

17. CHANGES IN UPPER WATER-COLUMN STRUCTURE AT SITE 925, LATE MIOCENE–PLEISTOCENE: PLANKTONIC FORAMINIFER ASSEMBLAGE AND ISOTOPIC EVIDENCE¹

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ABSTRACT

The relative abundance of all planktonic foraminifer species and the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of three species (*Globigerinoides sacculifer*, a mixed-layer dweller; *Neogloboquadrina dutertrei*, a thermocline dweller; and *Truncorotalia crassaformis*, a deep dweller) was determined in 25 samples at ~250 k.y. intervals through the last 6 m.y. at Ocean Drilling Program Site 925. Combined, the data indicate that mixed-layer depth was a minimum at the end of the early Pliocene (4.0 Ma) and gradually increased toward the Pleistocene.

The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ gradients in the mixed layer and the thermocline were derived by subtracting isotopic values of *Globigerinoides sacculifer* from *Neogloboquadrina dutertrei* and values of *N. dutertrei* from *Truncorotalia crassaformis*. Changes in $\delta^{18}\text{O}$ gradients were used as a proxy record for variation in thermocline strength and position, while changes in $\delta^{13}\text{C}$ gradients served a like purpose for productivity variation.

The early Pliocene was characterized by relatively high numbers of thermocline-dwelling taxa, relatively small mixed-layer $\delta^{18}\text{O}$ gradients, and relatively large $\delta^{13}\text{C}$ gradients. These indicators suggest that downwelling was at a minimum for the last 6 m.y. during this period at Site 925, the temperature difference between *G. sacculifer* and *N. dutertrei* habitats was small, and surface productivity was relatively great. After 2.5 Ma thermocline-dwelling species' numbers were relatively low, mixed-layer $\delta^{18}\text{O}$ gradients were relatively large, and mixed-layer $\delta^{13}\text{C}$ were relatively small. The increased pole-to-equator temperature gradient that accompanied the growth of Northern Hemisphere ice sheets caused the intertropical convergence zone to move toward the equator and exert a growing influence at Site 925 through the last 4 m.y.

INTRODUCTION AND BACKGROUND

Depth Ecology of Planktonic Foraminifers

A striking and useful aspect of planktonic foraminifer ecology is the vertical stratification of population maxima in the water column. The character of planktonic foraminifer assemblages is determined by the thermal structure and nutrient distribution in the upper water column. Depth stratification of species in the water column has been verified by numerous workers with respect to both modern thermal structure and nutrient distribution (e.g., Emiliani, 1954, 1971; Bé, 1960; Lidz et al., 1968; Bé et al., 1971; Shackleton and Vincent, 1978; Williams et al., 1979; Durazzi, 1981; Deuser et al., 1981; Fairbanks and Wiebe, 1980; Fairbanks et al., 1980, 1982; Deuser, 1987; Kroon and Ganssen, 1988; Deuser and Ross, 1989) and paleo-conditions (Shackleton, 1967; Douglas and Savin, 1978; Keller, 1985; Gasperi and Kennett, 1992, 1993; Norris et al., 1993, 1994; Hodell and Vayavananda, 1993). When the thermocline shoals in the photic zone, thermocline-dwelling foraminifers become a relatively larger percentage of the assemblage (Leckie, 1989). Different thermocline-dwelling species favor various levels of productivity (Fairbanks and Wiebe, 1980). The details of depth ecology are far from completely understood. The depth habitat of some species definitely changes during their ontogeny (e.g., Lohmann and Schweitzer, 1990), while the depth ecologies of some extinct species are still undetermined.

Vertical stratification is probably an adaptive strategy for partitioning resources. The partitioning of resources for maximum utilization by the largest possible number of organisms has often been observed in ecological communities (MacArthur et al., 1966; Ricklefs, 1979). The physiological mechanism in planktonic foraminifers that maintains this stratification is not known. However, collections made

in several locations around the world have consistently documented similar relative positions in the water column for several species, and $\delta^{18}\text{O}$ measurements generally corroborate tow-net and sediment-trap observations. A short coming of many of the older studies is that the depth rankings were not made with respect to thermal structure, but rather were made with respect to absolute depth. The absolute depth of a particular species habitat may vary greatly from one location to another depending on position of the seasonal thermocline (mean state or seasonal variation). For example, a species that lives at thermocline depths, such as *Menardella* (= *Globorotalia*) *menardii*, may be listed as a shallow or surface dweller in locations where the thermocline is near the surface and as an "intermediate" dweller in locations where the thermocline is deep. In this study the depth habitats of all species are described with respect to thermal structure.

Many extinct Pliocene species are the immediate ancestors of modern species. Where their ranges overlap in the fossil record, they often show covarying abundances, suggesting similar ecological niche boundaries. Isotopic measurements in some cases confirm that extinct species occupied depth habitats similar to those of closely related modern species (e.g., *Neogloboquadrina acostaensis* and *N. dutertrei* in Keller, 1985). Given these similarities, extant and extinct species have been combined in faunal groups to produce continuous faunal records (Dowsett and Poore, 1990).

Climatic and Oceanographic History

The West Antarctic ice sheet was established in the late Miocene (Shackleton and Kennett, 1975; Ciesielski et al., 1982; Haq, 1984). During the latest Miocene, the Mediterranean was isolated ("the Messinian salinity crisis") by falling sea levels, a consequence of the Antarctic ice volume increase (Shackleton and Kennett, 1975; McKenzie and Oberhänsli, 1985; Hodell et al., 1986). Except for an episode of strong glaciation between 4.6 and 4.3 Ma (Jansen et al., 1993), the period from 5.0 to 3.2 Ma was one of climatic warmth and general stability in the size of Antarctic ice sheets (Shackleton and Opdyke, 1977; Keigwin, 1979, 1982; Jansen et al., 1993). High-lati-

¹Shackleton, N.J., Curry, W.B., Richter, C., and Bralower, T.J. (Eds.), 1997. *Proc. ODP, Sci. Results*, 154: College Station, TX (Ocean Drilling Program).

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tude surface water seems to have warmed, while low-latitude water seems to have become relatively cool through this interval (Kennett and von der Borch, 1986). It was while the globe was in this climatic state that the tectonic uplift made the Isthmus of Panama subaerial, cutting off the low-latitude interoceanic connection between the Pacific and Atlantic basins (Berggren and Hollister, 1977; Thunell and Belyea, 1982). The final closing of the Central American seaway may have taken place in the mid-Pliocene (Kaneps, 1979; Keigwin, 1978, 1982; Duque-Caro, 1990), but Coates et al. (1992), using near-shore marine records, have placed the final closing at 3.8–3.7 Ma, which is older than the 3.4–3.2 Ma estimate given by Keigwin (1978, 1982) based on pelagic records. Farrell et al. (1995) estimated, on the basis of carbonate records from several (Leg 138) sites in the eastern equatorial Pacific, that the seaway may have been effectively closed as early as 4.5 Ma.

