration of abundance variations within the dominant foraminiferal species in order to document specific intervals of increased environmental stress on these foraminiferal populations. The effect of this environmental stress can most clearly be seen in terms of changes in the isotopically determined depth habitat preferences of individual species. Finally, we discuss and correlate these faunal turnover data with the stable isotope records of high and low latitude stratigraphic sequences in order to demonstrate how changes in marine productivity, thermal stratification and climate all contributed to the terminal decline in Paleogene planktic foraminiferal populations.

THE EOCENE-OLIGOCENE MASS EXTINCTION: A TAXIC EVALUATION

Micropaleontologists have long regarded the late Eocene through early Oligocene as a time of widespread extinction in the planktic foraminiferal fauna. Evidence for this view has traditionally come from two sources: i) the planktic foraminiferal classifications of Loeblich and Tappan (1964) and Blow (1979), and ii) Cifelli's (1969) analysis of the iterative evolution of major planktic foraminiferal morphotypes. One striking aspect of the systematic data used to characterize extinction patterns in these studies is the almost universal employment of rather coarse taxonomic groupings and stratigraphic intervals. These data typically consist of the observed stratigraphic ranges of either families or genera assessed to the nearest inclusive epoch (e.g., Harland et al., 1967; Sepkoski, 1982). This data set tends to distort the true extinction record in favor of abrupt changes. More recently, this picture of a sudden and pervasive late Paleogene biotic crisis in the deep sea has been given additional support through the discovery of a late Eocene deep-sea iridium anomaly (Ganapathy, 1982; Glass et al., 1982; Keller et al., 1987), the observation of multiple late Eocene microtektite and microspherule-bearing layers in both continental sections and deep sea cores (Keller et al., 1983; 1987; Miller et al., 1991; Hazel, 1989), and the extinction periodicity analyses of Raup and Sepkoski (1984, 1986; see also Sepkoski and Raup, 1985).

Since 1964 there have been three major Paleogene planktic foraminiferal classifications: Loeblich and Tappan (1964), Blow (1979), and Loeblich and Tappan (1988). While only a handful of new planktic foraminiferal species have been described during this interval, the supraspecific taxonomy has more than doubled, rising from four Eocene-Oligocene families representing seventeen genera (Loeblich and Tappan, 1964) to ten Eocene-Oligocene families representing thirty-nine genera (Loeblich and Tappan, 1988). The demographic effects of this ongoing taxonomic revision can be seen by plotting the total number of planktic foraminiferal families and genera present in the six Eocene-

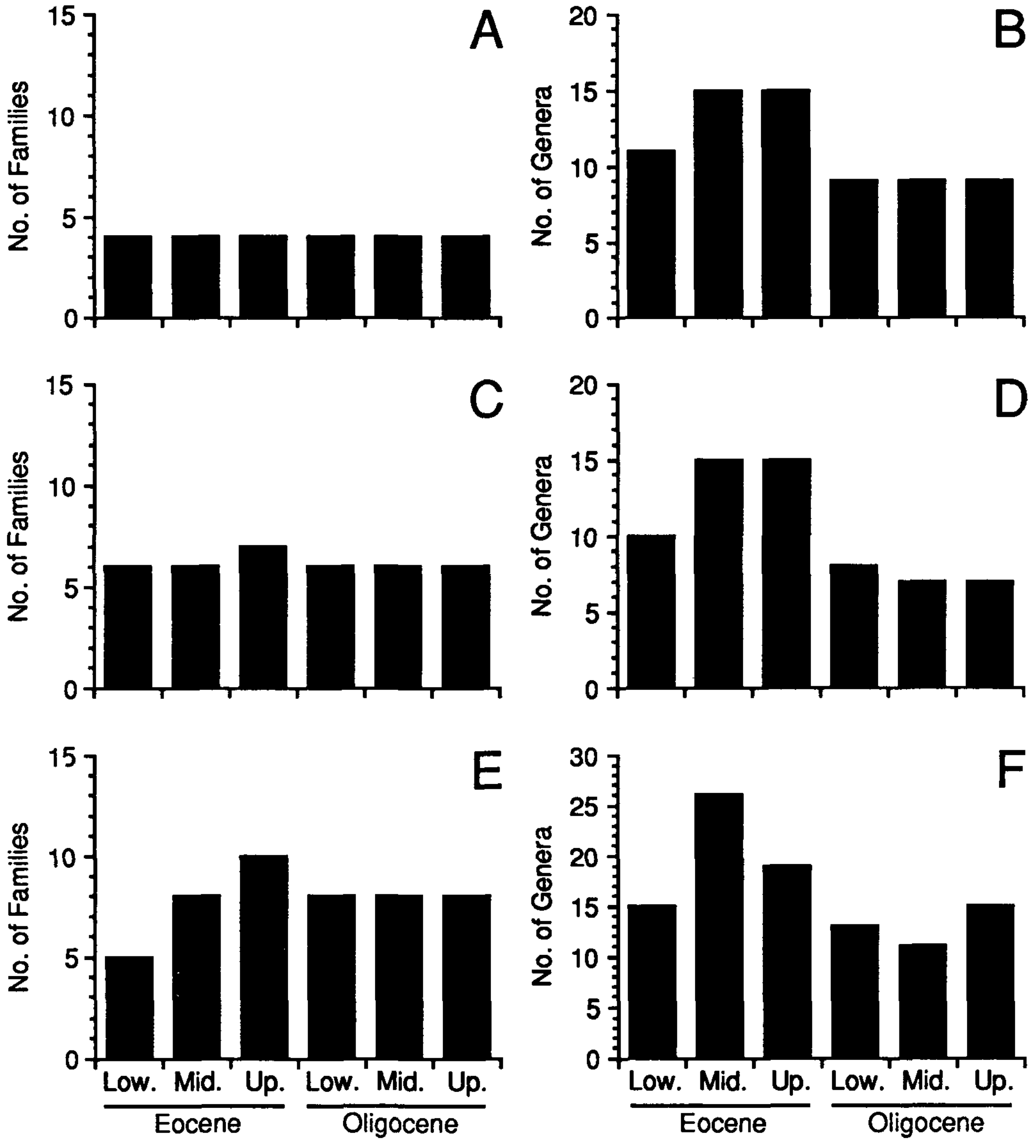

FIGURE 11.1. Histograms of planktic foraminiferal taxic (families and genera) richness for Eocene and Oligocene time based on Loeblich and Tappan (1964) [A-B], Blow (1979) [C-D], and Loeblich and Tappan (1988) [E-F].

Oligocene epochs for each classification (Figure 11.1). In essence, these diagrams describe two different taxic richness patterns in what are, for the most part, the same group of species.

The classifications of Loeblich and Tappan (1964) and Blow (1979) show similar patterns through the Eocene-Oligocene interval with little or no change at the family-level (Figures 11.1A and 11.1C), but a sudden rise in generic richness at the lower/ middle Eocene boundary followed by an equally sudden drop at the E/O boundary (Figures 11.1B and 11.1D). In contrast, Loeblich and Tappan's most recent classification (1988) exhibits a progressive increase in the Eocene family richness, followed by a slight decline at the E/O boundary. Unlike the previous classifications of Loeblich and Tappan (1964) and Blow (1979), however, Loeblich and Tappan's generic data exhibits an abrupt taxic richness *increase* in the middle Eocene followed by a more or less continuous decline into the middle Oligocene that, in turn, passes into another generic richness increase in the Upper Oligocene (Figures 11.1E and 11.1F). In addition, all three classifications exhibit marked discrepancies between taxic richness patterns assessed at different levels within the taxonomic hierarchy.

On the basis of these discrepancies, one is forced to conclude that: i) late Paleogene supraspecific taxic richness patterns are strongly influenced by the classification scheme employed; and ii) temporal trends in taxic richness observed at one level in the taxonomic hierarchy may not necessarily be representative of different levels. While the Loeblich and Tappan (1964) and Blow (1979) classifications have traditionally provided the main empirical support for recognizing the E/O boundary as a time of sudden and widespread change in planktic foraminiferal faunas, the greatly expanded generic classification of Loeblich and Tappan (1988) shows a gradual, rather than sudden, Eocene-Oligocene faunal turnover that is much more reminiscent of preliminary species-level data (e.g., Corliss et al., 1984). As a result of these very obvious sources of bias within various supraspecific planktic foraminiferal classifications, any rigorous evaluation of the Eocene-Oligocene planktic foraminiferal extinction record must employ species-level taxonomic data that have been resolved to a considerably more refined stratigraphic scale than that of nearest inclusive stage.

Fortunately, a large part of these species-level taxonomic/high resolution stratigraphic data have been summarized by Toumarkine and Luterbacher (1985) and Bolli and Saunders (1985). These biostratigraphic compendia list 109 species and subspecies of planktic foraminifera along with their associated stratigraphic ranges to (at least) the nearest inclusive biozone. Although these data do not represent an exhaustive census of all Eocene-Oligocene planktic foraminifera, they do include not only the majority of such taxa, but essentially all of the common, well-studied forms whose stratigraphic ranges have been reliably established. Moreover, those species and subspecies excluded from this dataset are predominately longer-ranging forms that are of little use in high-resolution biostratigraphic analyses and, if anything, would tend to obscure the very faunal turnover patterns we seek to study.

In order to evaluate these species- and subspecies-level data, taxic richness estimates [corrected for intrazonal turnover via Harper's (1975) index] were made for each of seventeen constituent Eocene and Oligocene planktic foraminiferal biozones as shown in Figure 11.2A. Starting at comparatively low values in the early Eocene, planktic foraminiferal taxic richness increased rapidly reaching a peak in the middle part of the middle Eocene, after which it underwent a progressive decline that extended through the Oligocene where it returned to early Eocene values. These patterns remain unchanged regardless of whether or not subspecies (light shading in Figure 11.2A) are excluded from consideration. Both species and species + subspecies data are also uncorrelated with variations in the temporal duration of the Eocene-Oligocene biozones (MacLeod, in press).

