BOUNDARY CONDITIONS OF ATLANTIC EOCENE OXYGEN MINIMUM ZONES

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Riassunto. Gli Heterohelicidi biseriali (Foraminiferi planctonici) si sono rivelati gli indicatori paleo-idrografici delle zone di minimo d'ossigeno in ambiente oceanico aperto. Dal confronto tra la diminuzione della ratio del carbonio isotopico negli Heterohelicidi biseriali e l'intensità del gradiente del carbonio isotopico nella colonna d'acqua è stato possibile individuare e descrivere l'intensità del minimo d'ossigeno durante l'Eocene.

Combinando i valori degli isotopi stabili con le percentuali delle specie—indice tra i Foraminiferi planctonici sono state individuate le condizioni limite delle zone di minimo d'ossigeno relative all'Eocene inferiore, medio e sommitale in Oceano Atlantico. Esse sono: *Eocene inferiore* — un modesto contrasto termico sia verticale che latitudinale, associato a movimenti di risalita ridotti e circolazione poco vigorosa in un oceano termosferico, moderatamente caldo e stabile, si traduce in una zona di minimo d'ossigeno poco intensa ed arealmente ristretta; *Eocene medio* — risalite più vigorose e contrasti termici sia verticali che areali più accentuati in seguito ad un raffreddamento al fondo ma non in superficie, associati ad una maggiore ventilazione della colonna d'acqua, si traducono in una zona di minimo d'ossigeno più intensa ed arealmente ben sviluppata; infine *Eocene superiore* — in un oceano psicrosferico, un contrasto termico, sia verticale che latitudinale, poco accentuato, risalite e circolazione atmosferica equatoriali limitate, unitamente ad una diminuzione dell'intensità delle correnti, si correlano con uno strato misto omogeneo, in cui la zona di minimo d'ossigeno non solo è scarsamente sviluppata ma si localizza al di sopra del termoclino invece che a media profondità.

Abstract. Biserial heterohelicid foraminifera are paleohydrographic indices for open ocean oxygen minimum zones. Comparison of the depletion of biserial heterohelicid carbon isotope ratios with the carbon isotope contrast through the water column is used to describe the strength of Eocene oxygen minima. Combining stable isotope values and percentages of planktonic foraminiferal index species, we describe the following boundary condition for early, middle and latest Eocene oxygen minimum zones in the Atlantic Ocean. *Early Eocene* — low meridional and vertical thermal contrasts, reduced upwelling and circulation vigor in a moderately warm, stable thermospheric ocean accompany a poorly developed, spatially restricted oxygen minimum. *Middle Eocene* — invigorated upwelling, large vertical and spatial thermal contrasts caused by cooling at the bottom but not at the surface together with increased ventilation of the water column accompany a strong, widely developed oxygen minimum; and *Late Eocene* — in a psychrospheric ocean low meridional and vertical thermal contrasts, reduced equatorial upwelling and atmospheric circulation with decreased current circulation vigor correlate with a homogeneous mixed layer in which an oxygen minimum is poorly developed above the thermocline, but not at mid depths.

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Introduction.

Stable isotope studies have been used to depict the relative habitats of planktonic foraminiferal species along temperature and oxygen profiles (Shackleton & Vincent, 1978; Kennett et al., 1985). Studies of biserial heterohelicid foraminifera suggest occupation of an oxygen minimum habitat (Boersma et al., 1979; Resig & Kroopnick, 1983). The possibility arises to use this group as tracers for the relative depths and geographic locations of open ocean oxygen minimum zones during climatic reorganization of the Eocene.

To depict the oceanographic settings of Eocene oxygen minima, a number of climatic and habitat monitors will be adduced. Oxygen isotope ratios depict the spatial distribution of near surface paleotemperatures and paleothermoclines. The distribution of Eocene tropical versus higher latitude planktonic foraminiferal index groups corroborate patterns in the near surface temperature estimates (Haq et al., 1977). Planktonic interspecific carbon isotope profiles depict not only the habitat of the heterohelicids, but carbon isotope and oxygenation gradients which they inhabited. Abundance of the biserial heterohelicids should then track the location and strength of oxygen minimum zones.

In this paper we discuss three very different intervals of the Eocene; the very warm interval of early Eocene Zone P8; middle Eocene Zones P11 to P14, the time of oceanic cooling and eutrophication (Lipps, 1970); and latest Eocene Zone P17, the interval of planktonic foraminiferal extinctions immediately preceding the Eocene/Oligocene boundary.

Methodologies.

The methodologies used in this paper have been discussed elsewhere (Haq et al., 1977; Boersma & Premoli Silva, 1983). All site locations are shown in Fig. 1. Planktonic foraminiferal species counts are made on three size fractions. In percentage plots the raw counts are combined in order to eliminate the size effect (Vincent, 1972; Boersma & Premoli Silva, 1983).

Oxygen isotope analyses are made by standard techniques in Shackleton's Cambridge laboratory. In estimating paleotemperatures no ice sheet effect is assumed prior to Miocene time (Savin et al., 1985). Near surface temperatures are estimated from the most oxygen isotopically negative species in each sample or from genera measured because they consistently produce the most negative values. These include the acarininids and the morozovellids in the early through middle Eocene (Douglas & Savin, 1978; Shackleton et al., 1985) and the biserial heterohelicids, the globoquadrinids, and occasionally the turborotaliids in the late Eocene (Poore & Matthews, 1984; Keigwin & Corliss, 1986). These are also the tropical–subtropical index groups through most of the Eocene (Stainforth et al., 1975). Their presence in shelf sediments is fur-
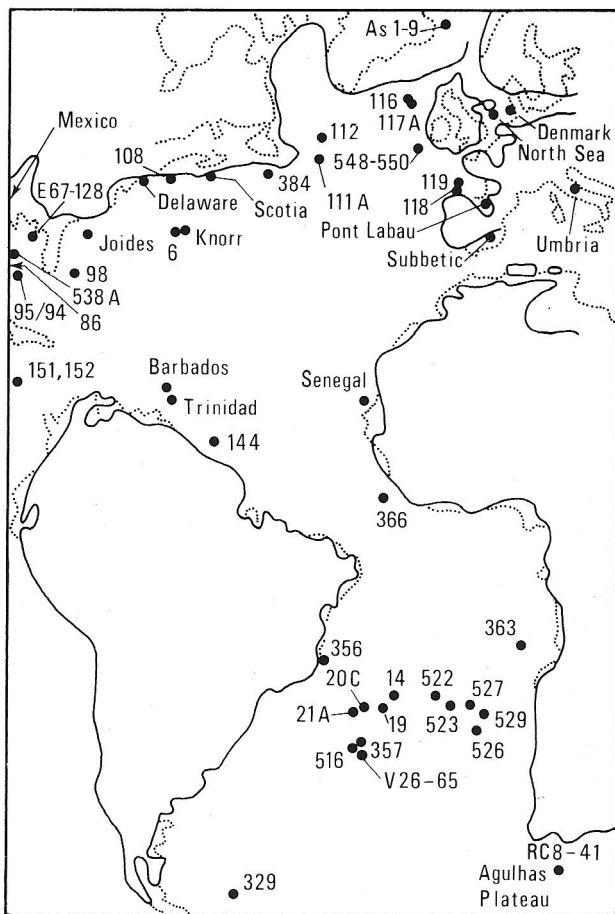
Fig. 1 — Location map of all Atlantic Ocean sites described in this study (from Boersma & Premoli Silva, 1983; Boersma et al., 1987; Premoli Silva & Boersma, in press).

ther indication of their shallow habitat (Harris & Jobe, 1951; Nagymarosy et al., 1986; Lindsay & McGowran, 1986).