The intensification of Northern Hemisphere cooling seems to have followed the closing of the seaway. Shackleton and Opdyke (1977) ascribed a large positive shift in the oxygen isotopic record on the Ontong Java Plateau at 3.2 Ma to the beginning of ice-sheet growth in the Northern Hemisphere, which agreed with an initial 3.0-Ma age estimate for the first appearance of ice-rafted debris in North Atlantic sediments (Berggren, 1972; Poore, 1981). Re-evaluation of biostratigraphy at Deep Sea Drilling Project (DSDP) Sites 111 and 116 caused Backman (1979; Shackleton et al., 1984) to date the first appearance of ice-rafted debris in North Atlantic sediments at about 2.5 Ma. However, $\delta^{18}\text{O}$ data from Site 806 in the western equatorial Pacific (Jansen et al., 1993) suggest that ice sheet growth was not a steady expansion from the 3.2 Ma enrichment, but rather a more complex enrichment pattern beginning after 3.7 Ma.

Other studies of North Atlantic records suggest that the interval from 3.1 to 2.45 Ma showed a trend toward progressively cooler sea-surface temperatures with increasing amplitude changes (Dowsett and Poore, 1990), and that cold episodes after 2.95 Ma began to be colder than the modern climate, but the warm intervals were also still significantly warmer (Raymo et al., 1992). After 2.5 Ma, a permanent enrichment of oxygen isotope values in North Atlantic DSDP cores marked what is probably the beginning of Northern Hemisphere glaciation (Thunell and Williams, 1983; Raymo et al., 1989). In this paper we will interpret changes in tropical planktonic foraminifer assemblages at Ocean Drilling Program (ODP) Site 925 as responses to changes in the position of the thermocline in the photic zone and consequent changes in the productivity of the upper water column from the late Miocene to the Pleistocene.

METHODOLOGY

This paper examines faunal and isotopic data at Site 925 in the western tropical Atlantic (Fig. 1) with a sampling interval of about 250 k.y. (Table 1). Absolute ages are assigned to samples using the astrochronologically tuned age models of Tiedemann and Franz (this volume), Bickert et al. (Chapter 16, this volume), and Shackleton and Crowhurst (this volume). Planktonic foraminifers are counted in 25 samples. Stable isotopes for *Globigerinoides sacculifer*, *Neoglobobulimina dutertrei* and *Truncorotalia crassaformis* are measured in the same samples. The difference between the $\delta^{18}\text{O}$ values of *G. sacculifer* and *N. dutertrei* (mixed-layer [ML] $\Delta\delta^{18}\text{O}$) are taken to represent the temperature difference between the surface and the ther-

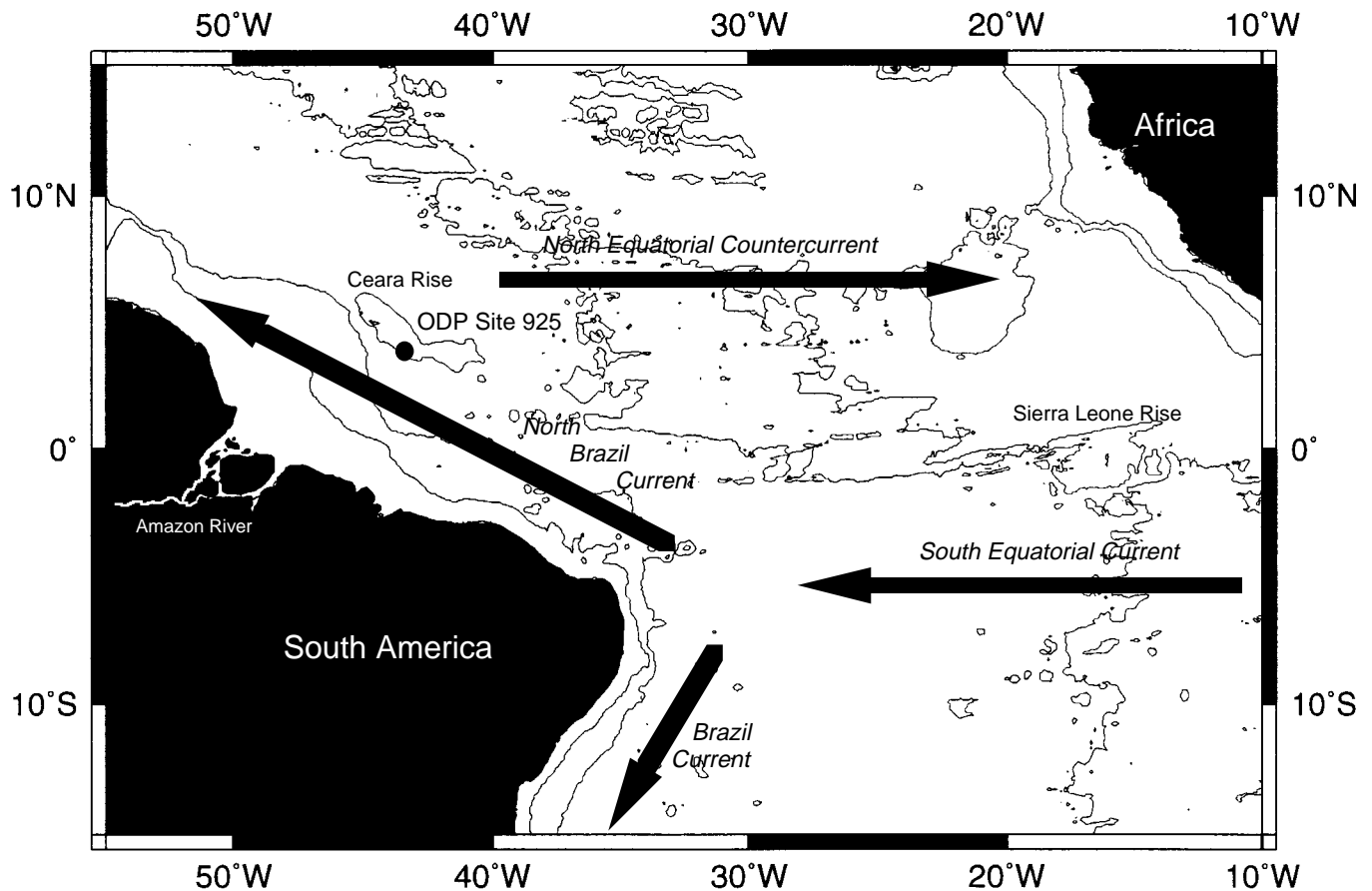


Figure 1. Location of Site 925 in the western tropical Atlantic.

Table 1. Sample depths and ages at Site 925.