The taxic richness data illustrated in Figure 11.2A represent the dynamic interplay between rates of extinction and origination. Separate tabulations of these extinction and origination data (Figures 11.2B and 11.2C) reveal several interesting aspects of this extended faunal transition. For instance, elevated numbers of species and subspecies extinctions were not confined to the two late Eocene biozones, both of which contain unambiguously impact-related debris layers. Instead, relatively high levels of planktic foraminiferal extinctions occurred throughout an interval from the middle Eocene to the early Oligocene (Figure 11.2B). But, while the elevated levels of species originations that characterize the early/middle Eocene boundary remain high throughout most of the middle and late Eocene, this relatively high late Eocene planktic foraminiferal origination rate undergoes a precipitous decline at the E/O boundary (Figure 11.2C). It is this failure of taxic origination in the early Oligocene rather than the acceleration of late Eocene extinction rates (for which there is no evidence) that drives the planktic foraminiferal faunal turnover at the E/O boundary. Irrespective of this highly provocative and previously unanticipated decline in species originations across the E/O boundary, the taxic richness data as a whole provide strong evidence in favor of the gradual Eocene-Oligocene planktic foraminiferal turnover

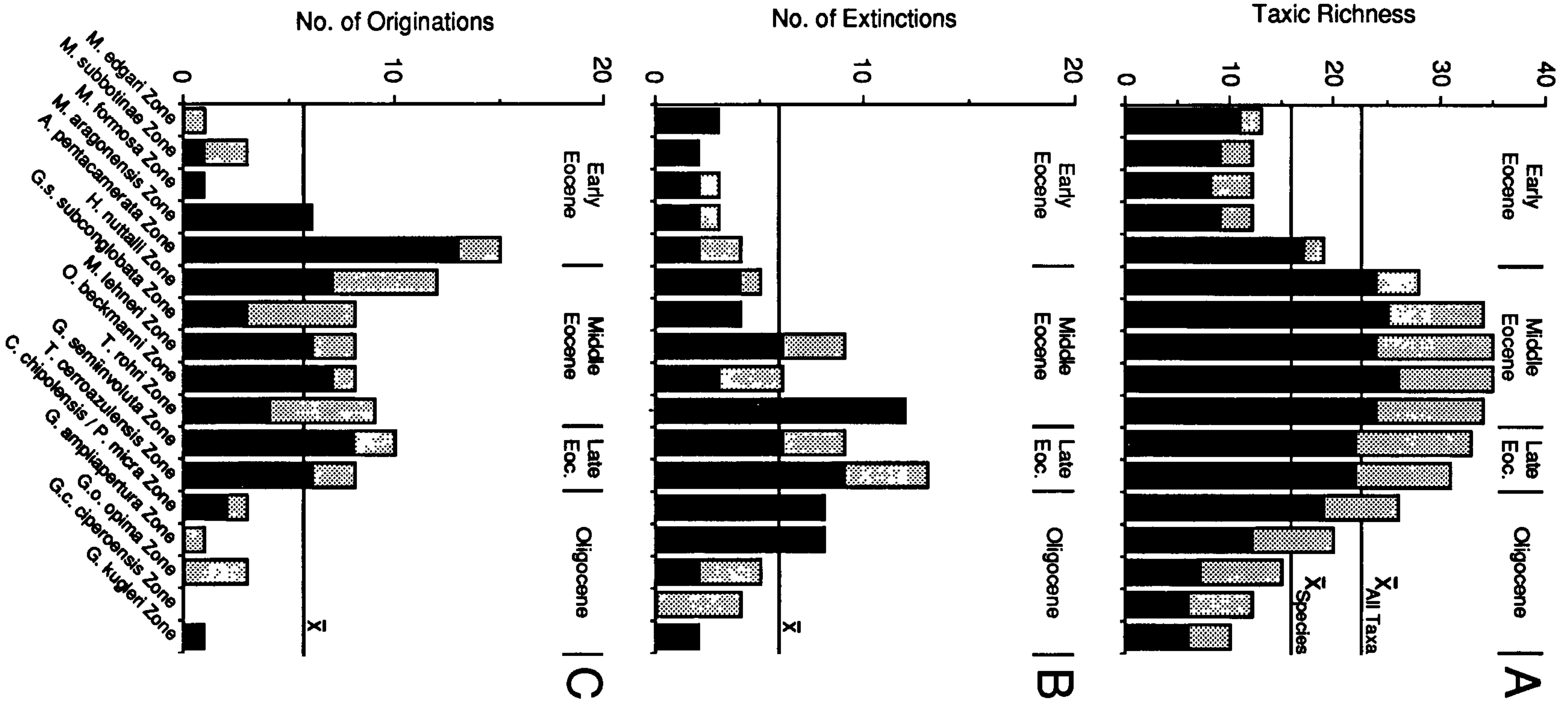

FIGURE 11.2. Histograms of estimated planktonic foraminiferal taxic (species and subspecies) richness (A), numbers of taxic extinction (B) and originations (C) in each of the seventeen Eocene and Oligocene planktic foraminiferal biozones. Black bars = species data, stippled pattern = subspecies data. Data from Toumarkine and Luterbacher (1985) and Bolli and Saunders (1985).

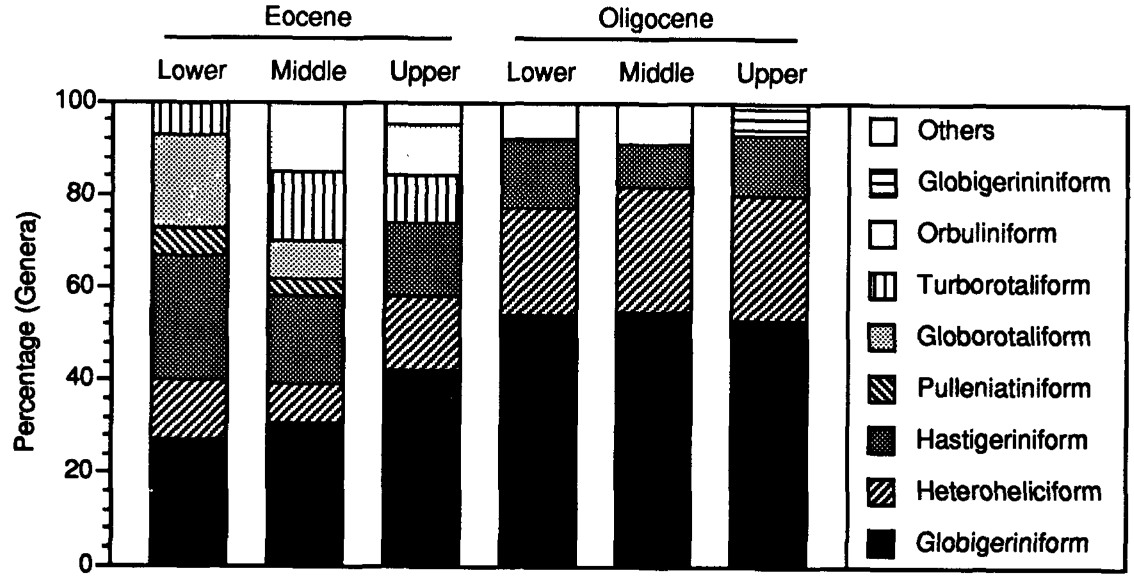

FIGURE 11.3. Morphotypic richness patterns for planktic foraminiferal faunas in each of the six Eocene-Oligocene epochs. Morphotypic classification based on Cifelli (1969): i) globigeriniform -- test consisting of a series of round chambers arranged in a trochospiral coil with a single umbilical aperture; ii) orbuliniform -- globigerine tests in which the final chamber envelops the previous coils; iii) turborotaliform -- globigerine tests with angular chambers and an acute periphery; iv) globorotaliform--globigerine tests with angular chambers and a true peripheral keel; v) pulleniatiniform -- globigerine tests in which axis of coiling migrates to a more umbilical position during ontogeny; vi) hastigeriniform -- planispirally coiled, bilaterally symmetrical tests; vii) globigeriniform -- globigerine tests that exhibit supplementary apertures on the spiral side; viii) heterohelicilform --tests with biserially or triserially arranged chambers. See text for discussion.

model reflected in the generic classification of Loeblich and Tappan (1988).

Was the Eocene-Oligocene faunal turnover the result of a preferential elimination of specific morphotypes that reflect either ecological similarities or functional equivalences? In his classic paper on iterative evolution in planktic foraminifera, Cifelli (1969) used seven morphotypic groupings of taxa to summarize the evolutionary history of planktic foraminifera. Based on changes in the relative abundance of these morphotypes he concluded that while both orbuliniform and globorotaliiform species went extinct before the beginning of the late Eocene, the hastigeriniforms continued to diversify into the late Eocene. Similarly, turborotaliiform morphotypes remained present throughout the Eocene but became extinct by the end of that epoch. By the late Oligocene, however, "all [morphotypes] except the globigerin[iforms] had disappeared" (Cifelli, 1969, p. 159).

In order to update Cifelli's (1969) analysis and determine the extent to which his characterization of the Eocene-Oligocene faunal transition remains valid, we have expanded Cifelli's original morphotypic classification to include a category for species exhibiting either biserial or triserial chamber arrangements (heterohelicilforms) along with an additional category for forms (e.g., *Cassigerinella*) that cannot be fit into any of the aforementioned groups. Results of our revised morphotypic characterization are shown in Figure 11.3.

While Cifelli's (1969) morphotypic analysis appears to be largely consistent with contemporary data (despite the revisions in our taxonomic view of the Eocene-Oligocene planktic foraminiferal transition), our results extend those of Cifelli in several important respects. Although Cifelli (1969) described the Oligocene planktic foraminiferal fauna as being exclusively globigeriniform in character, our expanded morphotypic classification shows that both globigeriniform and heteroheliciform taxa not only dominate the Oligocene planktic foraminiferal assemblage (at least in terms of numbers of genera), but that these morphotypes were also major constituents of the Eocene fauna. It is also important to note that regardless of the low taxic richness values that characterize in early Eocene planktic foraminiferal faunas (Figure 11.2), they nevertheless exhibit the highest morphotypic richnesses observed in the late Paleogene.

Cifelli (1969) concluded that the replacement of the morphotypically diverse middle and late Eocene planktic foraminiferal fauna by (what he described as) a nearly monotypic Oligocene assemblage (of globigeriniform species) was brought about by a reduction in the thermal differentiation of marine surface waters. This inference was based on the ecological preferences of morphologically similar Recent planktic foraminiferal species. Since that time, a large number of isotopic, taxonomic, and biogeographic data have supported the general model of late Paleogene climatic cooling. In the following sections we analyze the Eocene-Oligocene faunal transition based on current relative abundance data and the grouping of species according to their depth habitat preferences in order to explore the relationship between these patterns of taxonomic/morphotypic faunal turnover and physical changes in marine planktic habitats. This analysis will both refine the timing of the major planktic foraminiferal faunal turnover(s) and document the evolutionary/ecological fates of individual species groups in greater detail.

MAJOR FAUNAL TURNOVERS

Planktic foraminiferal assemblages are generally dominated by five to six species which may constitute up to 80% of the total number of individuals present. Changes in the relative abundance of these dominant species reflect changes in the physical and biological character of the local environment. Quantitative analysis of microfossil assemblages can therefore be used to examine the relationship between environmental change and planktic foraminiferal turnovers.