The biserial heterohelicid niche.

In the present study we attempt to establish the paleohydrographic indications of the biserial heterohelicids by describing the biserial heterohelicid niche. Conclusions about habitats derive from numerous tests and comparisons, including:

1) negative covariance of oxygen and carbon isotope ratios among arrays of species through the water column (Curry & Matthews, 1981);

2) biogeographic distribution patterns, as evidence on preference for warm, temperate, or cool water habitat (Berger, 1970);

3) comparison of benthic and cool—preferring planktonic carbon isotope records to corroborate the direction of change in the planktonic record (Boersma & Shackleton, 1977 b);

4) evidence for a high productivity water column, such as the abundance of siliceous fossils, to compare with carbon isotopic data suggesting depleted carbon isotope ratios under conditions of enhanced production (Broecker, 1974; Elmstrom & Kennett, 1985);

5) evidence of synchronous morphologic changes accompanying a habitat change presumed from the isotope data (Boersma & Premoli Silva, 1983);

6) analogies between Eocene and Recent foraminiferal wall structures and their implications for habitat preference (Bè, 1982);

7) consistency of vertical stratification patterns and inter—specific stable isotope differentials in cooler and warmer times, and in different latitudes and habitats (Boersma et al., 1987);

8) interpretation of relative habitats and isotope values rather than absolute numbers (Savin et al., 1985);

9) ecologic conditions surrounding the evolution of species and of genera;

10) specific and generic longevity as an indication of genetic and adaptive flexibility, compared to the breadth of the foraminiferal habitat as indicated by stable isotopes (Boersma & Premoli Silva, 1983);

11) patterns of solution susceptibility related to depth habitats (Berger, 1970);

12) comparison of $\delta^{13}C$ values with the bulk carbon record as a means of verifying that a species is a surface or a mesopelagic dweller (Shackleton et al., 1985);

13) isotopic evidence for tropical submergence (Ekman, 1953) expected under conditions of cool high latitudes and a strong tropical thermocline; and

14) comparison with habitats of modern biserial heterohelicids.

Biserial heterohelicids first evolved in the later Albian and with only two major apertural modifications, the group has survived into the present day. They first proliferated in the open ocean during the Cenomanian and throughout epicontinental seas which have been described as low in oxygen and high in salinity (Herm, 1966; Hamaoui, 1966). Paleogene biserial heterohelicids are found in neritic and other shallow water deposits (Harris & Jobe, 1951) where they display patterns typical of opportunistic and/or survivor species (Lindsay & McGowran, 1986). They survive into the present day in only a few tropical areas of the Indian and Pacific Oceans.

Paleogene biserial heterohelicids vary dramatically in abundance and in areal extent. From one planktonic zone to the next they may vary from 5 to 50% of a fauna, and within the same time period may change their area of preference from high latitudes to the tropics. During their numerous geographic migrations they underwent marked morphologic changes. For example during warm, highly productive times of the late Paleocene, biserial heterohelicids increase in size and thickness. During low productivity episodes of the early Oligocene they become elongate and thin (Poore & Gosnell, 1985; Boersma & Premoli Silva, 1983, 1986; Premoli Silva & Boersma, in press). Throughout the Paleogene their distributions and their stable isotope data suggest morphologic and ecological flexibility (Boersma & Premoli Silva, 1983).

Stable Isotope Evidence.

Studies have suggested that biserial heterohelicids occupied a mid depth oxygen minimum habitat (Tab. 1). In the Pacific Neogene, depleted carbon isotope values of the biserial heterohelicids were interpreted to represent a low oxygen habitat (Resig & Kroopnick, 1983). In the Pliocene of the equatorial Pacific *Streptochilus tokelauae* (= *S. globulosum*?) records intermediate oxygen isotope values, but very depleted carbon isotope values (Tab. 1, V18–262) and stratifies well below *Globigerinoides* among the cooler, but not the coolest group of globorotaliids. By analogy with the studies of Vincent & Shackleton (1980) *S. tokelauae* appears to occupy a mid depth habitat in an oxygen minimum zone located near the base of the mixed layer. These results have been reproduced in late Cretaceous, mid early through late Paleocene, early through middle Eocene, and early Oligocene materials (Douglas & Savin, 1978; Boersma et al., 1979; Boersma & Premoli Silva, 1983; Poore & Matthews, 1984; Keigwin & Corliss, 1986; Boersma et al., 1987).

Shackleton et al. (1985) have suggested that in the late Paleocene– early Eocene when the carbon isotope contrast through the water column is very large, a stronger oxygen minimum develops. At this time in the Atlantic when a large surface to bottom carbon isotope contrast accompanies warm near surface paleotemperatures, biserial heterohelicids register most depleted carbon isotope values (Tab. 2). There is a simultaneous change in the morphologies of the biserial heterohelicids. They tend to become more numerous, diversify morphologically, and especially in tropical areas they became larger (Boersma & Premoli Silva, 1983). The large, thick specimens of *C. wilcoxensis* typical in the intermediate size fractions of late Paleocene sediments, are an example of this trend. Size increase with habitat warming under conditions of heightened production has been documented also for modern planktonics.

Their numerous episodes of geographic emmigration and abundance changes each accompanied a shift in the oceanic carbon isotope contrast. For example, the minimal carbon isotope gradient at the Cretaceous/Tertiary boundary is associated with a low productivity water column (Percival & Fischer, 1977; Romein & Smit, 1981). On sedimentologic evidence it has been suggested that the Atlantic water column was low in oxygen, especially in the north and at depth (Tucholke & Vogt, 1979; Boersma et al., 1979; Zachos & Arthur, 1986). At this time the biserial heterohelicids proliferated through latitude (Boersma & Premoli Silva, 1983). Similarly, during the latest Eocene episode of minimal surface to bottom carbon isotope contrasts, the biserial heterohelicids proliferated (Boersma & Premoli Silva, 1986).

Recent biserial heterohelicids have been found in Holocene sediments (Resig & Kroopnick, 1983) and in the tops of carbonate–rich cores from the Ontong–Java Plateau in the equatorial Pacific. They average around 35–100 microns or less in length and, to date, have not been found in plankton tows.