Core, section, interval (cm)	Depth (mbsf)	Tuned age (Ma)
154-925-		
1H-1, 65-67	0.65	0.01
2H-3, 65-67	8.15	0.22
3H-2, 65-67	16.15	0.47
4H-1, 65-67	24.15	0.75
4H-6, 65-67	31.65	1.01
5H-5, 65-67	39.65	1.30
6H-3, 55-57	46.05	1.52
7H-2, 65-67	54.15	1.80
7H-6, 65-67	60.18	2.00
8H-5, 65-67	68.15	2.24
9H-3, 65-67	74.65	2.49
10H-2, 65-67	82.65	2.77
10H-6, 65-67	88.65	3.07
11H-5, 65-67	96.65	3.25
12H-3, 65-67	103.15	3.49
13H-1, 66-68	109.66	3.78
13H-5, 73-75	115.73	3.97
14H-3, 65-67	122.15	4.19
14H-7, 10-12	127.60	4.36
15H-5, 65-67	134.65	4.71
16H-3, 65-67	141.15	4.99
17H-1, 65-67	147.65	5.31
17H-5, 65-67	153.65	5.57
18H-3, 66-68	160.16	5.92
19H-1, 65-67	166.65	6.14

Note: Tuned ages are derived from astrochronologic age models produced by Bickert et al. (Chapter 16, this volume), Tiedemann and Franz (this volume), and Shackleton and Crowhurst (this volume).

moocline, and the difference between *N. dutertrei* and *T. crassaformis* (thermocline [TH] $\Delta\delta^{18}\text{O}$) represent the temperature difference between the (seasonal) thermocline and sub-thermocline waters. These values are compared with changes in the faunal data in an attempt to locate the position of the thermocline relative to the photic zone. The timing of changes in the conjectured position of the thermocline through the last 6 m.y. is considered as a possible response to climatic and oceanographic events set in motion by the closing of the Central American seaway and the onset of large-scale Northern Hemisphere glaciation.

Sample Preparation

Samples of 10 cm³ were collected shipboard at set intervals (one per core). Sample material was soaked in a neutral solution of water, Calgon, and hydrogen peroxide until it disaggregated. Sediment that did not disaggregate readily was agitated on a shaking table and/or placed on a hot plate equipped with a rotating magnet. Disaggregated sediment was wet sieved through a 63- μm screen. The >63- μm fraction was dried either in an oven or on a hot plate (<100°C).

Six to 10 specimens of each species were picked from the 355–425- μm fraction of each sample. Stable isotope measurements were made using a phosphoric acid bath at 90°C on a VG OPTIMA gas ratio mass spectrometer with an automated Isocarb carbonate reaction device attached. Precision of measurements is 0.05‰ for carbon and 0.08‰ for oxygen based on replicate standards. The values are reported relative to the Pee Dee belemnite (PDB) standard, and calibrations to PDB have been done using National Institute of Standard and Technology (NSB) 19 and the University of California, Santa Cruz in-house standards.

Reconstruction of Water-column Structure

Oxygen and carbon isotope ratios were measured for three planktonic species at ~250-k.y. intervals through the last 6 m.y. At least three species were needed to characterize the structure of the upper water column: a mixed layer-, a thermocline-, and a deep-dwelling

species to record the stable isotope values above, within and below the thermocline. Ravelo and Fairbanks (1992) introduced this strategy, using *Globigerinoides sacculifer*, *Neogloboquadrina dutertrei*, and *Globorotalia tumida* from core-top sediments to describe surface-water hydrography across the tropical Atlantic. They found that the range of $\delta^{18}\text{O}$ values recorded in foraminiferal calcite was proportional to the observed temperature differences between the surface and the bottom of the photic zone at three sites with different hydrographic regimes (Ravelo and Fairbanks, 1992).

It is generally accepted that the oxygen isotopes of *Globigerinoides sacculifer* record conditions in the surface mixed layer (e.g., Shackleton and Vincent, 1978). Ecologic studies of modern *G. sacculifer* suggest that it does not spend its entire life cycle in the mixed layer, but may enter the upper thermocline to reproduce (Berger, 1971; Hemleben et al., 1989). Lohmann (1995) has shown that interpretation of the isotopic signal of some specimens of *G. sacculifer* may be complex due to the accretion of gametogenic calcite and partial dissolution of primary calcite. Isotopic analyses in this study were performed only on non-saccate specimens of *G. sacculifer*. *G. sacculifer* was present in all 25 samples examined.

The oxygen isotopic record of *Neogloboquadrina dutertrei* represents conditions in the thermocline (Curry and Matthews, 1981). Tow-netting (Jones, 1967; Fairbanks and Wiebe, 1980; Fairbanks et al., 1982) and sediment-trap work (Thunell et al., 1983; Curry et al., 1983; Thunell and Reynolds, 1984) have revealed that this species is closely associated with the nutricline, which is found in the upper part of the thermocline where the rapid change in water density slows the sinking rate phytoplankton creating a maximum concentration (Fairbanks and Wiebe, 1980). Ravelo and Fairbanks (1992) suggested that *N. dutertrei* calcifies at the same temperature on opposite sides of the tropical Atlantic, apparently remaining near the thermocline regardless of its depth. Curry and Matthews (1981) examined core-top material in the Indian Ocean and found that *N. dutertrei* calcifies at approximately 20°C through a wide range of depths. There are also data to support the assumption of the isothermy of *N. dutertrei* depth habitat in the Pleistocene (Ravelo and Fairbanks, 1992), but in the Pliocene there is no data at present. The above studies were done in the low latitudes, and in higher latitudes *N. dutertrei* is found in water cooler than 20°C (Bé, 1977). The 20°C value is here regarded as a tropical asymptote; *N. dutertrei* was assumed not to calcify in warmer water. *N. dutertrei* was present in 21 out of 25 samples examined. Specimens of sufficient size were not found at 4.71, 5.57, 5.92, and 6.14 Ma.

The deep-dwelling foraminifer most frequently present at Site 925 was *Truncorotalia crassaformis*. It appeared in 15 out of 25 samples in two stratigraphically disjunct and isotopically different ranges. Modern thermocline depth in the Ceara Rise region is 100–150 m below sea surface (Molinari and Johns, 1994). This hydrographic condition prevents a large supply of nutrients from reaching the photic zone, where they can be absorbed into the pelagic food web by phytoplankton. Consequently the 'rain' of organic matter to the zone below the thermocline at Site 925 has probably been very light through some of the last 6 m.y. and has sustained only low numbers of planktonic foraminifers adapted to a habit at the bottom of the thermocline.

The oxygen isotope signal includes both global ice volume and local temperature components. All species experience the ice-volume effect equally because the ratio of ^{18}O to ^{16}O changes universally at time scales greater than the mixing time of the world ocean (500–600 yr). However, each species records the temperature of its immediate environment uniquely. Therefore, if one species' isotope value is subtracted from another, then the difference will be equivalent to the temperature difference of their respective records (Berger et al., 1978), assuming that the ice-volume components of the isotope signal are equal.