Relative species abundance data for planktic foraminifera from DSDP sites in low and middle latitude Pacific, Atlantic and Indian Oceans as well as onshore marine sections in Spain and the U.S. Gulf Coast have been published for over 20 middle Eocene to Oligocene sequences (Keller, 1983a, 1985, 1986; Keller et al., 1987; Molina et al., 1988). Although individual species abundances vary among these sections, the overall trends in their biostratigraphy and extinction record are similar. Figure 11.4 illustrates this record for Indian Ocean DSDP Site 219. Site 219, as well as most other deep-sea sections, have short hiatuses or nondeposition events in the middle Eocene (*M. lehneri*/*T. rohri* Zone, *O. beckmanni* Zone missing), at the middle/late Eocene boundary (*T. rohri*/*G. semiinvoluta* Zone) and in the late Eocene (*G. semiinvoluta*/*T. cerroazulensis* Zone, Keller, 1983a, 1986; Keller et al., 1987).

Among the dominant species there was a gradual replacement of warm-tolerant tropical species by successively more temperate and cold-tolerant taxa. For example, in Site 219 the middle Eocene *G. subconglobata* Zone is dominated by *Acarinina bullbrooki*, *A. planodorsalis* and *A. broedermanni*, all of which terminally decline at the top of this zone and into the following *M. lehneri* Zone. In the succeeding *T. rohri* Zone, *T. rohri* and *Globigerinatheka* spp. (excluding *G. semiinvoluta*) dominate and terminally decline in abundance at the top of the zone. A notably cooler water temperate faunal assemblage dominates the early late Eocene *G. semiinvoluta* Zone (*Globorotaloides carcoselleensis*, *Globigerinatheka semiinvoluta*, *Pseudohastigerina micra*; Figure 11.4) only to be replaced by a still colder water fauna in the late Eocene *T. cerroazulensis* Zone dominated by *Subbotina angiporoides*, *S. linaperta*, and *Globigerina ouachitaensis*. The appearance of successively more cold-tolerant elements within the dominant planktic foraminiferal fauna through the middle and late Eocene results from the migration of cooler water taxa into lower latitudes and coincides with global climatic cooling.

At the Site 219 E/O boundary, however, a significant change in planktic foraminiferal species diversity is conspicuously absent. Only *Turborotalia cerroazulensis*, which constitutes less than 8% of the total fauna, disappears at this boundary (Figure 11.4). Overall, the

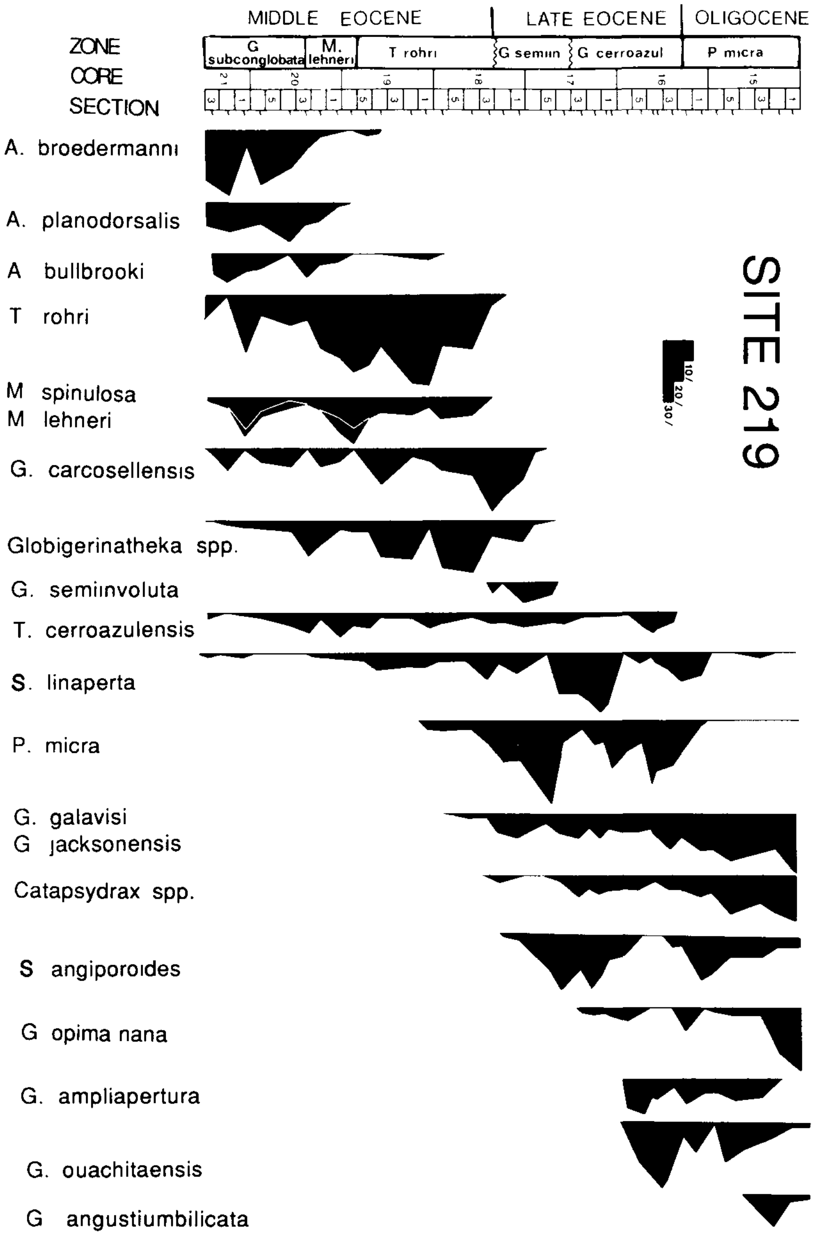

FIGURE 11.4. Abundance distribution of dominant planktic foraminiferal species in Indian Ocean DSDP Site 219. Wavy lines mark hiatuses, tick marks in core-sections indicate sample positions.

dominant cool-temperate taxa that appeared during the latest Eocene continued across the boundary into the early Oligocene (Figures 11.4, 11.5; Keller, 1983a, 1985, 1986); suggesting a simple continuation of the late Eocene cooling trend. The next major faunal turnover begins in the late early Oligocene near the *G. ampliapertura/ G. opima* Zone boundary and continues into *G. opima* Zone (Figure 11.5). In this interval, most of the surviving Eocene taxa (e.g., *Pseudohastigerina micra, Globigerina ampliapertura, Subbotina angiporoides, S. linaperta, S. utilisindex, Subbotina galavisi, G. jacksonensis*) decline in abundance and disappear. At the same time *Globorotalia opima* appears and predominates in the zone bearing its name,

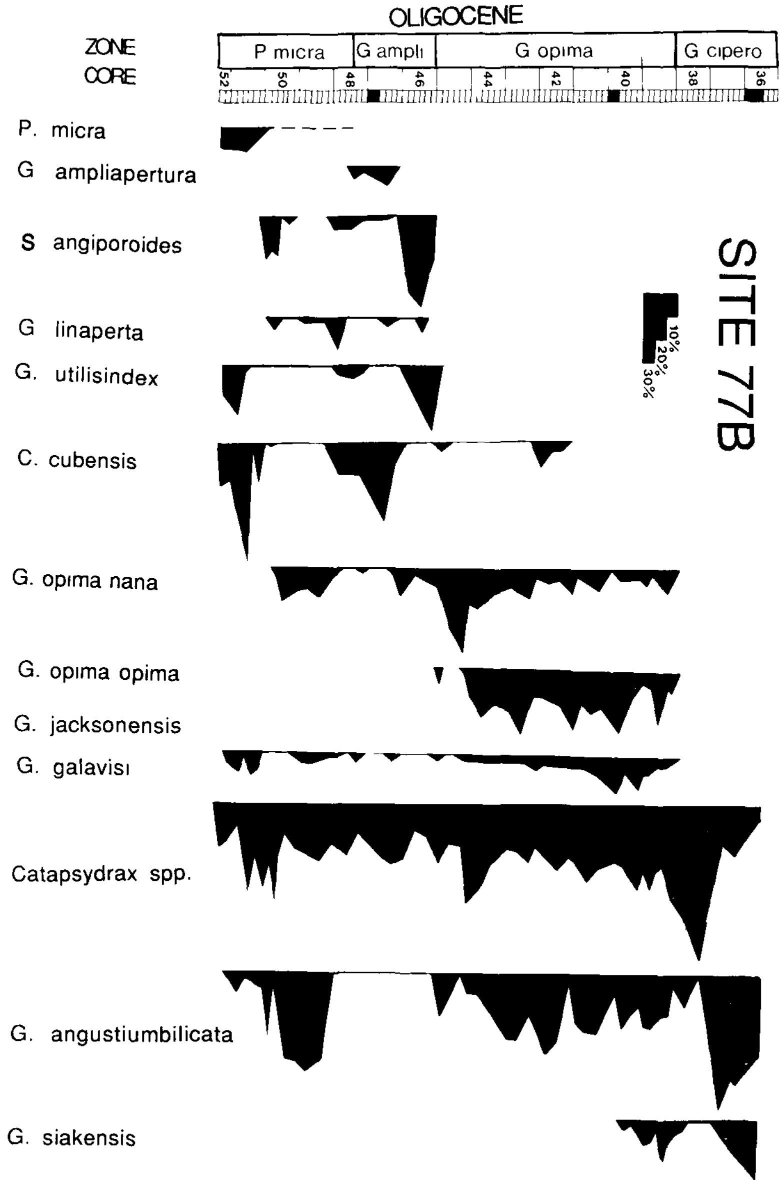

FIGURE 11.5. Abundance distribution of dominant planktic foraminiferal species in east equatorial Pacific DSDP Site 77B.

followed by increased abundance of *Tenuitella angustiumbilicata*, and the appearance of *Globorotalia siakensis*, *G. pseudocontinuosa*, *Globigerina ciperoensis*, and *G. angulisuturalis* (Figure 11.5; Keller, 1983a,b; 1984; 1985). These faunal turnovers represent global climatic and oceanographic changes as well as a major evolutionary transition from a relatively warm-tolerant and diverse middle Eocene fauna to a cold-tolerant, low diversity Oligocene assemblage.