Location	Species	$\delta^{18}O‰$	$\delta^{13}C‰$
PALEOCENE			
356, 29—3	G. cretacea	− 2.49	0.21
	C. MORSEI	− 1.78	0.80
	P. eugubinus	− 1.36	1.50
465A, 3—1	C. MORSEI	− 1.11	1.39
	G. cretacea	1.06	0.92
	H. monmouthensis	1.04	1.81
465A, 3—3	C. MORSEI	− 1.40	1.76
	G. cretacea	− 1.17	1.24
	P. eugubinus	− 0.88	1.95
V22—126	A. mckannai	− 0.50	3.70
	P. australiformis	0.22	2.36
	C. CRINITA	0.35	2.31
357,30cc	TUBITEXTULARIA	− 1.65	0.85
	H. monmouthensis	− 1.14	1.20
95,10—4	A. mckannai	− 1.62	2.92
	S. trilocularis	− 0.87	1.71
	C. WILCOXENSIS	− 0.41	1.57
	Z. AEGYPTIACA	− 0.46	1.25
EOCENE			
277, 38—2	M. aragonensis	− 1.34	2.89
	C. MIDWAYENSIS	− 0.70	1.29
	Subbotina sp.	− 0.68	1.60
529, 24—2	M. aragonensis	− 0.83	2.23
	A. bullbrooki	− 0.63	1.34
	C. WILCOXENSIS	− 0.63	0.70
	A. pseudotopilensis	− 0.57	1.62
V27—202	Acarinina sp.	− 0.17	1.57
	P. MICRA	− 0.17	0.77
	Globigerina sp.	0.26	0.98
357, 20—2	C. CUBENSIS	0.08	1.52
	P. micra	0.17	1.22
	Catapsydrax	0.24	1.23
OLIGOCENE			
357, 15—2	P. nana	0.21	1.56
	G. ouachitaensis	0.20	1.04
	STREPTOCHILUS	0.50	0.41

366, 8–4	C. CUBENSIS	− 1.23	0.85
	«G.» ampliapertura	− 0.42	0.59
	Catapsydrax	0.32	0.54
167, 14cc (Douglas & Savin)	C. CUBENSIS	− 0.68	1.08
	G. galavisi	− 0.63	0.88
	G. prasaepis	− 0.59	0.82
	G. ouachitaensis	− 0.54	0.85
	P. nana	− 0.45	0.52

MIOCENE

357, 4–3	O. universa	0.48	2.37
	S. seminulina	0.57	2.48
	G. ruber	0.60	2.34
	O. universa	0.66	2.49
	G. nepenthes	1.05	1.96
	Gl. conomiozea	1.11	2.29
	G. dehiscens (bullate)	1.27	2.24
	Gl. scitula	2.06	1.66

PLIOCENE

357, 2cc	G. sacculifer	0.86	1.83
	Gl. margaritae	1.00	0.60
	Gl. scitula	1.95	0.28
357, 3–5	Globigerinoides	0.58	2.18
	G. sacculifer	1.02	2.17
	Gl. scitula	1.86	0.54
V18–262	G. sacculifer	− 0.65	2.34
	G. fistulosus	− 0.58	2.97
	N. dutertrei	− 0.49	1.54
	O. universa	− 0.35	2.60
	S. dehiscens	− 0.34	1.25
	Gl. tumida	0.07	2.06
	S. TOKELAUAE	0.39	− 0.37
	G. venezuelana	0.51	0.76
	Gl. tosaensis	1.80	1.35
62, 11–1 (Resig & Kroopnick)	G. sacculifer	− 2.21	2.13
	Gl. tumida	− 1.30	1.40
	S. GLOBULOSUM	− 1.07	− 0.97

Table 1 – Representative stable isotope analyses of Tertiary planktonic foraminifera, including the biserial heterohelicids indicated in CAPITAL LETTERS. *Pseudohastigerina micra* often records similar carbon isotope ratios to those of the heterohelicids, and its values are also CAPITALIZED. During times when the oxygen and carbon isotope gradients among the planktonics are large and surface carbon isotope ratios are very positive, the biserial heterohelicids occupy an intermediate position and register some of the most negative carbon isotope values. Other smooth–walled species, such as *Gl. scitula*, also consistently register some of the most negative carbon isotope values. Data from Douglas & Savin, 1978; Boersma & Shackleton, 1977a, b; 1981; Boersma et al., 1979; Resig & Kroopnick, 1983; Boersma et al., 1987; Boersma & Shackleton, unpublished data.

Site	$\delta^{13}C$		$\delta^{18}O$
	Warm Planktonic	Cool Planktonic	Cool Planktonic
Early Eocene			
527	2.88	1.89	− 0.03
525	2.90	1.84	− 0.38
525	2.69	1.80	− 0.27
548	3.83	0.61	− 1.59
21	2.85	1.44	− 0.33
356	2.82	0.69	− 0.45
356	3.42	0.77	− 1.19
277	2.89	1.60	− 0.68
Middle Eocene			
RC14−29	3.26 − 2.89	1.62	0.10
21	3.26	1.69	0.50
357	3.17 − 2.89	0.55	− 0.73
357	2.59 − 2.30	1.16	− 0.27
357	3.43	1.23	− 0.56
V27−202	1.57	0.98	− 0.26
Late Eocene			
526	2.92	1.88	0.56
529	2.77 − 2.13	1.92	0.53
548	1.35*	1.19	0.55

Table 2 − Carbon isotope values among the warmest (most oxygen isotopically depleted) and coolest (most oxygen isotopically enriched) planktonic species at numerous Atlantic and a few Pacific and Indian Ocean sites during the Eocene. The oxygen isotope ratio for the coolest−preferring species is also given. Enriched oxygen isotope values suggest that the form was living at cooler temperatures at that time. A star beside the planktonic value indicates that it may not have been the most negative at the site, but was the most negative among those measured. Data is derived from Boersma et al. (1987).

The area is overlain today by very warm 28°−26°C, not well oxygenated water into which a low oxygen tongue penetrates at a depth near 200 meters. This produces a large oxygen gradient through only a moderate depth and temperature differential, and a strong upper water column oxygen minimum located near 200 m depth (Craig et al., 1981). Present also is an alkalinity anomaly located in the upper water column only of this area. In this area biserial heterohelicids register mid depth temperatures and carbon isotope ratios suggestive of a strong oxygen minimum (Tab. 1).

While we cannot prove equilibrium precipitation and/or a preference for low oxygen (or related) conditions in the Tertiary, circumstantial evidence suggests this is a realistic interpretation of biserial heterohelicid ecology. Comparison with their habitat today partially confirms this idea.

Biserial heterohelicid stable isotope values and oceanic oxygenation.

The purpose of this discussion is to demonstrate a link between the stable isotope values of the biserial heterohelicids and the oxygenation of the water column in which they live. Any attempt to reconstruct oceanic oxygenation and/or temperatures from fossil stable isotope data, however, depends on establishing: 1) the fact that measured oxygen isotope values are related to ocean temperatures; 2) that measured carbon isotope values are related to the oxygen profile in the water column; and 3) if and how values registered in the fossils are reflective of past temperatures and the carbon isotope ratio in total CO_2 of ambient seawater.

While initial studies documented oxygen isotopic disequilibrium precipitation of calcite by numerous planktonic species (Kahn, 1979; Berger et al., 1978), recent analyses have demonstrated the retention of differences between habitats within versus below the mixed layer. Bouvier—Soumagnac & Duplessy (1985) measured three species from culture, plankton tows and the seabed which demonstrated small (0.2—0.3 per mil), but statistically significant differences between the foraminiferal oxygen isotope ratios and the equilibrium value. However, the slope of the relationship linking temperature to the difference between foraminiferal oxygen isotope ratios and water oxygen isotope ratios is the same as that measured for equilibrium conditions. From whatever ontogenetic or gametogenic process, shells of one species deposited below the mixed layer were both larger and heavier than those from within the mixed layer. In the open ocean these forms registered the carbon isotopic impoverishment predictable for forms below the mixed layer.