“Difference curves” were calculated and presented as proxies for the temperature differences between the depths of calcification for three species. The equation

$$ML \Delta\delta^{18}O = N. dutertrei \delta^{18}O - G. sacculifer \delta^{18}O$$

represents the temperature range between the sea surface and the thermocline ($ML \Delta\delta^{18}O$). The equation

$$TH \Delta\delta^{18}O = T. crassaformis \delta^{18}O - N. dutertrei \delta^{18}O$$

represents the temperature range from the thermocline into the water below it ($TH \Delta\delta^{18}O$).

It is the rate of temperature change in the upper water column (i.e., the character of the thermocline) that serves as the organizing parameter for populations of planktonic foraminifer species (Fairbanks and Wiebe, 1980; Ravelo et al., 1990; Ravelo and Fairbanks, 1992). If we inspect depth rankings of planktonic foraminifers from different locations in the modern ocean, they are generally similar in order, but the $\delta^{18}O$ values that bracket the limits of each species' depth range vary widely (e.g., compare Shackleton and Vincent, 1978 and Deuser, 1987). The $\delta^{18}O$ values in a given sample correspond to relative water temperature, but the depth ranking order of the assemblage is determined by the structure of the upper water column with only secondary regard for temperature (Ravelo and Fairbanks, 1992).

Basic to the interpretation of carbon isotope records is the assumption that lower $\delta^{13}C_{\text{carbonate}}$ values represent more nutrient-rich conditions. Organisms (and organic matter) are enriched in ^{12}C due to fractionation by metabolic processes. Oxidation of organic matter by actively feeding organisms and by heterotrophic bacteria releases ^{12}C back into the environment (Berger et al., 1978). $ML \Delta\delta^{13}C$ describes the gradient of $\delta^{13}C$ value in the mixed layer. Steep $\delta^{13}C$ gradients indicate strong stratification between *G. sacculifer* and *N. dutertrei* habitats. $TH \Delta\delta^{13}C$ describes the $\delta^{13}C$ gradient between *N. dutertrei* and *T. crassaformis* habitats.

In this study the influence of salinity on isotopic values is assumed to be minor, although it is conceivable that the southward migration of the intertropical convergence zone (ITCZ) and its attendant rain could lower the oxygen isotopic values of *G. sacculifer* at Site 925.

For the faunal counts the >150- μm fraction was separated from the dried sample with a dry sieve. This fraction was divided with an Otto microsplitter until there was an amount small enough to evenly cover a picking tray. The picking tray was scored to divide its surface into quadrates. All specimens in a given quadrate were identified to species and removed to a gummed archive slide. To assure an unbiased collection of specimens, quadrates were cleared in a random pattern across the tray until >300 specimens had been counted (Imbrie and Kipp, 1971).

Low-resolution data do not preserve the high-frequency variation that is inherent in both the faunal and isotopic records. An estimate of variance is made for all the Site 925 data presented by using high-resolution data sets from other tropical sites. Although the variance around the observed value is probably not normally distributed, a standard deviation was calculated, and an error of two standard deviations is included in Figures 2–7. This technique smooths the data and preserves only the larger trends. Obviously it is optimal to have an estimate of variability based on data from the same site, but failing that it is better to use the variability observed at other sites, rather than have no estimate of error at all.

The taxonomy of Kennett and Srinivasan (1983) is largely followed in this study with modifications noted in Chaisson and Leckie (1993) and Chaisson and Pearson (this volume).

RESULTS

Isotopic Records

Globigerinoides sacculifer $\delta^{18}O$ values at Site 925 do not change significantly between 6.14 and 2.49 Ma (Fig. 2; Table 2). The average value is -1.59‰ through this interval. After 2.49 Ma the average value of *G. sacculifer* $\delta^{18}O$ (-0.82‰) is higher. *Neogloboquadrina dutertrei* $\delta^{18}O$ record follows a pattern similar to that of *G. sacculifer* (Fig. 2; Table 2), but the values are slightly higher, averaging -1.00‰ between 5.31 and 2.49 Ma, and increasing to -0.02‰ after 2.49 Ma.

Unlike *G. sacculifer* and *N. dutertrei*, *Truncorotalia crassaformis* $\delta^{18}O$ decreases through the Pliocene portion of its range (Fig. 2; Table 2). The average value of *T. crassaformis* $\delta^{18}O$ in the early to late Pliocene (3.97–2.24 Ma) is 0.46‰ , but in the late Pliocene to Pleistocene (2.35–1.91 Ma) the average value increases to 2.29‰ . A similar large increase in the value of all truncorotaliids is observed in the late Pliocene of the southwest Pacific (Spencer-Cervato, pers. comm., 1995).

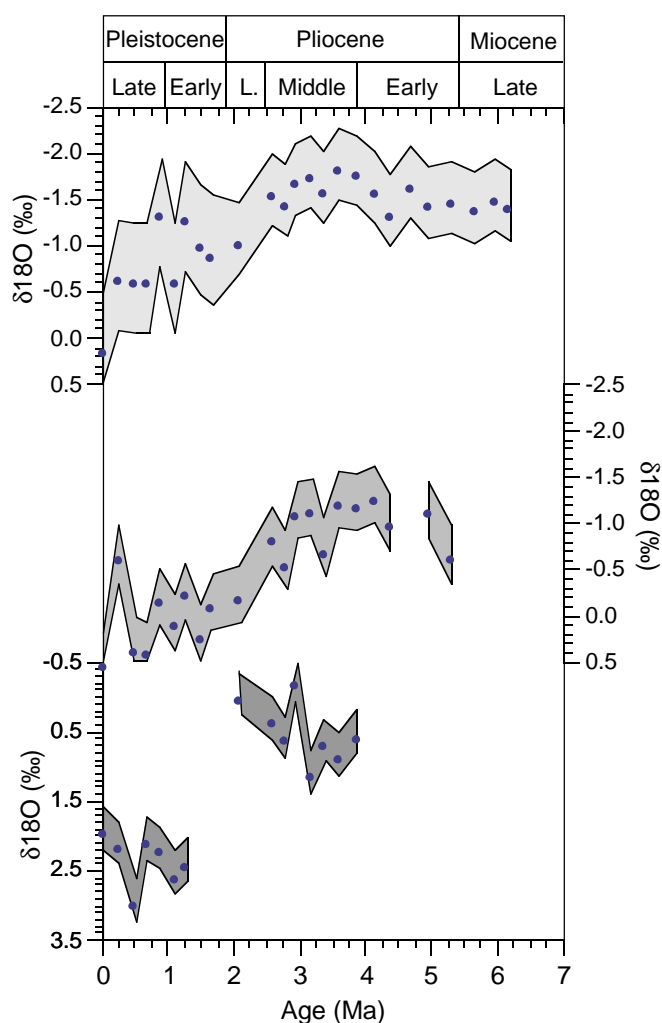


Figure 2. Oxygen isotope curves for *Globigerinoides sacculifer* (upper, light gray), *Neogloboquadrina dutertrei* (middle, medium gray), and *Truncorotalia crassaformis* (lower, dark gray). Gray areas around points are an estimate of variability derived from high resolution data provided by Jansen et al. (1993) and Billups et al. (this volume).