DEPTH STRATIFICATION OF PLANKTIC FORAMINIFERA

Planktic foraminifera live in the upper portion of the oceanic water column with the highest density of individuals in the upper 100 m and few individuals below 400 m depth (Bé and Tolderlund, 1971; Bé et al., 1971). Within this interval, species are depth stratified with many species remaining at relatively constant depths while others migrate downward during their life cycle (Lidz et al., 1968; Berger, 1969, Bé and Hemleben, 1970; Bé and Tolderlund; Williams et al., 1979; Fairbanks et al., 1980, 1982). The relative depth habitat of individual fossil species can be determined from oxygen and carbon isotope ranking. This depth ranking is typically based on the relative values of $\delta^{18}O$, with the lower $\delta^{18}O$ values characterizing species that predominantly inhabit warmer surface waters while higher $\delta^{18}O$ values indicate species living either at greater depths or within cooler water masses. Although some recent spinose taxa have been observed to calcify their tests out of equilibrium with the surrounding sea water (Fairbanks, 1980, 1982), the stable isotopic depth ranking of Recent species exhibits a general agreement with the vertical stratification observed from plankton tow studies (Williams et al., 1979; Williams and Healy-Williams, 1980) despite the presence of seasonal temperature variations, the non-equilibrium isotopic fractionation of some foraminiferal species (e.g., *Cibicidoides*), and other vital effects. Consequently, the stable isotopic ranking of species can be used to subdivide the standing foraminiferal fauna into species groups which predominantly inhabit surface, intermediate and deep water sectors within the upper part of the oceanic water column.

These data, when coupled with assessments of relative abundance changes for individual species inhabiting each depth sector, can, in turn, be used to infer changes in the water mass stratification and the physical expansion or contraction of particular depth-related habitats. Physical oceanographic changes such as these are presumably driven by external factors, such as variations in temperature, salinity, and density. Thus, once species have been isotopically ranked, it is then possible to construct vertical temperature profiles of marine surface waters and construct a detailed paleoecological description of species extinctions and originations in terms of the historical record of the occupation of depth-related planktic habitats.

In the present study, stable isotopic ranking of planktic foraminifera in middle Eocene through Oligocene sections was used to understand the oceanographic and evolutionary changes underlying planktic foraminiferal faunal turnovers. Preliminary stable isotopic depth rankings for most common species have been provided by Saito and Donk (1974), Douglas and Savin (1973; 1975; 1978) Boersma and Shackleton (1981), Boersma and Premoli-Silva (1983, 1989), Shackleton et al. (1985), Keigwin and Corliss (1986), Corliss and Keigwin (1986) and our own unpublished data. Based on this composite data set, we have compiled a preliminary depth stratification of species grouped into surface, intermediate and deep water dwellers (Table 11.1; Keller and MacLeod, in press). Although further isotopic ranking of species is still necessary to refine the relative positions of species in the water column, the data presented here are sufficient to demonstrate the potential of this tool for understanding the general pattern of planktic foraminiferal evolution and species diversity and their relationship to changing climatic and oceanographic regimes.

By analogy with present oceanic conditions, we have assumed that the isotopically lightest species inhabited the surface (mixed) layer that constitutes the uppermost 100 m of the water column (Table 11.1). Intermediate dwellers are inferred to have occupied the interval below the surface (mixed) layer and at or just below the permanent (as opposed to the seasonal) thermocline that resides between 100 m to 250 m below the surface. Deep water dwellers are inferred to have lived below the permanent thermocline (Berger, 1969; Bé and Tolderlund, 1971; Williams et al., 1979; Williams and Healy-Williams, 1980; Fairbanks et al., 1980, 1982).

Middle Eocene-Oligocene depth stratification

The relative abundance of dominant species groups in surface, intermediate and deep water habitats is illustrated in Figure 11.6 based on data from the equatorial Pacific DSDP Site 77B for the Oligocene interval and Indian Ocean DSDP Site 219 for the Eocene interval. Within each depth habitat, species have been grouped by common temporal trends. For example, species that evolved during the same time span are grouped together and followed

TABLE 11.1. Relative depth ranking of middle Eocene to Oligocene planktic foraminifera based on oxygen isotope variations.

Surface

Middle Eocene	Late Eocene	Oligocene
Acarinina bullbrooki (●)	Chiloguembelina cubensis (⊙)	Globigerina ampliapertura (⊙)
A. broedermanni (●)	Truncoroaloides rohri (●)	Pseudohastigerina barbadoensis (⊙)
A, planodorsalis (●)	Globigerinatheka semiinvoluta (●)	Globigerina officinalis
Muricoglobigerina senni (●)	G. index (●)	G. ouachitaensis
	Turborotalia cerroazulensis (●)	G. angustumbilicata
	T. cunialensis (●)	Globorotalia siakensis
	Hantkenina alabamaensis (●)	G. pseudokugleri
	Pseudohastogerina barbadoensis (⊙)	G. mendacis
	Globigerina ampliapertura	
	G. officinalis	
	G. ouachitaensis	
	G. angustiumbilicata	

Intermediate

Middle Eocene	Late Eocene	Oligocene
Morozovella lehneri (●)	Subbotina linaperta	Subbotina linaperta
M. spinulosa (●)	S. angiporoides	S. angiporoides
M. aragonensis (●)	S. utilisindex	S. utilisindex
Truncorotaloides rohri (●)	Globigerina eocaena	Globigerina eocaena
Globigerinatheka semiinvoluta (●)	G. galavisi	G. galavisi
G. index (●)	G. euapertura	G. praebulloides
	G. medizzai (●)	Pseudohastogerina micra
	Pseudohastigerina micra	Globoquadrina dehiscens
	Globorotaloides carcosellensis (●)	Globorotalia opima opima
		G. opima nana

Deep

Middle Eocene	Late Eocene	Oligocene
Globigerinatheka spp.	Globoquadrina venezuelana	Globoquadrina venezuelana
	G. pseudovenezuelana	G. pseudovenezuelana
	G. tripartita	G. tripartita
	Catapsydrax spp.	G. praedehiscens
		Catapsydrax spp.

●Species included in solid (black) pattern on Figure 11.6.

⊙Species included in dark stipple pattern of surface and intermediate columns of Figure 11.6.

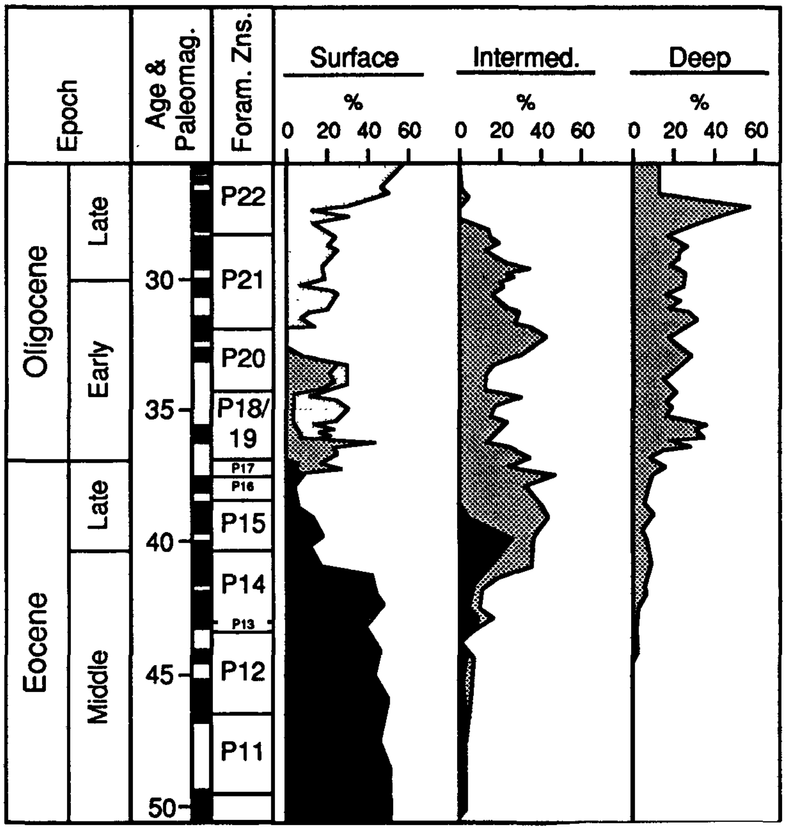

FIGURE 11.6. Relative depth stratification of the predominant constituents of the middle Eocene to Oligocene planktic foraminiferal fauna. Relative abundance of species grouped into surface-, intermediate- and deep-dwelling forms based on relative oxygen isotope ranking. Eocene data from DSDP Site 219, Oligocene data from DSDP Site 77B. Time scale based on Berggren et al. (1985). Faunal changes within each group are illustrated by different stipple patterns. Species included in the solid (black) pattern are marked by (O) in Table 11.1. Species included in the dark stipple area of the surface column are marked by a (O) in Table 11.1. Species listed in other stipple patterns as listed in Table 11.1 for surface-, intermediate- and deep-dwelling forms. See text for discussion.

through to their extinction with different shading patterns being used to delineate these temporally-related groups of taxa. In this way three major species groups can be identified in the surface (mixed) layer, but only two and one group in the intermediate and deeper sectors respectively. These results indicate that evolutionary diversification preferentially took place within the surface layer and secondarily at the intermediate depths of the thermocline. Our data also suggests that little evolutionary activity took place below the permanent thermocline (see also Hart, 1980).

In addition, Figure 11.6 illustrates that the transition from one faunal assemblage to another was generally a gradual process that occurred over a period 10^5 to 10^6 yrs. This transition pattern was typically characterized by a sharp terminal decline in numerical abundance and the lingering of these numerically rare species during the rise to dominance of the succeeding faunal group. Where abrupt faunal changes are observed, this is generally due to artifacts of the stratigraphic record such as short hiatuses and carbonate dissolution (Keller, 1983a, 1985, 1986; Keller et al., 1986; MacLeod and Keller, in press).

The major faunal turnovers noted in the

species abundance plots (Figures 11.4, 11.5) discussed earlier can be recognized in the depth stratified assemblage groups of Figure 11.6. The middle to late Eocene faunal turnover was characterized by the decline and eventual extinction of the warm surface water fauna (solid pattern) and a correlative increase in the cooler water intermediate fauna (dark stipple, Figure 11.6). A new, but for the most part short-lived, cooler surface water fauna (e.g., *G. ampliapertura, T. angustiumbilicata, Chiloguembelina cubensis*) evolved in the latest Eocene and disappeared again in the late early Oligocene (dark stipple), except for *T. angustiumbilicata* that predominates throughout the Oligocene. This surface water fauna was accompanied by a temporary decrease in the intermediate-dwelling species group (Figure 11.6). For the most part, *T. angustiumbilicata* was the dominant surface dweller (except for a short interval of increased carbonate dissolution in the *G. opima* Zone (Keller, 1983a), and intermediate and deep dwellers were abundant during the Oligocene at Site 77B. In the latest Oligocene (*G. ciperoensis* Zone) the surface group increased dramatically, partly due to the evolution of several new species (e.g., *Globorotalia siakensis, G. mayeri, G. kugleri, Globigerina ciperoensis, G. angulisuturalis*, Keller, 1983b), and was accompanied by a correlative decrease in the numbers of intermediate and deeper dwelling species.