In an upwelling environment, the foraminiferal shells recorded a cold temperature signal linked to intense upwelling. Adults were also smaller in size in this situation. It is thought that when high nutrient contents prevail, reproduction occurs earlier (Duplessy et al., 1981a).

Carbon isotope analyses demonstrated that when strictly limited and narrow size fractions are analyzed, shell carbon isotope variations reflect those of the surficial mixed layer, as well as conditions below the mixed layer. In sediment the size effect among species precipitating most of their calcite below the mixed layer was negligible. In conclusion, carbon isotopic impoverishment below the mixed layer as well as in the sediment reflects deposition in a colder water with a low carbon isotope ratio (Bouvier—Soumagnac & Duplessy, 1985).

The notion that the carbon isotopic composition of seawater is related to ambient oxygen levels has been suggested in numerous studies. For example, Kroopnick (1980) documented the relation between [13]C—depleted water in the region of the dissolved O_2 minimum in Atlantic surface waters. He attributed this minimum to the addition to the water column of CO_2 derived from the oxidation of [13]C—depleted organic matter. In deeper water, also, the car-

bon isotope ratios were correlated with oxygenation, determined by the origin of, and *in situ* processes occurring within, each water mass.

In order to reconstruct the *relative* habitats of extinct planktonic foraminifera, several types of studies have been made: 1) attempts to document deviations from equilibrium; 2) comparison of estimated synoptic mixed layer paleo–isotherms with the present distribution of mixed layer isotherms; and 3) comparison of vertical carbon and oxygen isotope profiles with measured temperatures and oxygenation through the water column.

Using planktonic foraminiferal oxygen and carbon isotope ratios Shackleton & Vincent (1978) reconstructed profiles of dissolved oxygen and predicted, based on oxygen isotopes, at what depths such oxygenation values should be found. Comparison with measured oxygen isotope/temperature values suggested that the foraminiferal data had correctly depicted those profiles in the Agulhas Current region. By plotting measured paleo–isotherms delimited in analyses of one planktonic foraminiferal species from surface sediments, these same authors demonstrated that the planktonics approximated the distribution of near summer, mixed layer isotherms in the same region (Vincent & Shackleton, 1980).

Studies of size–related variation in isotopic composition have demonstrated patterns similar to those determined in culture and plankton tow data (Douglas & Savin, 1978; Poore & Matthews, 1984; Shackleton et al., 1985; Keigwin & Corliss, 1986). As with modern materials, it is necessary to pick size–graded samples of adults of one species. Shackleton et al. (1985) also demonstrated that when appropriate size fractions were used, forms occupying warmer and cooler habitats could be identified. Their occupation of these habitats was corroborated by carbon isotopic impoverishment of the cooler dwelling forms.

While small species and size fractions demonstrate carbon isotopic depletion and approach bulk carbon values, taken to represent nannofossil carbonate, minimum depletion was registered by the cooler dwelling species. Among the species which live deeper in the water column, the effect of ontogenetic stage on isotopic composition is much smaller. Because these species were living below the depth regions with a strong vertical $\delta^{13}C$ gradient, a minimal change in carbon isotopic composition is evidence against a disequilibrium effect (Berger et al., 1978).

Numerous tests have been made to differentiate the surface from the deeper habitat. For Paleocene/Eocene boundary species the occupation of a warmer versus a cooler, presumably deeper habitat was tested by examination of forms from cooler latitudes (Shackleton et al., 1985). In the cooler region species showed a parallel pattern of size change, but with isotopically enriched oxygen isotope values, and a smaller differential between the warmest and the

coolest registering species, as would be expected in the higher latitude site. By plotting size—normalized carbon isotope data for each species grouping against the bulk sediment $\delta^{13}C$ value, the authors also showed the systematic difference in depth habitat for various groups. The surface and deep groups were monitoring conditions respectively above and below the main gradient in dissolved oxygen concentration.

To study the character of the carbon isotope gradient through the upper water column, these same authors traced the difference between the surface and subsurface $\delta^{13}C$ as a function of the $\delta^{13}C$ in bulk sediment. As the surface $\delta^{13}C$ value is enriched, the difference between the two regions increases. This implies that at the time that surface waters were most carbon isotopically positive, the intensity of the underlying oxygen minimum was enhanced.

Models for the development of Eocene Oxygen Minima.

Wyrtki (1962, 1971) asserted that the development of an oxygen minimum zone can be the result of several processes: *in situ* oceanographic conditions contributing to the utilization of oxygen through the water column, circulation of deeper watermasses, and lateral advection of low oxygen water layers. Each of these processes has produced mid depth or shallow oxygen minima in different areas of the ocean today. To interpret the presence and genesis of Eocene oxygen minima, the carbon isotope profiles must first be examined in order to separate which maxima and/or minima correspond to fluctuations in oxygen content, and which to alteration of the distribution of carbon isotopes through the water column.

Atlantic Eocene paleooceanography and ecological biogeography.

In this section we will characterize the three intervals of the Eocene using several biotic and chemical tracers: the distribution of estimated near surface paleotemperatures, the steepness of vertical thermal gradients, the distributions of foraminiferal index groups which are related to the temperature data, the character of the carbon isotope profile through the water column, and the distribution of heterohelicid foraminifera which trace the development and strength of oxygen minimum zones.

Early Eocene.

The early Eocene has long been considered the warmest series of the Tertiary (Frakes & Kemp, 1973; Frakes, 1979). Early Eocene near surface paleotemperature estimates are uniformly high (Fig. 2). Although we have no tropical measurement, estimated temperatures range from highs near 21°C in the area of the Mediterranean outflow, to near 18°−19°C in the subtropics.
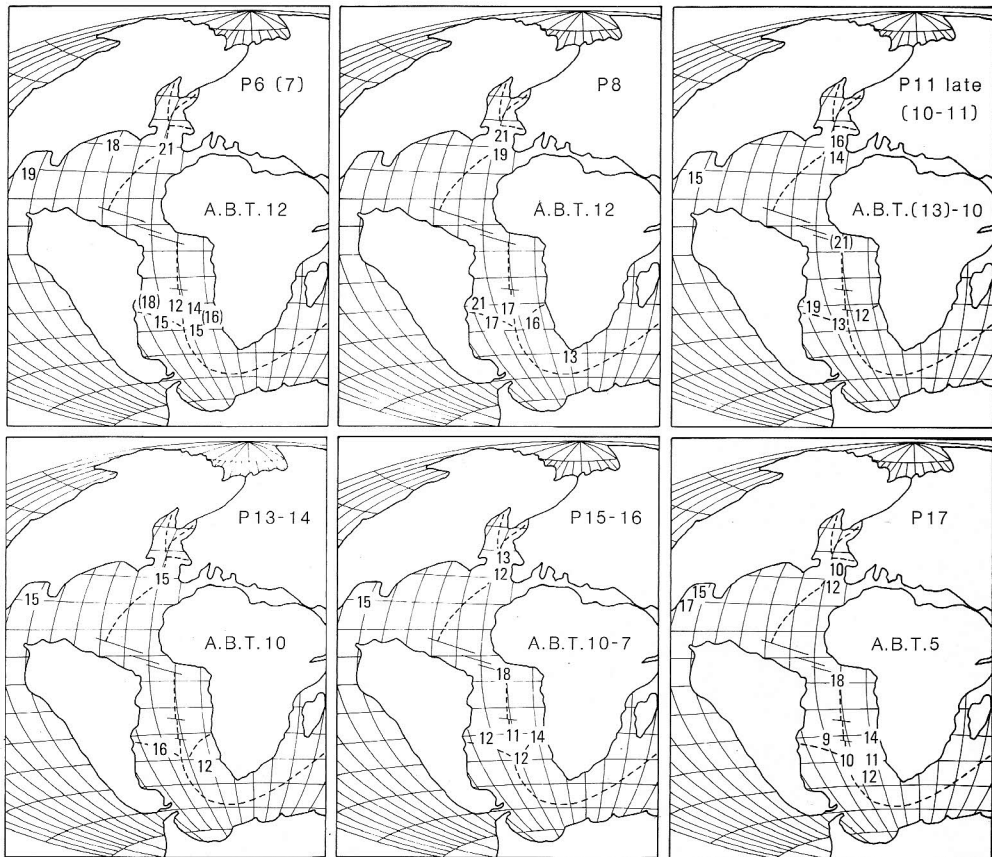
Fig. 2 — Atlantic Eocene estimated near surface paleotemperatures. Temperatures are estimated from the oxygen isotopic compositions of the most negative (warmest) species in each sample. A.B.T., average bottom water paleotemperature, derived from analysis of uvigerinids, or corrected to a uvigerinid value according to the correction factors in Shackleton et al. (1984). Data from Boersma et al. (1987). Biozones from Berggren et al. (1985).