Table 2. Oxygen isotope values.

Age (Ma)	sac	dut	cra	ML	TH
0.01	0.11	0.51	1.91	0.40	1.80
0.22	-0.67	-0.66	2.12	0.01	2.79
0.47	-0.64	0.33	2.92	0.97	3.57
0.75	-0.64	0.37	2.04	1.01	2.69
1.01	-1.36	-0.20	2.17	1.16	3.52
1.30	-0.65	0.06	2.54	0.71	3.20
1.52	-1.31	-0.27	2.35	1.04	3.66
1.80	-1.05	0.20		1.25	
2.00	-0.94	-0.14		0.79	
2.24	-1.07	-0.22	-0.03	0.84	1.04
2.49	-1.59	-0.84	0.32	0.75	1.91
2.77	-1.47	-0.59	0.57	0.88	2.05
3.07	-1.72	-1.14	-0.23	0.58	1.49
3.25	-1.78	-1.15	1.07	0.63	2.86
3.49	-1.62	-0.73	0.63	0.89	2.25
3.78	-1.87	-1.25	0.83	0.62	2.70
3.97	-1.81	-1.23	0.52	0.58	2.32
4.19	-1.62	-1.31		0.31	
4.36	-1.37	-1.01		0.36	
4.71	-1.68				
4.99	-1.48	-1.15		0.33	
5.31	-1.51	-0.67		0.85	
5.57	-1.42				
5.92	-1.54				
6.14	-1.44				

Notes: sac = *Globigerinoides sacculifer*; dut = *Neogloboquadrina dutertrei*; cra = *Truncorotalia crassaformis*; ML = [*N. dutertrei* - *Gs. sacculifer*]; TH = [*Gr. crassaformis* - *N. dutertrei*].

G. sacculifer $\delta^{13}\text{C}$ values at Site 925 decline from 2.97‰ at 6.2 Ma to 1.76‰ at 2.24 Ma (Fig. 3; Table 3). *G. sacculifer* and *N. dutertrei* $\delta^{13}\text{C}$ values converge slightly between 5.31 and 3.07 Ma (Fig. 3; Table 3). After a transitional period between 3.07 and 2.00 Ma, they converge very closely.

Compared with its $\delta^{18}\text{O}$ values, the *T. crassaformis* $\delta^{13}\text{C}$ record changes very little at Site 925 (Figs. 2, 3). In the Pliocene it generally parallels the *N. dutertrei* $\delta^{13}\text{C}$ record, and in the Pleistocene it follows the oscillations in *G. sacculifer* and *N. dutertrei* $\delta^{13}\text{C}$ values up to 0.47 Ma, whereafter it diverges toward more negative values. Overall the $\delta^{13}\text{C}$ record of *T. crassaformis* shows a slight negative drift, less pronounced than that of *G. sacculifer*, and opposite that of *N. dutertrei*.

The difference between *N. dutertrei* and *G. sacculifer* $\delta^{18}\text{O}$ ($\Delta\delta^{18}\text{O}$) is 0.4‰ at 4.99 Ma and increases gradually until 1.80 Ma (Fig. 4A; Table 2). From 1.80 Ma to the latest Pleistocene the difference generally decreases with one reversal of the trend between 1.30 Ma and 1.01 Ma.

ML $\Delta\delta^{13}\text{C}$ changes little between 3.97 and 3.49 Ma (Fig. 4B; Table 3) and has an average value of 1.42‰. Values generally decline after 3.49 Ma, but seem to stabilize again after 2.00 Ma. The average value from the latest Pliocene through the Pleistocene is 0.45‰. The ML $\Delta\delta^{13}\text{C}$ record is nearly a mirror image of the ML $\Delta\delta^{18}\text{O}$ record.

The most prominent attribute of the TH $\Delta\delta^{18}\text{O}$ curve is the very large positive shift recorded across the Pliocene/Pleistocene boundary, where it is unfortunately broken by the absence of *T. crassaformis* at 2.00 and 1.80 Ma (Fig. 4C). While *N. dutertrei* $\delta^{18}\text{O}$ values increase through this interval, the greater part of TH $\Delta\delta^{18}\text{O}$ change is due to the large Pleistocene increase in *T. crassaformis* $\delta^{18}\text{O}$ values.

TH $\Delta\delta^{13}\text{C}$ has a trend toward increasing values after 3.07 Ma (Fig. 4D). The coarseness and discontinuity of the record make further interpretation difficult.

Faunal Abundance Records

To compare the faunal record with the isotopic record at Site 925 and to make an estimate of the faunal response to hydrography in the Ceara Rise region through the last 6 m.y., counts of individual species

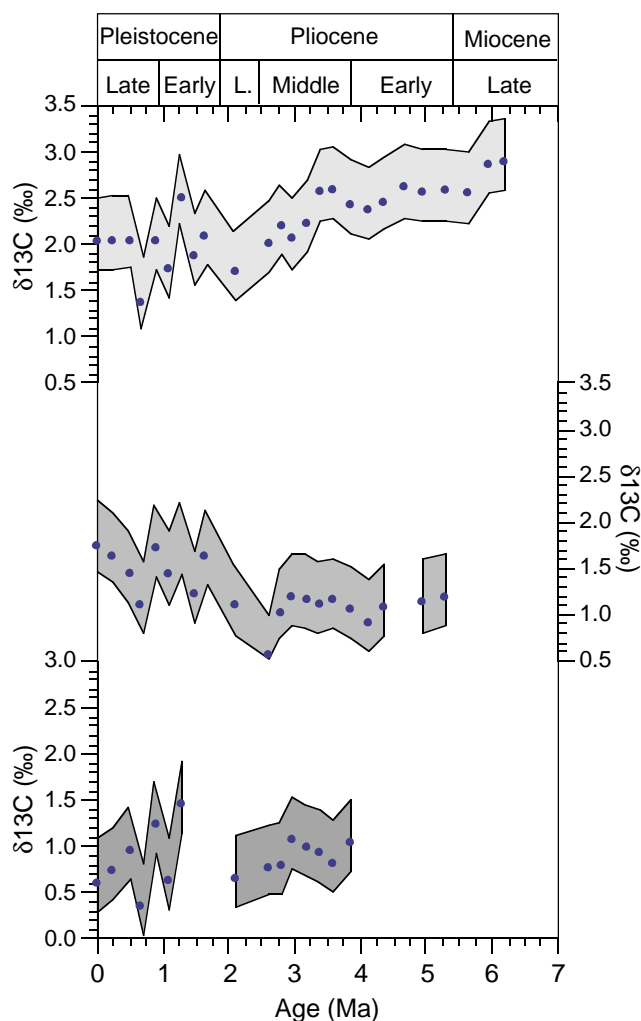


Figure 3. Carbon isotope curves for *Globigerinoides sacculifer* (upper, light gray), *Neogloboquadrina dutertrei* (middle, medium gray), *Truncorotalia crassaformis* (lower, dark gray). Gray areas around points are an estimate of variability derived from high resolution data in Billups et al. (this volume).