Middle to late Eocene faunal turnover

Where and how in this long term climatic cooling trend did the so-called late Eocene-Oligocene mass extinctions occur? Figure 11.6 illustrates the presence of a major middle to late Eocene faunal turnover with its climax near the middle/ late Eocene boundary and a second faunal turnover of lesser magnitude during the late early Oligocene. Although this turnover cannot be characterized as a mass extinction, the numbers of taxa evolving and becoming extinct during the middle to late Eocene clearly identify this interval as marking a major ecological crisis for planktic foraminiferal populations. Figure 11.7 details this faunal turnover and shows that the relative abundance of all taxa becoming extinct at DSDP Site 219 constitute over 80% of the middle Eocene fauna. The decline in numerical abundance of surface dwellers, that began in the *G. subconglobata* Zone (Figure 11.4), continued through the *M. lehneri* Zone, accelerating into the upper part of the *T. rohri* Zone where it resulted in the extinction of several surface-dwelling species (e.g., *Truncorotaloides rohri, Morozovella lehneri* and *M. spinulosa*; Figures 11.4, 11.7). The surviving surface dwellers (e.g., *Globigerinatheka* spp., *Turborotalia cerroazulensis* s.l.) and one intermediate-dwelling species (*Globorotaloides carcoselleensis*) declined rapidly near the top of the *G. semiinvoluta* Zone. Since few surface-dwelling species survived to the E/O boundary (Figures 11.4, 11.7), the faunal turnover appears to have affected warm-tolerant surface dwellers first, followed successively by more cold-tolerant taxa. In contrast, only one intermediate-dwelling species disappeared during this interval, whereas the remaining intermediate-dwelling taxa survived well into the Oligocene. This middle to late Eocene faunal decline was accompanied by the rise to dominance of a new fauna, strikingly different in both taxonomic and ecologic composition. This new fauna consists primarily of intermediate-dwelling forms with a few deep-dwelling species whose number increased throughout the late Eocene and Oligocene. Only near the E/O boundary did a new surface-dwelling species group evolve (Figure 11.7). This interval of accelerated faunal turnover spanned approximately 4 m.y.

What caused this increase in the relative faunal turnover rate? Based on available isotopic data, this event most likely reflects major changes in the temperature-depth gradient between the ocean surface and the permanent thermocline that presumably decreased as a result of global cooling (Savin et al., 1975; Savin and Yeh, 1981; Barrera et al., 1990). Accompanying changes in the isotopic composition of planktic foraminifera during this interval indicate that this cooling trend reduced the vertical heterogeneity of the upper marine water column largely through surface water cooling which, in turn, would have been accompanied by a reduction in depth-related planktic habitats as well as a contraction of tropical biogeographic provinces. Increased vertical and latitudinal thermal gradients were likely accompanied by decreased oceanic circulation, diminished upwelling, and reduced nutrient

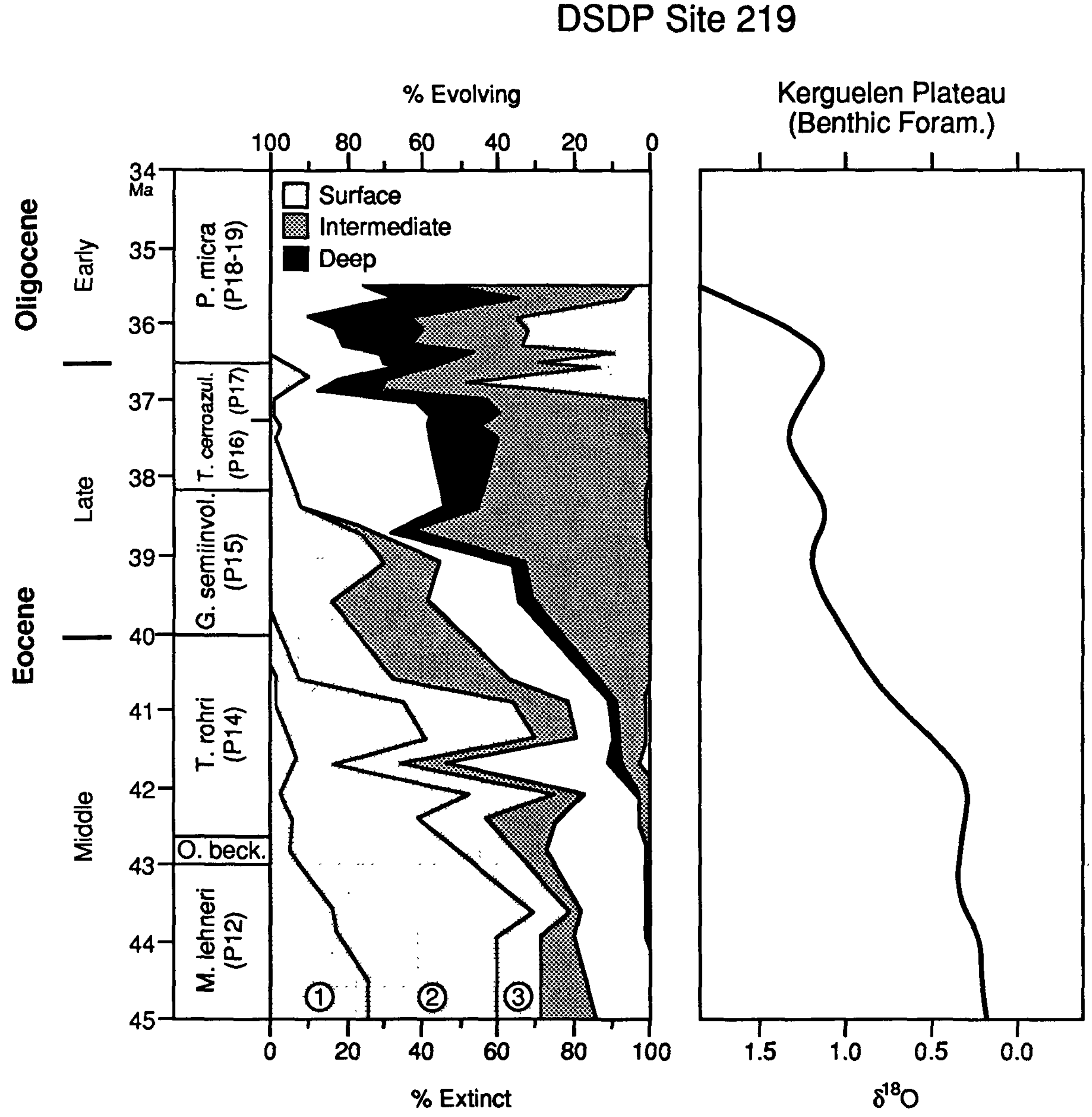

FIGURE 11.7. Middle Eocene to early Oligocene faunal turnover at Indian Ocean DSDP Site 219 based on the relative abundance of species going extinct and of species evolving in surface, intermediate and deep water sectors as determined from oxygen isotopic ranking. White zone in the center of the figure represents the relative proportion of the (undifferentiated) planktic foraminiferal fauna persisting throughout the interval. Benthic foraminiferal (*Cibicidoides*) $\delta^{18}O$ curve for ODP Sites 689 and 690; see Figure 11.11. Note that during the late middle to late Eocene, extinction predominantly takes place within surface-dwelling assemblage, including a successive pattern of disappearance among the following groups: 1. *Acarinina broedermanni, A. planodorsalis, A. bullbrooki*; 2. *Truncorotaloides rohri, Morozovella lehneri, M. spinulosa*; 3. *Globigerinatheka* spp. Time scale based on Berggren et al. (1985).

resources (an inference supported by the southern high latitude $\delta^{13}C$ record as discussed below). Our data thus provide empirical support for Cifelli (1969) and Lipps (1970, 1986) prior attribution of the middle to late Eocene faunal turnover as primarily resulting from habitat destruction, brought on by global cooling, via altered oceanographic patterns.

Oligocene faunal turnover

The second interval characterized by accelerated rates of faunal turnover spans the early/late Oligocene boundary, a time period characterized by the decline and eventual extinction of nearly all surviving Eocene species. The numerical abundance of these taxa and that of the evolving species is illustrated in Figure 11.8 for Site 77B along with the benthic $\delta^{18}O$ record (Keigwin and Keller, 1984). In this faunal turnover the species becoming extinct consisted primarily of surface-dwelling forms that evolved during the latest Eocene (e.g., *Globigerina ampliapertura, Pseudohastigerina spp.*) and the intermediate-dwelling Eocene survivors (e.g., *Subbotina linaperta, S. angiporoides, S. utilisindex, Globorotalia opima nana, Subbotina galavisi, G. jacksonensis*). These taxa begin their decline at approximately 30.5 Ma and disappear altogether between 28 to 29 Ma. This decline and eventual extinction was accompanied by a major global cooling (1.0 per mil for $\delta^{18}O$) that reached its maximum at 29 Ma (see Savin et al., 1975; Savin, 1977; Keigwin and Keller, 1984; Figure 11.8). Among the species that originate during this time interval was the relatively short-lived intermediate-dwelling form *Globorotalia opima* (restricted to *G. opima* Zone) and small globigerine and globorotaliid surface dwellers (e.g., *Globorotalia siakensis, G. mayeri, G. kugleri, G. mendacis, Tenuitella angulisuturalis*; Keller, 1983b). These taxa first appear in the late *G. opima* and *G. ciperoensis* Zones and survive well into the early Miocene. The evolution and diversification of these surface dwellers was accompanied by a significant global warming (1.0 per mil for $\delta^{18}O$; see Savin et al., 1977; Shackleton et al. 1984; Keigwin and Keller, 1984; Oberhänsli, 1986; Barrera and Huber, 1991). *Tenuitella augustiumbilicata* constitutes a relatively unaffected dominant faunal component of this faunal turnover in surface waters whereas *Catapsydrax* and *Globoquadrina* predominate in deeper waters (Keller, 1983a). The intermediate-dwelling fauna was much reduced during the Oligocene with the exception of a short interval near the *G. ampliapertura/G. opima* Zone boundary (Figure 11.8).

These changes in the depth stratification of Oligocene planktic foraminifera imply that the middle to late Eocene cooling trend continued through the early late Oligocene. Moreover, the Oligocene was much cooler than the late Eocene as indicated by; i) stable isotope data (Figures 11.9, 11.10; Savin et al., 1975; Shackleton et al., 1984; Barrera and Huber, 1991); ii) increased abundances of cold-tolerant deep-dwelling species; and iii) a correlative decrease in both intermediate- and surface-dwelling groups (Figure 11.6). The elimination of the late Eocene survivors at both surface and intermediate depths near the early/late Oligocene boundary and in the early late Oligocene, along with the near absence of newly evolving species until the late Oligocene, indicates a further reduction in depth-related habitats since the late Eocene (Figures 11.5, 11.6, 11.8).