Early Eocene vertical thermal gradients in tropical regions are near 9°C (Fig. 3), in contrast with gradients over 20°C in the warmest regions today (Craig et al., 1981). It is the very warm deeper water and higher latitude temperatures of the Eocene which distinguish it from the later Paleocene. It is not maximal tropical near surface temperatures, then, but the geographic and vertical extent of the thermosphere which makes the Eocene seem warmer (Boersma et al., 1987).

The ratio of warm to cool water planktonic foraminiferal index species depicts an expanded tropical bioprovince (Fig. 4). In the tropics the ratio of warm dwelling to cooler index species was approximately 12 to 1; in the proto –Gulf Stream near 40°N latitude warm outnumbered cooler index species ap-
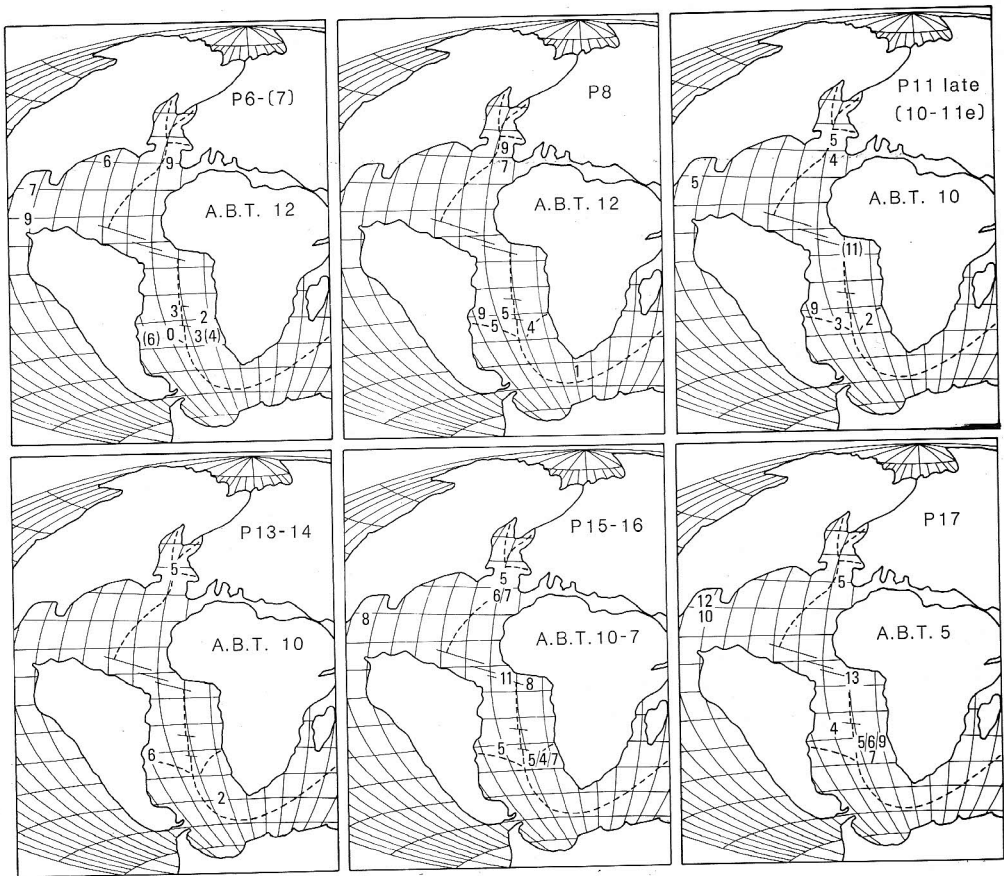
Fig. 3 — Atlantic Eocene estimated surface to bottom paleotemperature gradients. At each locality the average bottom water paleotemperature (A.B.T.) was subtracted from estimated near surface paleotemperatures in Fig. 2. See caption of Fig. 2 for explanation. Data from Boersma et al. (1987).

proximately 5 to 1. During the slightly cooler episode in Zone P7 tropical ratios were even greater, near 20 to 1; even in the proto−Brazil Current system near 30°S, tropical species outnumber higher latitude indices by 4 to 1.

The biserial heterohelicids, which underwent major habitat contraction and individual size reduction across the Paleocene/Eocene boundary, were neither widespread nor abundant during the early Eocene (Fig. 5). Only during Zone P8 did they comprise slightly larger numbers of higher latitude faunas. Throughout this interval intra−generic diversity was low and individual size, even in upwelling areas, remained small (Beckmann, 1957; Premoli Silva & Boersma, in press).