are combined into faunal groups (*sensu* “counting categories” of Dowsett and Poore, 1990). Percentage data for individual species is in Appendix A. Many of the extant planktonic foraminifer species have been present in the tropical oceans throughout the last 6 m.y., but there were several extinctions and first appearances in the mid-Pliocene (Wei and Kennett, 1986). The groups assembled in this paper (Table 4) are after Dowsett and Poore (1990), who established covariance between the quantitative biostratigraphies of some Pliocene species and their modern descendants, and based on the phylogenetic relationships presented by Kennett and Srinivasan (1983).

Stratigraphic Groups

In addition to using ecological criteria to subdivide the planktonic foraminifers, the sediment assemblage is partitioned according to the stratigraphic range of each species. Taxa are classified as “Miocene–Pliocene” if their first appearance is before 7 Ma and they become extinct before the Holocene. That is, most of their stratigraphic range is in the Miocene or earlier. Taxa are considered “Pliocene–Pleis-

Table 3. Carbon isotope values.

Age (Ma)	sac	dut	cra	ML	TH
0.01	2.10	1.82	0.67	-0.28	-1.15
0.22	2.11	1.71	0.80	-0.40	-0.91
0.47	2.11	1.51	1.03	-0.61	-0.48
0.75	1.45	1.17	0.41	-0.28	-0.76
1.01	2.09	1.77	1.30	-0.32	-0.47
1.30	1.79	1.50	0.70	-0.29	-0.80
1.52	2.58	1.82	1.52	-0.77	-0.30
1.80	1.93	1.30		-0.64	
2.00	2.16	1.71		-0.45	
2.24	1.76	1.16	0.71	-0.60	-0.45
2.49	2.09	0.61	0.83	-1.48	0.22
2.77	2.26	1.10	0.85	-1.16	-0.25
3.07	2.12	1.26	1.13	-0.86	-0.13
3.25	2.30	1.24	1.06	-1.06	-0.19
3.49	2.62	1.17	1.00	-1.45	-0.17
3.78	2.66	1.22	0.90	-1.44	-0.32
3.97	2.50	1.12	1.11	-1.38	-0.02
4.19	2.44	0.98		-1.47	
4.36	2.53	1.15		-1.38	
4.71	2.67				
4.99	2.62	1.20		-1.42	
5.31	2.65	1.26		-1.40	
5.57	2.62				
5.92	2.94				
6.14	2.97				

Notes: sac = *Globigerinoides sacculifer*; dut = *Neogloboquadrina dutertrei*; cra = *Truncorotalia crassaformis*; ML = [*N. dutertrei* - *Gs. sacculifer*]; TH = [*Gr. crassaformis* - *N. dutertrei*].

toecene" if they appear after 7 Ma, but do not survive into the modern ocean. Taxa are called "extant" if they exist in the modern ocean, regardless of the time of their first appearance. See Table 5 for a species list.

Miocene–Pliocene taxa account for fully half of the assemblage from the bottom of the section to the middle Pliocene, declining slightly from nearly 60% at 4.71 Ma to 50% at 3.78 Ma (Fig. 4A; Table 6). At 2.61 and 2.49 Ma the Pliocene fraction expands to maintain the Neogene component of the fauna (= Miocene–Pliocene + Pliocene–Pleistocene components) at ~45%, but both groups decline drastically between 2.49 and 2.24 Ma to only 10% of the assemblage. The expansion of the Pliocene–Pleistocene portion of the assemblage at 2.77 and 2.49 Ma is due to large numbers (11% and 13%, respectively) of *Globorotalia miocenica* in those two samples. The slight recovery of the Miocene–Pliocene fraction at 2.49 Ma is due largely to the Neogene globoturborotalitids (27%) and *Globigerinoides obliquus* at 2.49 Ma (23%).

Mixed-layer Dwellers

The dominant faunal elements of the mixed-layer dwellers include the *Globigerinoides sacculifer* group, *Globigerinoides ruber* group and *Globigerinina glutinata*. *Dentoglobigerina altispira* is significant during the early to middle Pliocene and *Globoturborotalita rubescens* is significant in the Pleistocene (Figs. 5, 6). From 5.31 to 3.07 Ma, mixed-layer dwellers make up about 60% of the planktonic foraminifer fauna. After 2.77 Ma, the abundance of this group increases through the late Pliocene to constitute nearly 80% of the assemblage through much of the Pleistocene.

The *Globigerinoides ruber* group constitutes >30% of the assemblage at 5.92 Ma and declines to a low of 15% at 4.71 Ma (Fig. 6C; Table 6). It increases steadily from 4.71 Ma to a high at 1.80 Ma, when it constitutes 50% of the planktonic foraminifer fauna. A steep decline to 10% at 0.75 Ma is followed by a recovery to >40% at the top of the section.

The abundance of the *Globigerinoides sacculifer* group increases sharply between 6.14 and 5.57 Ma and then declines throughout the early and middle Pliocene, reaching a low at 2.49 Ma (Fig. 5D; Table 6). Two samples in the late Pliocene (2.00 Ma) and early Pleistocene (1.80 Ma) have large numbers of the *Globigerinoides sacculifer*