Stable isotopic data of Site 77B suggest that this early/ late Oligocene faunal turnover was the result of renewed global cooling that was probably augmented by Antarctic glaciation during the Paleogene. As before, this global cooling would have been expected to reduce vertical and latitudinal thermal gradients, upwelling, and oceanic circulation, all of which would have resulted in habitat destruction for planktic biotas. In the late Oligocene this cooling trend was reversed, however, with low latitude climatic warming, and the diversification of surface-dwelling forms, indicating an increase in the thermal differentiation of marine surface waters, a deepening of the permanent thermocline, and (probably) increased upwelling and nutrient supply.

EOCENE TO OLIGOCENE ANTARCTIC COOLING

The general trends of the late Paleogene paleoclimatic history are well understood (as discussed earlier), whereas relatively high resolution stable isotopic records have only recently been recovered from sediments in the southern

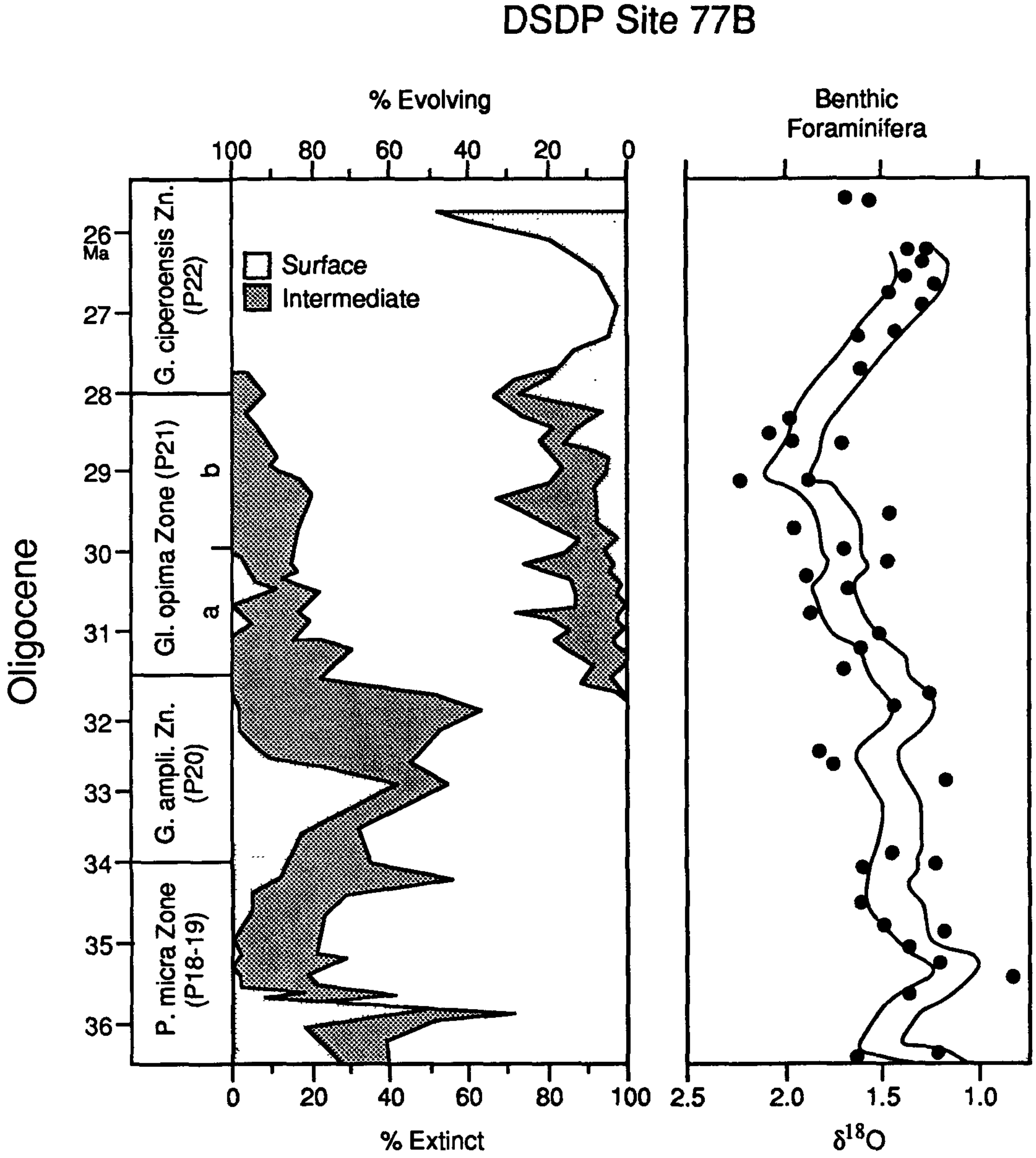

FIGURE 11.8. Oligocene faunal turnover in east equatorial Pacific DSDP Site 77B based on relative abundances of species going extinct and of species evolving in surface, intermediate and deep water sectors as determined by oxygen isotope ranking of species. White zone in the center of the figure represents the relative proportion of the (undifferentiated) planktic foraminiferal fauna persisting throughout the interval. Benthic foraminiferal (*Cibicidoides*) $\delta^{18}O$ curve for Site 77B from Keigwin and Keller (1984). Time scale based on Berggren et al. (1985).

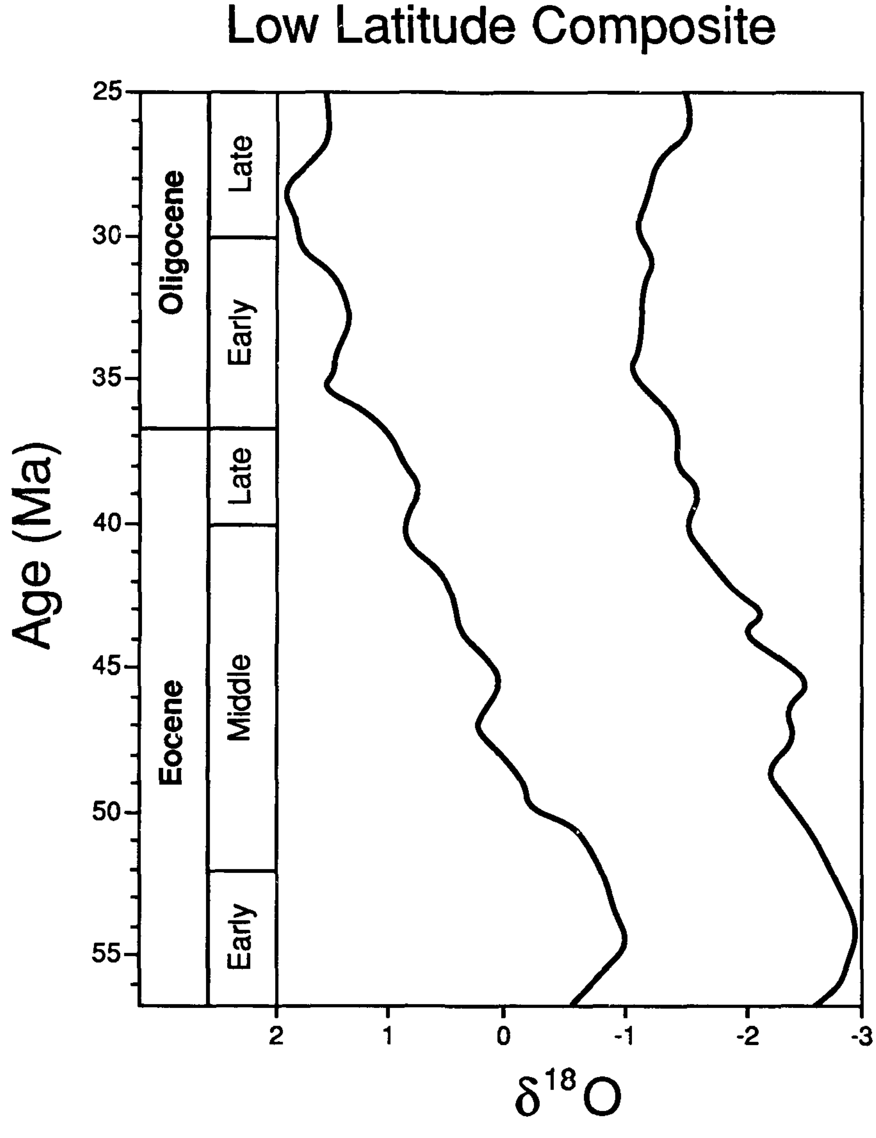

FIGURE 11.9. Composite oxygen isotope curves for tropical shallow-dwelling planktic foraminifers and benthic foraminifers as modified from Prentice and Matthews, 1988. Isotopic data from Poore and Mathews (1984) and Shackleton et al. (1984). Time scale based on Berggren et al. (1985).

oceans near Antarctica on ODP Legs 113 and 119. These high latitude isotopic records together with low and mid-latitude records have yielded the necessary climatic data that document the nature of the late Paleogene cooling and its relationship to the planktic foraminiferal turnovers.

Figure 11.9 presents the composite $\delta^{18}O$ record for planktic and benthic foraminifera from low and mid-latitudes as modified from Prentice and Matthews (1988). This $\delta^{18}O$ record most closely reflects the prevailing temperature conditions at Sites 219 and 77B during the time of the middle Eocene to Oligocene faunal turnovers. Unfortunately, no corresponding composite $\delta^{13}C$ record is available at this time. In Figures 11.10 and 11.11 we illustrate the $\delta^{18}O$ and $\delta^{13}C$ records from the Kerguélen Plateau (Sites 738, 744) and Maude Rise (Sites 689, 690). These data are based on Stott et al. (1990) and Barrera and Huber's (1991) analyses of the planktic foraminiferal taxa *Acarinina* and

Chiloguembelina (reflecting near-surface water conditions), *Subbotina* and *Globorotaloides suteri* (reflecting conditions at or below the thermocline), and the benthic foraminifer *Cibicidoides* spp.. (recording water conditions on the ocean floor [= intermediate water at these locations]). Short-time fluctuations in the raw isotopic data have been removed by interpolating the data to a constant temporal spacing (500,000 years) and then applying a smoothing filter (Sheppard's five-term filter; see Whittaker and Robinson, 1929) to remove any remaining single point anomalies. This data smoothing procedure is preferable to the more commonly employed equally-weighted average filters in that it efficiently represents the overall trend of the isotopic time series while simultaneously minimizing the distortion brought about through the temporally forward or backward migration of local extrema. The isotopic records of these three groups reflect variations in surface productivity along with the thermal differentiation of marine surface waters during the Eocene-Oligocene Antarctic climate cooling trend.