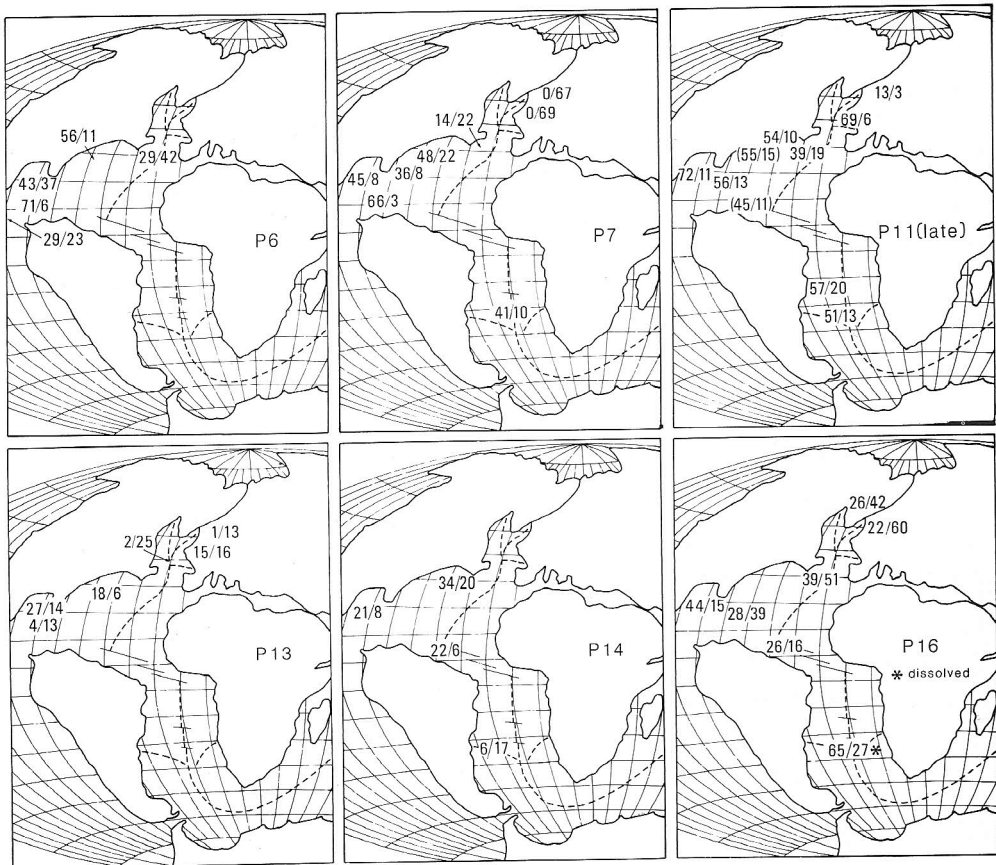The carbon isotope profile for early Eocene Zone P8 at Site 356 in the

Fig. 4 — The ratio of lower to higher latitude index species (the L:H ratio) at numerous Atlantic localities during the Eocene. Index species were determined in each zone of the Eocene (Boersma & Premoli Silva, 1986; Boersma et al., 1987; Premoli Silva & Boersma, in press). Lower latitude indices include all morozovellids or globo-quadrinids, some acarininids, globigerinathekids, and turborotaliids. Higher latitude indices include the tenuitellids, catapsydracids, globorotaloids, low--spired subboti-nids, and planorotalitids prior to the later middle Eocene, and biserial heterohelicids in the late Eocene. The combined percentages of these index species were then plotted on Eocene time--slices at the localities shown in Fig. 1.

proto—Brazil Current system (Fig. 1) is representative of lower latitude regions with high near surface paleotemperatures (Fig. 6). The interspecific gradient is the broadest of the Eocene, ranging from highs near 3.2 per mil in the warmest group, the morozovellids, to values near 0.5 per mil registered by the low-spired subbotinids, and near 0.00 per mil among benthic cibicidids. While we cannot specify the depths which species occupied, the subbotinids are the Eocene high latitude index group (Gradstein & Srivastava, 1980) and register oxygen isotope
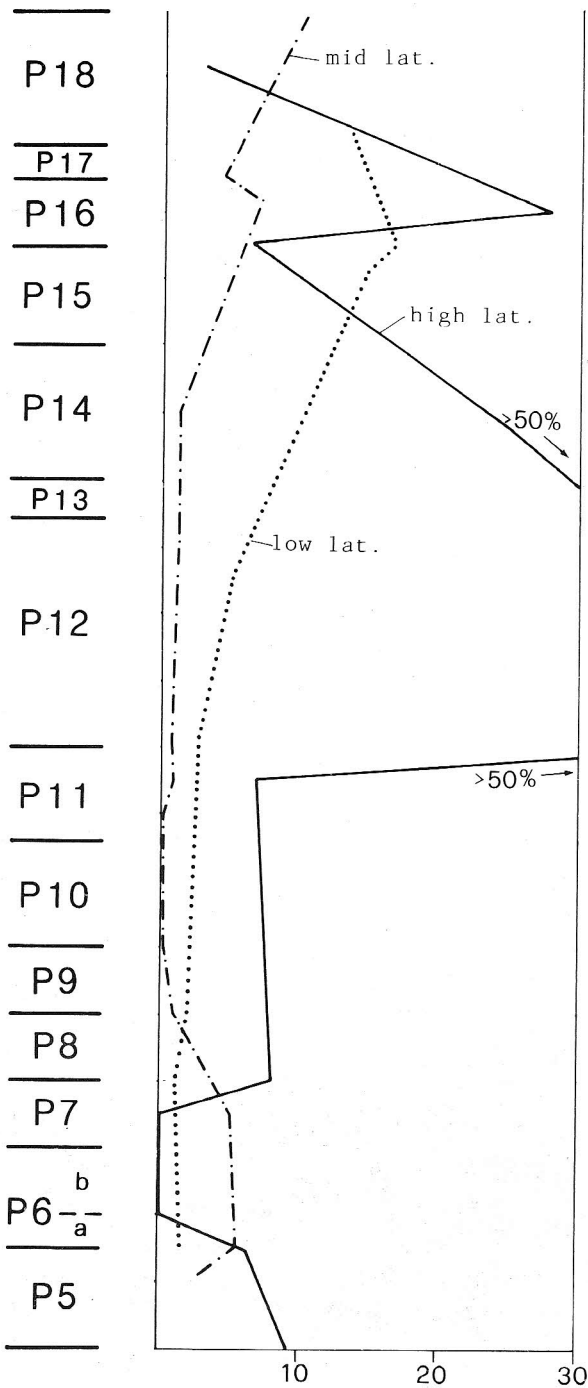
Fig. 5 — Percentages of biserial heterohelicids at lower, middle and higher latitudes through each planktonic foraminiferal zone of the Eocene and into the early Oligocene in the Atlantic (Premoli Silva & Boersma, in press). Biochronology follows Berggren et al. (1985).

values consistent with a cooler water habitat (Douglas & Savin, 1978; Boersma et al., 1979; Boersma & Premoli Silva, 1986). This suggests that we have measured the carbon isotope gradient through that part of the upper water column occupied by planktonic foraminifera.

These oxygen—carbon plots (Fig. 6) allow interpretation of the carbon isotope profile along the foraminiferal thermocline. The early Eocene carbon isotope profile lacks a discrete minimum level, but contains two zones: enriched values and a strong gradient above the thermocline and depleted values and a low gradient in and below the thermocline, decreasing slightly down to the bottom.

Middle Eocene.

Climate change of the middle Eocene involved decreasing near surface and bottom water temperatures (Boersma & Shackleton, 1977a; Oberhänsli et al., 1984). Equatorial values near 21°C and southern boundary current estimates near 19°C resemble those of the early Eocene (Fig. 2). Both North and South temperate latitudes become cooler. Low paleotemperature estimates in the Gulf of Mexico suggest that subtropical source regions were supplying cooler surface waters to the subtropical gyres (Boersma et al., 1987).

Vertical thermal contrasts of the middle Eocene (Fig. 3), while similar in degree to those of the early Eocene, are spatially different. At this time gradients decrease in the North Atlantic coeval with the cooler near surface temperatures. In this situation the thermocline would shoal through the surface water column (Kennett et al., 1985). By the end of the middle Eocene a divergence in near surface and bottom water paleotemperature records suggests the thermal isolation of higher latitudes and decreased heat transport in South Atlantic boundary currents (Williams et al., 1985).