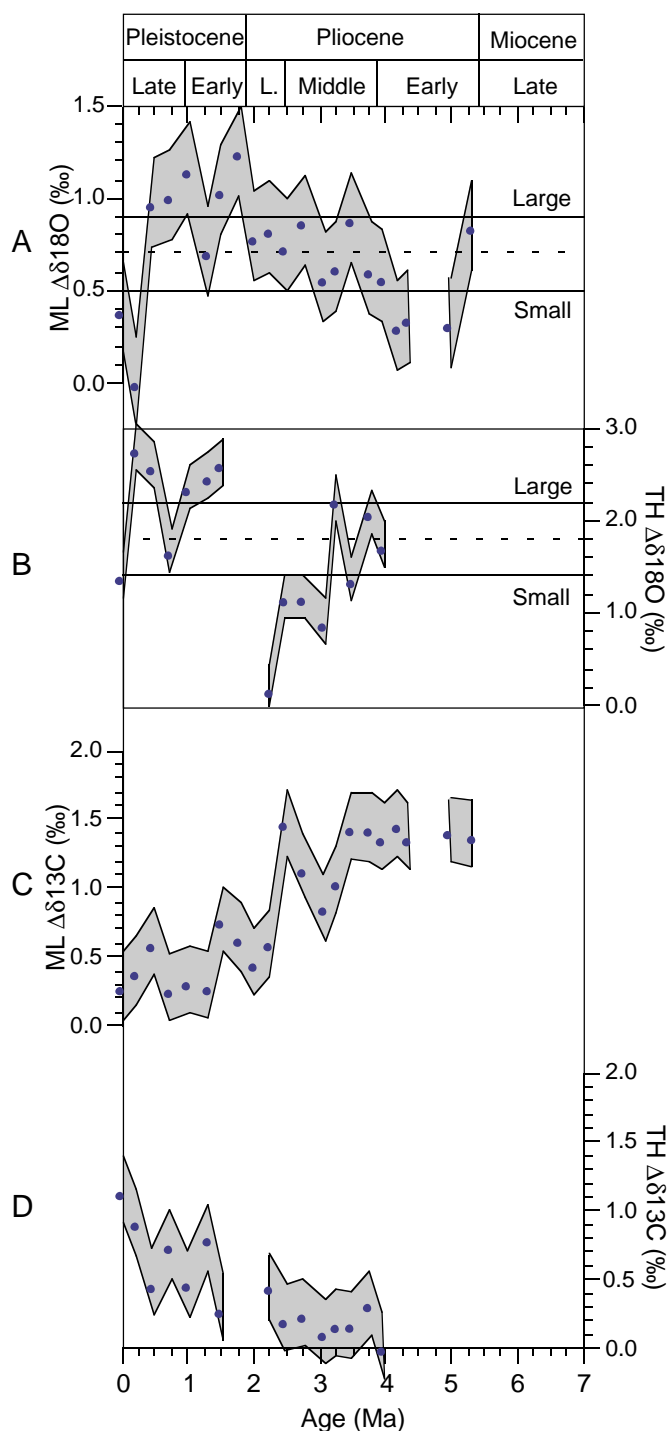


Figure 4. Oxygen and carbon isotope "difference" curves. A. *Neogloboquadrina dutertrei* $\delta^{18}\text{O}$ - *Globigerinoides sacculifer* $\delta^{18}\text{O}$. B. *Truncorotalia crassaformis* $\delta^{18}\text{O}$ - *Neogloboquadrina dutertrei* $\delta^{18}\text{O}$. C. *N. dutertrei* $\delta^{13}\text{C}$ - *G. sacculifer* $\delta^{13}\text{C}$. D. *T. crassaformis* $\delta^{13}\text{C}$ - *N. dutertrei* $\delta^{13}\text{C}$. Gray areas represent two standard deviations around data points, and are based on high resolution data provided by Jansen et al. (1993) and Billups et al. (this volume).

Table 4. Species in faunal groups.

Mixed layer	Thermocline
<i>Globigerinoides ruber</i> group	Pulleniatinids
<i>Globigerinoides ruber</i>	<i>Pulleniatina obliquiloculata</i>
<i>Globigerinoides obliquus</i>	<i>Pulleniatina primalis</i>
<i>Globigerinoides extremus</i>	
<i>Globigerinoides sacculifer</i> group	Thermocline globorotaliids
<i>Globigerinoides sacculifer</i>	<i>Menardella limbata</i>
<i>Globigerinoides trilobus</i>	<i>Menardella menardii</i>
<i>Globigerinoides quadrilobatus</i>	<i>Menardella miocenica</i>
<i>Globigerinoides fistulosus</i>	<i>Menardella multicamerata</i>
<i>Orbulina universa</i>	<i>Menardella pertenuis</i>
	<i>Hirsutella cibaoensis</i>
Surface phytoplanktivore group	<i>Hirsutella juanai</i>
<i>Globoturborotalita rubescens</i>	<i>Hirsutella margaritae</i>
<i>Globigerinita glutinata</i>	<i>Globoconella inflata</i>
<i>Dentoglobigerina altispira</i>	<i>Globoconella triangula</i>
	<i>Globorotalia plesiotumida</i>
	<i>Globorotalia merotumida</i>
	<i>Globorotalia tumida</i>
	Neogene globoturborotalitids
	<i>Globoturborotalita woodi</i>
	<i>Globoturborotalita apertura</i>
	<i>Globoturborotalita nepenthes</i>
	<i>Globoturborotalita decoraperta</i>
	Tropical neogloboquadrinids
	<i>Neogloboquadrina dutertrei</i>
	<i>Neogloboquadrina humerosa</i>
	<i>Neogloboquadrina acostaensis</i>

Table 5. Species in stratigraphic groups.

Miocene–Pliocene taxa	Pliocene–Pleistocene taxa
Mixed-layer dwellers	Mixed-layer dwellers
<i>Globigerinoides obliquus</i>	<i>Globigerinoides fistulosus</i>
<i>Globigerinoides extremus</i>	<i>Beella praedigitata</i>
<i>Globoquadrina baromoensis</i>	
<i>Dentoglobigerina altispira</i>	
Thermocline dwellers	Thermocline dwellers
<i>Globoturborotalita nepenthes</i>	<i>Menardella miocenica</i>
<i>Globoturborotalita decoraperta</i>	<i>Menardella multicamerata</i>
<i>Globoturborotalita apertura</i>	<i>Hirsutella margaritae</i>
<i>Globoturborotalita woodi</i>	<i>Globoconella triangula</i>
<i>Menardella limbata</i>	<i>Neogloboquadrina humerosa</i>
<i>Hirsutella cibaoensis</i>	<i>Pulleniatina primalis</i>
<i>Hirsutella juanai</i>	
<i>Globorotalia plesiotumida</i>	
<i>Globorotalia merotumida</i>	
<i>Neogloboquadrina acostaensis</i>	
<i>Sphaeroidinellopsis seminulina</i>	
<i>Sphaeroidinellopsis paenadehiscens</i>	
<i>Sphaeroidinellopsis kochi</i>	
<i>Globigerinella obesa</i>	
Deep dwellers	Deep dwellers
<i>Globoquadrina venezuelana</i> *	<i>Truncorotalia tosaensis</i>
	Extant taxa
Mixed-layer dwellers	Thermocline dwellers
<i>Globigerina falconensis</i>	<i>Globigerinoides conglobatus</i>
<i>Globigerina bulloides</i>	<i>Menardella menardii</i>
<i>Globoturborotalita rubescens</i>	<i>Hirsutella scitula</i>
<i>Globoturborotalita tenulla</i>	<i>Globoconella inflata</i>
<i>Globigerinoides sacculifer</i>	<i>Globorotalia tumida</i>
<i>Globigerinoides ruber</i>	<i>Neogloboquadrina pachyderma</i>
<i>Orbulina universa</i>	<i>Neogloboquadrina dutertrei</i>
<i>Globorotalia unguolata</i>	<i>Pulleniatina obliquiloculata</i>
<i>Turborotalita quinqueloba</i>	<i>Sphaeroidinella dehiscens</i>
<i>Turborotalita humilis</i>	<i>Globigerinella calida</i>
<i>Beella digitata</i>	<i>Candeina nitida</i>
<i>Globigerinita glutinata</i>	
<i>Globigerinella aequilateralis</i>	Deep dwellers
	<i>Truncorotalia crassaformis</i>
	<i>Truncorotalia truncatulinoides</i>
	<i>Globorotaloides hexagona</i>
	<i>Tenuitella</i>