CLIMATE COOLING-δ^{18}O RECORD

The δ^{18}O records of both the Maude Rise (ODP Sites 689, 690) and Kerguelen Plateau (Sites 738, 744) as well as the composite low latitude record, show very similar temperature trends for benthic foraminiferal species that resided within the intermediate to deep water mass. Maximum Cenozoic warming occurred between 53 Ma and 55 Ma (Figures 11.9-11.11). Thereafter, intermediate water temperatures decreased by about 12°C-15°C (3.5 per mil) in both high and low latitudes reaching a maximum low in the early Oligocene. At the same time high latitude surface water temperatures also cooled by 12°C-15°C (3.5 per mil) whereas low latitude temperatures cooled by 6°C-8°C (1.5-2.0 per mil). The majority of this cooling occurred during the middle and late Eocene. Although in its early stages this cooling trend appears to be gradual, marked drops in intermediate water temperatures of about 0.5 per mil can be identified between 52-50 Ma (early/middle Eocene boundary) and between 47-48 Ma. Thereafter, two pronounced increases in δ^{18}O values of intermediate waters, (each averaging 1.0 to 1.5 per mil in high latitude) span the middle/late Eocene boundary (39-43 Ma) and the E/O boundary (35-37 Ma). These major high latitude cooling episodes are associated with ice-rafted debris in the Kerguelen Plateau sites both above the E/O boundary and near the middle/late Eocene boundary (dated at 34.5-36.5 Ma, and about 42.0 Ma, Barrera et al., 1990; Barrera and Huber, 1991; Ehrmann, 1991). Such glacio-marine sediments provide strong evidence for a major episode of East Antarctic glaciation beginning during the late middle Eocene and intensifying throughout the Oligocene. Based on the composite low latitude δ^{18}O record, Prentice and Matthews (1988) have concluded that glaciation began at about 40 Ma though their interpretation of these data differs from ours in that they assume that low latitude temperatures remained constant throughout the interval.

Comparison of the low latitude faunal turnover of Indian Ocean Site 219 (paleolatitude ~2°S) with the high latitude benthic δ^{18}O record from Kerguelen Plateau sites, shows a close correlation between the onset of major global cooling and Antarctic glaciation at about 42 Ma and the onset of the major middle to late Eocene faunal turnover (Figure 11.7). In fact, the faunal turnover (largely a record of the progressive elimination of warm-tolerant surface-dwelling species) parallels the decline in surface and intermediate water temperatures at both high and low latitude sites (Figures 11.9, 11.10). Moreover, the disappearance of this warm surface water fauna that was predominately composed of globorotaliform morphotypes, was nearly complete by 38 Ma; thus coinciding to the end of the first major cool event. The second major cooling in the early Oligocene corresponds to the elimination of surface-dwelling taxa that evolved during the latest Eocene cooling (Figures 11.7, 11.8), and the onset of cold climatic conditions also correlate well with the early/late Oligocene faunal turnover.

δ^{18}O AND δ^{13}C GRADIENTS

The δ^{18}O gradients between planktic foraminifers in surface, near-surface and benthic foraminifers reflect thermal stratification of the water column, whereas δ^{13}C gradients generally reflect changes in surface water productivity. Figures 11.10 and 11.11 illustrate

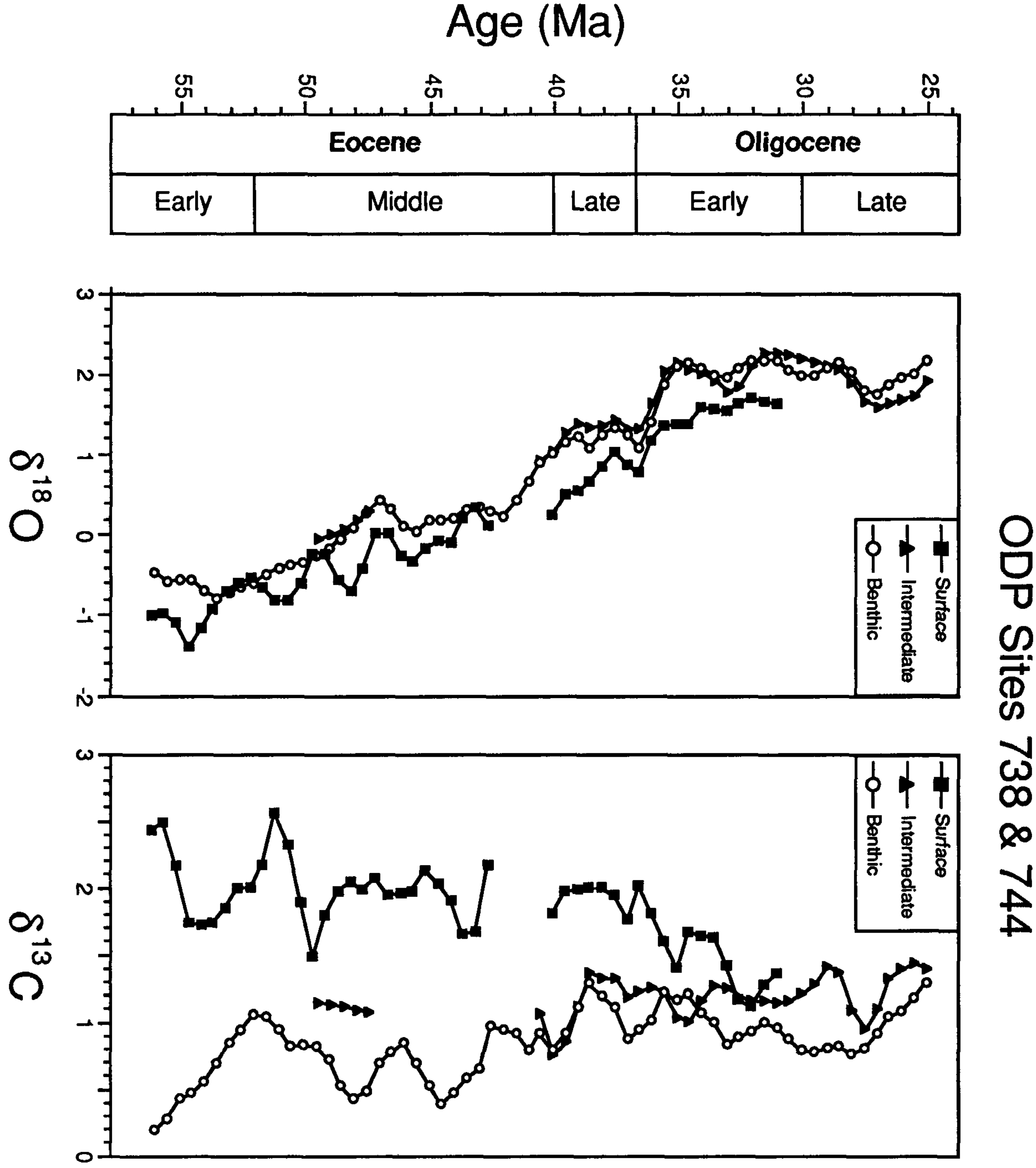

FIGURE 11.10. Eocene-Oligocene oxygen and carbon isotope curves for surface- (*Acarinina* spp. [from 43-52 Ma] and *Chiloguembelina* spp. [from 30-40 Ma]), and intermediate- (*Globorotaloides suteri*) dwelling planktic foraminifera along with benthic foraminifera (*Cibicidoides* spp.) from Kerguelen Plateau, ODP Sites 738, 744, southern Indian Ocean. Data from Barrera and Huber, in press. Time scale based on Berggren et al. (1985). See text for discussion.

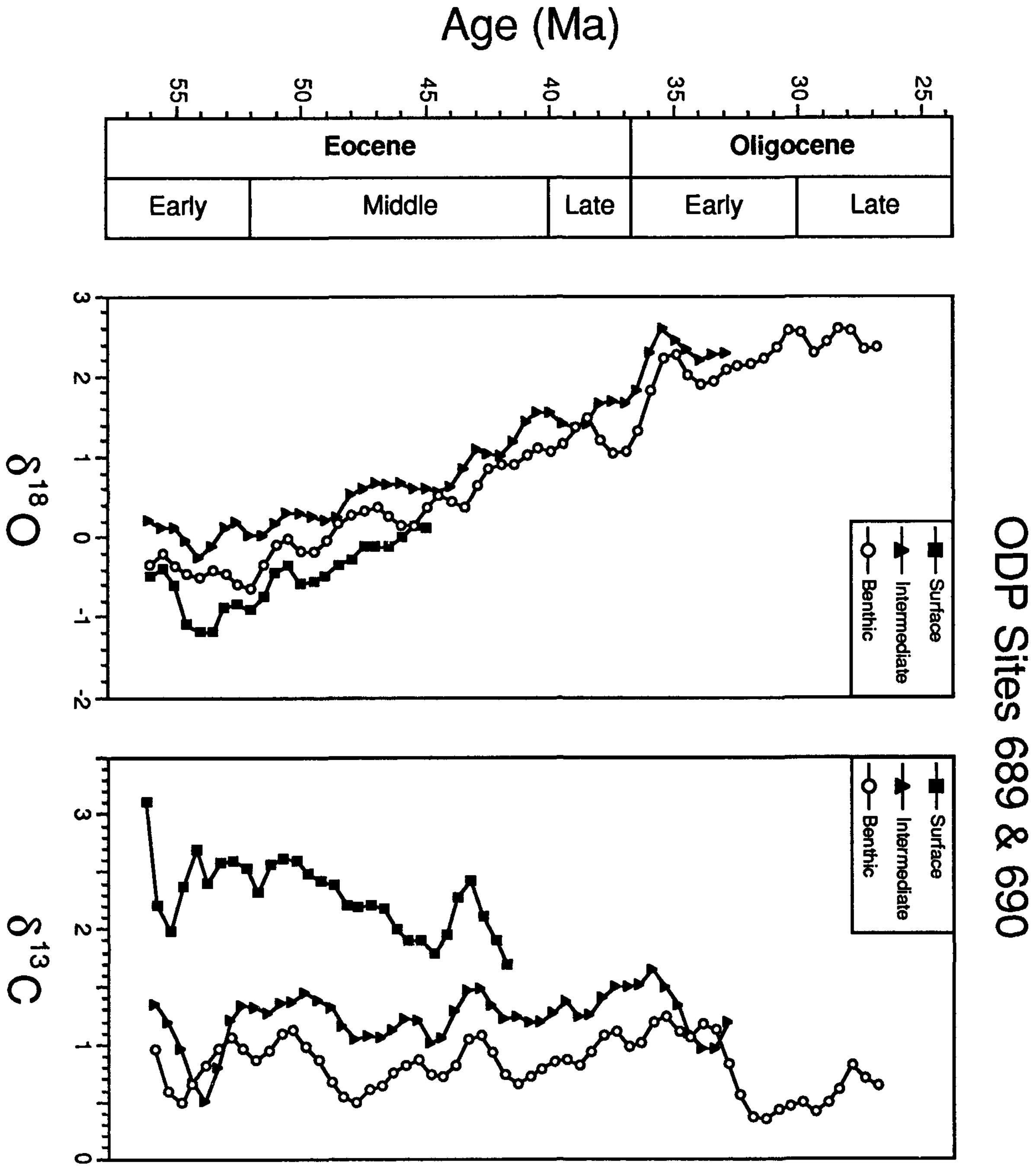

FIGURE 11.11. Eocene-Oligocene oxygen and carbon isotope curves for surface- (*Acarinina* spp.) and intermediate- (*Subbotina* spp.) dwelling planktic foraminifera and benthic foraminifera (*Cibicidoides* spp.) from Maude Rise, ODP Sites 689, 690, Wedell Sea, Antarctica. Data from Barrera and Huber, in press. Time scale based on Berggren et al. (1985). See text for discussion.