Reorganization of warm and cool water index species (Fig. 4) parallels these gradient changes. By the middle Eocene the warm water indices were different: globigerinathekids, and to a lesser degree, the acarininids became the dominant tropical—subtropical indices. These forms are typical of vigorously circulating boundary currents and upwellings, and seem to represent cooler, more eutrophic environments (Boersma et al., 1987). In Zone P11 distribution of the globigerinathekids and acarininids to near every site in this study accounts for the increased lower to higher latitude index ratios.

Biserial heterohelicids diversify, proliferate, and expand latitudinally during the middle Eocene (Fig. 5). Beginning in Zone P11 they account for over 50% of high latitude faunas, many of which are not well preserved, however. Their expansion at lower latitudes is delayed until the end of the middle Eocene. In tropical areas their presence is associated with high numbers both of acarininids and the siliceous fossils which proliferate at this time (Berger & von Rad, 1972; McCoy & Zimmerman, 1977).

The carbon—oxygen plot (Fig. 6) demonstrates a more complexly stratified water structure. A slight carbon isotope gradient is registered within the thermocline which is occupied by the warmest—preferring planktonics. A minimum zone is located below this thermocline. Underlying species register the maximal carbon isotope gradient over a small temperature range, but there is little gradient below in either the carbon or the oxygen isotope curve.
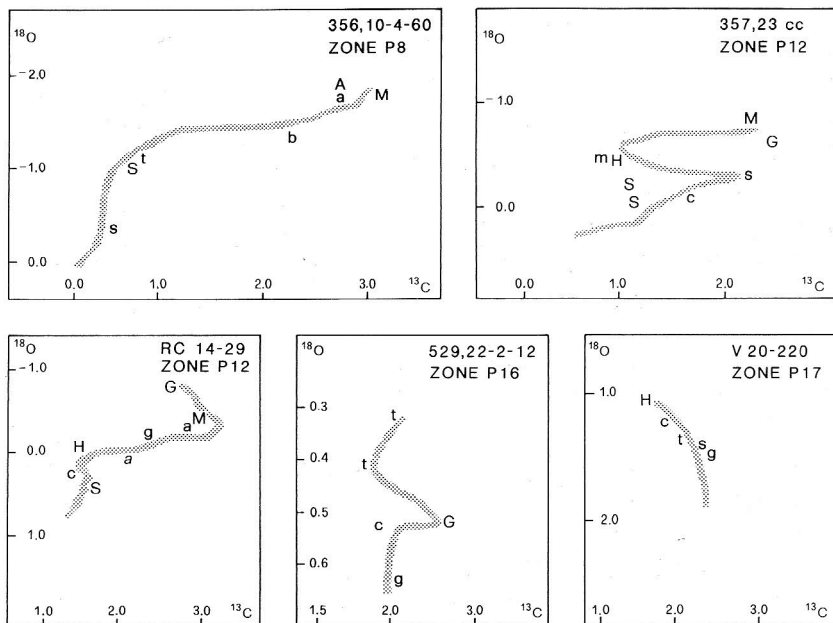
Fig. 6 — Carbon—oxygen isotope plots of arrays of planktonic foraminifera through the Eocene in the Atlantic Ocean. Site locations are shown on Fig. 1. Species abbreviations include: M) large morozovellids; m) biconvex morozovellids; A) coarsely muricate acarininids; a) other acarininids; G) globigerinathekids; t) turborotaliids; H) biserial heterohelicids; S) low—spired subbotinids; s) mixed subbotinids; c) catapsydracids; g) globorotaloids; b) benthics. Data from Boersma et al. (1987).

Latest Eocene.

Because of the evidence for extensive middle and late Eocene upwelling (Lipps, 1970) we have speculated that our near surface paleotemperature estimates for the later middle and late Eocene may reflect isothermal shallowing in upwelling regions. In fact, it was impossible to find a lower or lower middle latitude sample of this age lacking radiolarians. For this reason we may have not estimated maximal late Eocene near surface tropical temperatures (Boersma et al., 1987) such as the larger invertebrates require in lower latitude shelf seas (Adams et al., 1986).

The cooling trend continues through the late Eocene and culminates in minimal Eocene age paleotemperatures during Zone P16 time (Oberhänsli & Toumarkine, 1985; Williams et al., 1985). While temperatures in boundary currents cool, tropical areas of the gyres register temperature decreases near $1°-2°C$ (Fig. 2). As a result, there is a sort of thermal homogenization in the near surface zone of subtropical and temperate areas (Boersma et al., 1987). As bottom paleotemperature estimates decrease to their Eocene minima, the temperature gradient from intermediate to bottom water depths increases for the first time in the Eocene. Cooled bottom water temperatures produce the much larger surface to bottom gradients (Fig. 3). This is particularly evident in tropical regions where there was little change in near surface temperatures (Keigwin, 1980; Keigwin & Corliss, 1986).

Thermal homogenization is paralleled by faunal homogenization and the cosmopolitan distributions of many cool–preferring species (Fig. 4). Only in the northwestern Gulf of Mexico and offshore South America do tropical index species outnumber higher latitude types, by 3 to 1 and 2 to 1 respectively. Elsewhere, especially in the temperate zone, tropical and higher latitude indices (and incidentally mid latitude indices) occur in a ratio of almost 1 to 1. The maintenance of these ratios to the latitude of Rockall Bank and into the North Sea best demonstrates the extent of this faunal homogenization.

Despite a decrease, biserial heterohelicids comprise a moderate percentage of both higher and lower latitude assemblages (Fig. 5). At northwestern higher latitudes, especially where dissolution is pronounced, samples consist primarily of biserial heterohelicids and tenuitellids. And in the few continuous sequences across the Eocene/Oligocene boundary, sample fine fractions are highly dominated by biserial heterohelicids (Boersma & Premoli Silva, 1986).

The minimal carbon isotope contrast among planktonic foraminifera in Zone P17 (Fig. 6) reflects a global decrease in the oceanic carbon isotope gradient (Hsü et al., 1985). Gradient changes among the planktonic foraminifera are due to more depleted values among the warm–preferring species and enriched values among the cooler dwelling species. In Vema Core 20–220 located near 3,000 m paleodepth in the southernmost Brazil Basin (Tab. 1), biserial heterohelicids occupy minimum values above the other, cooler dwelling planktonic species (Fig. 6). This gradient is atypical, however, and in most instances the values of the cooler dwelling species are slightly more negative (around 0.2–0.4 per mil less) than those of the overlying biserial species (see values in Keigwin & Corliss, 1986; Boersma et al., 1987).

The oxygen–carbon plot (Fig. 6) demonstrates both minimal carbon isotope and vertical thermal gradients of the Eocene. In additional records this minimal carbon isotope gradient is located above the thermocline indicated by oxygen isotope ratios. That is, the greatest carbon isotope gradient was located at the top of the thermocline occupied by latest Eocene planktonic foraminifera.

Discussion

Early Eocene.

Biotic and isotopic evidence is consistent with a warm, sluggish, two—layer early Eocene ocean, oxygenated at the surface, less well oxygenated below, and lacking a mid depth oxygen minimum. A stable stratification lacking strong contrasts is suggested. Evidence suggesting low rates of overturn and upwelling through this time include:

1) restriction of siliceous biofacies to equatorial regions, and to a lesser degree, in western boundary currents and higher latitudes (McCoy & Zimmerman, 1977; Premoli Silva & Boersma, 1986).

2) occurrence of warm water siliceous indices, the radiolarians, rather than the cooler water diatoms (Fenner, 1984);

3) low planktonic foraminiferal species richness, near 42 species, is typical of cooler, low productivity times (Cifelli, 1969; Boersma & Premoli Silva, 1983);

4) benthic foraminiferal indices suggesting sluggish circulation (Tjalsma & Lohmann, 1983);

5) low thermal contrasts, both meridional and vertical.

A broad carbon isotope gradient through the mixed layer and through a minimal, probably deep thermocline in a thermospheric ocean allows diversification and high abundances only of the warmest water planktonic foraminiferal species in the mixed layer, but not beneath (Kennett et al., 1985). This would promote low diversity. The exclusion of the biserial heterohelicids, usually members of the cooler dwelling groups, may be attributed to the same mechanism.

Middle Eocene.

Middle Eocene carbon isotope profiles depict a broad carbon isotope contrast containing depleted carbon isotope ratios indicative of a well developed oxygen minimum located within the thermocline occupied by the planktonic foraminifera (Fig. 7). In many localities this carbon isotope contrast is as broad as that of the early Eocene, but it is registered at lower temperatures and through a lower thermal gradient (Fig. 2, 3).

Cooling, eutrophication and enhanced circulation vigor and upwelling during the middle Eocene, particularly its later half (Lipps, 1970), are suggested by:

1) Layer A cherts (Ewing et al., 1970);

2) maximal Eocene planktonic foraminiferal diversity, 64 species, suggesting maximal habitat diversification (Boersma et al., 1987);

3) vast expansion of siliceous biofacies (McCoy & Zimmerman, 1977);

4) expansion of the psychrospheric benthics, suggesting an increased higher latitude influence (Benson, 1984; Tjalsma & Lohmann, 1983; Boersma, 1985);

5) proliferation of the globigerinathekids, paleohydrographic indices for actively circulating boundary currents (Premoli Silva & Boersma, in press);

6) expansion of the diatoms (Fenner, 1984);

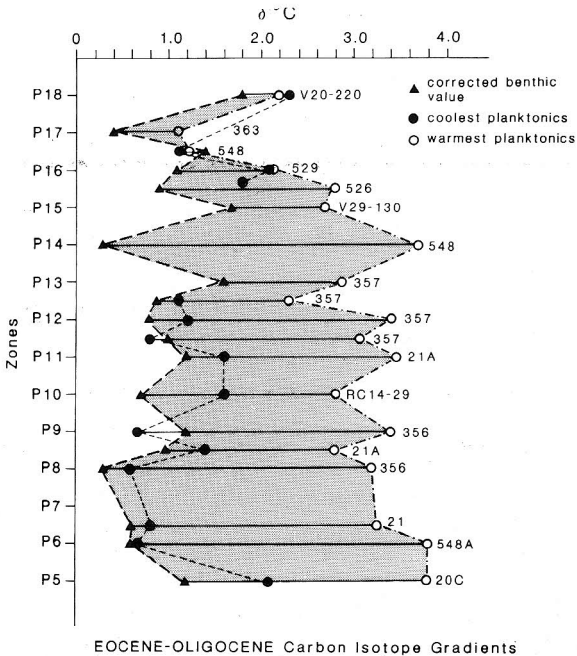EOCENE-OLIGOCENE Carbon Isotope Gradients

Fig. 7 — Near surface to bottom carbon isotope gradients at numerous Atlantic locations through the course of the Eocene and across the boundary into early Oligocene Zone P18. Curve includes also the values for the coolest planktonic in each analysis, usually *Catapsydrax*, a low–spired subbotinid, or a globigerinid. Benthic measurements were made on a cibicidid or corrected to cibicidid values according to the factors listed in Shackleton et al. (1984). All data from Boersma et al. (1987).

7) decline of the mid water benthic foraminiferal index for sluggish circulation and increased corrosivity at the bottom (Tjalsma & Lohmann, 1983); and

8) steeper thermoclines due to bottom water cooling (Fig. 2, 3).

Middle Eocene planktonic foraminiferal diversification includes not only the warm water species, but numerous temperate and cool water forms (Gradstein & Srivastava, 1980). Kennett et al. (1985) have suggested that a cooler thermocline usually lies shallower and is associated with higher abundances of deeper living species. Clearly niches above, within and below the mixed layer were produced during the cooling episode of the middle Eocene (Boersma et al., 1987).

The proliferation of the biserial heterohelicids (Fig. 5) in times and areas of high production is consistent with our conclusions on their habitat. As in the late Paleocene, their spread is coincident with a strong thermocline in a high productivity ocean.

Late Eocene.

Unique conditions developed through the course of the late Eocene. Despite an initially high surface to bottom carbon isotope contrast (Fig. 7), in Zone P17 the warmest preferring planktonics register depleted values causing a surface to bottom contrast below 1 per mil. Indices for diminished upwelling and production after this time include:

1) concentration of belts of siliceous production at higher latitudes (Fenner, 1986);
2) diminished equatorial siliceous production and wind speeds (Fenner, 1986);
3) low planktonic foraminiferal species richness, 43 species in the Atlantic (Boersma & Premoli Silva, 1986);
4) faunal homogeneity, characteristic of other times of low productivity (Boersma et al., 1979; Boersma & Premoli Silva, 1983) and low rates of sediment accumulation (Zachos & Arthur, 1986).

At this time in extra tropical areas the biserial heterohelicids demonstrate an inverted stratification relative to other planktonic species (Tab. 1). Their position at the top of the stratification ordering is typical of times, such as the earliest Paleocene, when low surface to bottom carbon isotope gradients coincide with reduced thermal contrasts through the upper water column (Tab. 2). Typical of such times are two different types of carbon isotope profile. In boundary current areas where there is a strong thermocline (Site 356, Tab. 1), there is a depletion in carbon isotope values through the thermocline, showing little gradation to the bottom. At the edges of the upwelling belt (Site 465A, Tab. 1) where the thermocline is diminished, the carbon isotope contrast is also low, but values registered by the warmest planktonic are more depleted than those below. This second type is analogous to the late Eocene situation.

In latest Eocene carbon isotope profiles the gradient in carbon isotope ratios is located above the thermocline. Biserial heterohelicids register values above this gradient (Tab. 1). The anomalous position of the biserial heterohelicids above the foraminiferal thermocline is difficult to reconcile with a cool, oxygen minimum habitat.

Conclusions

In summary, boundary conditions for a poorly developed oxygen minimum include low meridional and vertical thermal contrasts, reduced upwelling and circulation vigor, in a moderately warm stable, thermospheric ocean.

Boundary conditions for the strong, widespread oxygen minimum of the later middle Eocene include invigorated upwelling, high vertical and thermal contrasts caused by cooling at the bottom but not at the surface, a ventilated surface and bottom zones separated by a strong oxygen minimum in a maximally stratified situation which provides maximal niche differentiation for planktonic foraminifera.

Boundary conditions for a poorly developed oxygen minimum in a psychrospheric ocean include low meridional and vertical thermal contrasts, reduced equatorial upwelling and atmospheric circulation, decreased current circulation vigor, and a homogeneous mixed layer in which an oxygen minimum develops above the thermocline near the ocean surface, but not at mid depths.

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