these gradients for the Kerguelen Plateau (Sites 738, 744) and Maude Rise (Sites 689, 690). It is interesting to note that at both Sites 738 and 744, the $\delta^{18}O$ values of *Globorotaloides suteri* are nearly the same as those of *Cibicidoides* spp., suggesting a very shallow thermal gradient. This implies that water temperatures between the base of the thermocline and the ocean floor differed by only a few degrees, considering a disequilibrium fractionation of *Cibicidoides* of about 0.5 per mil (paleodepth between 1500 m and 1800 m during middle Eocene to Oligocene time, Barrera and Huber, 1991). Surface water $\delta^{18}O$ values (*Acarinina*), however, average about 0.5 per mil lighter and are more variable reflecting both warmer overall surface temperatures and the presence of substantial climatic fluctuations. Similarly, higher sea surface temperatures than those below the thermocline are observed at Sites 689 and 690 on Maude Rise (Figure 11.11). But, as opposed to the Kerguelen Plateau sites, $\delta^{18}O$ values of *Subbotina* spp. average 0.2 to 0.5 per mil heavier than for *Cibicidoides* spp. This implies that bottom water temperatures were similar, or only about 1°C lower than just below the thermocline. High latitude southern ocean surface to deep thermal gradients show no significant changes between middle Eocene and Oligocene time. Low latitude surface to deep thermal gradients also remain essentially unchanged through the Eocene but increase slightly during the Oligocene (Figure 11.9).

In contrast, $\delta^{13}C$ gradients between surface, near-surface (below thermocline) and the ocean floor show significant changes between Eocene and Oligocene time. Unlike the $\delta^{18}O$ gradients, the $\delta^{13}C$ gradient patterns between Maude Rise and Kerguelen Plateau sites appear to be very similar. The $\delta^{13}C$ difference is greatest between surface water (*Acarinina, Chiloguembelina*) and the ocean floor (*Cibicidoides*), but decreases steadily between early Eocene and Oligocene. During the early Eocene this difference averages about 1.5 per mil, decreasing to 1.0 per mil during the middle Eocene, to 0.5 per mil during the late Eocene and then declining to nearly 0.0 in the early Oligocene (Figures 11.10, 11.11). The progressive decrease in this $\delta^{13}C$ gradient is primarily due to the steadily decreasing $\delta^{13}C$ values of surface dwellers and secondarily to a slight increase of about 0.5 per mil in *Cibicidoides* during the late Eocene. Both benthic (*Cibicidoides*) and subsurface (*Subbotina, Globorotaloides suteri*) values remain relatively stable through the Eocene, although they mirror fluctuations observed in the surface $\delta^{13}C$ record and decrease in the early Oligocene.

If formed under equilibrium conditions, $\delta^{13}C$ ratios of foraminifers reflect the isotopic composition of dissolved CO_2 in ambient sea water. These values vary primarily with the level of surface water productivity. Because ^{12}C is preferentially removed during photosynthesis, surface waters are enriched in the heavier ^{13}C and bottom waters are enriched in the lighter ^{12}C through the return of this isotopic species to the ocean via oxidation at depth (Deuser and Hunt, 1969; Kroopnick, 1974). The gradual decrease in the vertical $\delta^{13}C$ gradient between surface, and subsurface and benthic foraminifers observed between middle Eocene and Oligocene time therefore may reflect a progressive decrease in primary marine productivity. Within this general trend, a major drop in surface productivity parallels the latest Eocene cooling (37-38 Ma) and ends in the early Oligocene (34 Ma) when surface productivity was only marginally higher than that of the subsurface planktic foraminifers (*Subbotina* spp., *Globorotaloides suteri*). Surface water productivity appears to have remained low through the early Oligocene. A similar decrease in the values for surface waters from the middle Eocene through late Oligocene has been observed from tropical North Pacific sites (Savin et al., 1975).

DISCUSSION AND CONCLUSIONS

The remarkable correspondence between middle Eocene to Oligocene planktic foraminiferal turnovers with major Antarctic glaciation accompanied by steadily declining global surface water temperatures in both high and low latitudes (Figures 11.9-11.11) and decreasing surface productivity suggest that changes in climate and productivity are the primary forces driving planktic foraminiferal faunal turnovers during this interval. Each of the two subintervals within this period that are characterized by elevated rates of faunal change (Figures 11.7, 11.8) and associated with times of accelerated temperature and productivity declines. If declining productivity-nutrient supply was the primary driving force behind these biotic patterns, random extinctions resulting from increased inter-specific competition within all depth-related habitats would be expected. But, if changes in the planktic habitat itself, brought about by a decrease in the temperature-density differentiation of marine surface waters, was the primary driving force, the resulting extinctions should exhibit a marked ecological structure. During the middle Eocene to Oligocene cooling trend, in particular, a decrease in warm-tolerant surface-dwelling species accompanied by an increase in more cold-tolerant deep-dwelling taxa would be expected.

The latter was indeed the case during the middle to late Eocene when virtually all warm surface dwellers were successively eliminated and more cold-tolerant intermediate-dwelling forms increased in relative abundance (Figure 11.7) [*Note*: the obvious discrepancy between our interpretation and that of Poore and Matthews (1984) will be addressed by Barrera et al., in prep.]. Regrettably, the role of lower surface productivity in this faunal turnover remains unclear at this time. It is possible that the composite $\delta^{13}C$ data reflect less efficient utilization of available nutrient resources due to surface water habitat reduction (note decreased diversity and numerical abundance of planktic foraminifers), rather than reduced nutrient supply per se. Despite this uncertainty, however, the middle to late Eocene faunal turnover appears to have been driven primarily by surface cooling and associated changes in the temperature-density differentiation of the surface waters and secondarily by the productivity-nutrient relationship.

In contrast, the early to late Oligocene faunal turnover occurred at a time of already cool and relatively stable surface water stratification, but greatly reduced productivity-nutrient supply. In fact, surface productivity at this time decreased to nearly the same levels as intermediate-dwelling forms (e.g., *Subbotina* spp., *Globorotaloides suteri*, Figures 11.9, 11.10). If available nutrient supply were a controlling factor, one would expect increased competition primarily in the photic zone (surface layer) and thermocline (intermediate) layer. This appears to have been the case. Species extinctions occurred in surface and intermediate layers seemingly at random, although it is interesting to note that only Eocene survivor taxa actually disappeared. The preferential extinction of Eocene survivors during this interval suggests strongly implies elimination through competition for a limited nutrient supply.

Our study indicates that evolutionary turnover in the middle Eocene through Oligocene planktic foraminiferal fauna occurred primarily in surface and secondarily in intermediate water groups, whereas deep-dwelling forms remained essentially unaffected. Morphologic diversity was highest among surface dwellers (which included globorotaliform, turborotaliform and pulleniatiniform morphotypes--Figure 11.3, Table 11.1), lower among the intermediate-dwelling species group (including heteroheliciform, hastigeriniform and globigeriniform morphotypes) and lowest among deep dwellers (predominately globigeriniform morphotypes). This pattern of decreasing morphologic diversity with depth may be related to the high density of phytoplankton above the thermocline thereby promoting the elaboration of specialized morphologies to either actively capture or more efficiently graze different types of prey. Phytoplankton are known to be a primary food source for many modern planktic foraminiferal species including juveniles of omnivorous and carnivorous taxa which are too small to effectively prey upon zooplankton (Hemleben et al., 1989). In addition, greater variability in test morphology may also be related to the high physical water density in the thermocline layer that may offer greater freedom in terms of test shape variation (e.g., less stringent selection pressure on morphological attributes that affect an individual's ability to maintain its position within the water column). In contrast, the low morphologic variability of predominantly globigeriniform test shapes below the thermocline layer may reflect a more omnivorous or scavenging trophic pattern that coincides with reduced nutrient supply, along with higher selection pressures on morphological attributes that contribute to the organism's ability to maintain its position in the water column.

Our relative depth classification of Paleogene planktic foraminiferal morphotypes contrasts strongly with that of Hart (1980).

Whereas Hart (1980) attempted to predict the depth distribution of Cretaceous through Recent genera based on the observed distribution of Recent morphological analogues along with some preliminary oxygen isotopic data from middle Cretaceous species, our results are based on the empirically assessed relative isotopic ranking of individual Paleogene species. These data reveal the existence of previously unanticipated levels of intra-generic heterogeneity within the stable isotopic biochemistry of these Paleogene faunas. This implies that their ecology, distribution, and trophic structure may have differed substantially from that of their Recent counterparts (see also Shackleton et al., 1985). In addition, this observed intra-generic ecological heterogeneity calls into question the conclusions of studies (e.g., Stanley et al., 1988) that attempt to use Hart's (1980) genus/ biocharacter-based depth classification to account for differences in the evolutionary histories of major planktic foraminiferal clades.

In summary, abundant faunal and isotopic data strongly suggests that changes in climate and productivity are the primary driving force in the Eocene to Oligocene faunal turnovers. There is no evidence of catastrophic extinctions, or sudden species abundance changes, directly associated with any of the three well documented microspherule layers in the *G. semiinvoluta* and *T. cerroazulensis* Zones (Keller et al., 1983, 1987; Keller, 1986; Glass and Burns, 1987; Miller et al., 1991). Nor is there evidence that these extraterrestrial impact events triggered the climatic change, since climate cooling precedes the emplacement of impact-related debris.

ACKNOWLEDGEMENTS

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