Notes: *Gasperi and Kennett (1992, 1993) suggest that this species may have become a mixed-layer dweller in the late Miocene. This depth ecology may have been maintained into the Pliocene.

group, but the remainder of the Pleistocene numbers return to early to middle Pliocene levels.

Globigerinita glutinata is a small, non-spinose foraminifer with a micro-perforate test. Although it lives in the mixed layer, it is largely a phytoplanktivore (Hemleben et al., 1989), while the *Globigerinoides* are omnivores, including varying amounts of zooplankton in their diet (Bé et al., 1977; Hemleben and Spindler, 1983; Spindler et al., 1984; Hemleben et al., 1989). The peaks in its record do not correspond to those of the *Globigerinoides* (Figs. 6A, 5C, 5D).

From a low of <5% at the bottom of the section, *G. glutinata* increases to reach peaks (>15%) at 2.49 Ma and at 3.97 Ma (Fig. 6A; Table 6). This trend is opposite that of the *Globigerinoides sacculifer* group and similar to that of the *Globigerinoides ruber* group, but *G. glutinata* reaches a maximum earlier and declines abruptly to <10% of the assemblage between 2.49 and 1.52 Ma, a period during which both *Globigerinoides* groups are plentiful. Similarly, it reaches a high of >20% at 1.01 and 0.75 Ma, while the *Globigerinoides* groups are declining.

Globoturborotalita rubescens abundance peaks (~25%) at 0.75 Ma, concordant with *Globigerinita glutinata* (Figs. 6A, 6B) and opposite the *Globigerinoides* groups (Figs. 6B, 5C, 5D). It decreases to 5% of the assemblage in the top two samples of the section during the recovery of the *Globigerinoides* groups.

Dentoglobigerina altispira disappeared globally at ~3 Ma and it declines abruptly to virtual extinction at Site 925 after reaching a maximum of 20% of the assemblage at 3.78 Ma (Fig. 6C), an interval of low abundance for the *Globigerinoides* groups and a peak for *Globigerinita glutinata*. Thus two separate factions in the mixed layer group are apparent: the *Globigerinoides* and a group that includes *Globigerinita glutinata* and *Globoturborotalita rubescens* in the Pleistocene and *G. glutinata* and *Dentoglobigerina altispira* in the Pliocene. *Dentoglobigerina* is a genus with no modern descendants. Single specimens found in samples younger than 3.07 Ma at Site 925 are contaminants.

Thermocline Dwellers

Thermocline-dwelling foraminifers are most numerous in the early Pliocene (Fig. 7A; Table 6). They gradually decline in abundance from 4.71 Ma to latest Pleistocene, interrupted by brief recoveries to early Pliocene levels at 2.77 and 0.47 Ma. The decline from 2.77 to 1.52 Ma is the most precipitous (~50% to ~10%). The coarse temporal resolution of this study likely misses other brief increases in thermocline-dwelling taxa in response to Pleistocene climatic fluctuations.

The tropical neogloboquadrinids include *Neogloboquadrina dutertrei*, *N. humerosa* and *N. acostaensis*. *N. acostaensis* is present in only two samples in the lower Pliocene at Site 925 and never exceeds 1% of the assemblage. The neogloboquadrinid group often (15 samples) accounts for >10%, but rarely (five samples) accounts for >15% of the assemblage (Fig. 7B; Table 6). At ~4.0 Ma, *N. humerosa* reaches 7% (its maximum) and *N. dutertrei* 12% of the assemblage, the maximum share for this group at Site 925. Tropical neogloboquadrinids decline through the rest of the Pliocene to a minimum (<5%) at 1.80 Ma in the early Pleistocene with sharp recoveries to ~15% at 3.07 and 2.24 Ma. In the Pleistocene, the group has two more similar recoveries at 0.96 and 0.47 Ma. Overall tropical neogloboquadrinid abundance varies inversely with respect to that of the *Globigerinoides ruber* group. This is to be expected for two groups that constitute eutrophic and oligotrophic end-members, respectively, of the ecological spectrum of planktonic foraminifer faunal groups.

“Thermocline” globorotaliids exclude *Globorotalia unguolata*, which is a mixed-layer denizen (Shackleton and Vincent, 1978) and *Truncorotalia crassaformis*, *T. truncatulinoides*, and *T. tosaensis*, which are all deep-dwelling taxa. Menardellid species are the dominant element of the group at Site 925, while tumidiform species are secondary and all other species (*Hirsutella cibaoensis*, *H. margaritae*

Table 6. Faunal abundance percentages.

Faunal group	Age (Ma)												
	0.01	0.22	0.47	0.75	1.01	1.30	1.52	1.80	2.00	2.24	2.49	2.77	3.07
Stratigraphic groups													
Miocene–Pliocene	0	0	0	0	2	1	3	2	3	5	30	34	23
Pliocene–Pleistocene	0	2	0	0	0	0	0	2	0	4	13	11	7
Mixed-layer dwellers	83	73	54	74	75	76	74	73	71	69	65	50	55
Thermocline dwellers	9	25	45	24	24	20	26	14	28	30	34	49	43
<i>Globigerinoides ruber</i> group	44	41	31	11	30	29	50	50	30	30	44	28	33
<i>Globigerinoides sacculifer</i> group	19	24	9	9	14	24	10	17	38	35	3	6	12
Surface phytoplanktivores	20	7	13	42	31	21	14	6	3	4	16	13	11
Pulleniatinids	0	2	0	0	1	5	5	3	7	8	0	0	0
Neogene globoturborotalitids	0	0	0	1	0	1	2	0	0	3	6	28	13
Thermocline globoturborotalitids	0	11	23	12	1	0	4	1	7	0	14	12	8
Tropical neogloboquadrinids	6	2	17	6	14	4	6	3	4	13	9	7	17

Faunal group	Age (Ma)											
	3.25	3.49	3.78	3.97	4.19	4.36	4.71	4.99	5.31	5.57	5.92	6.14
Stratigraphic groups												
Miocene–Pliocene	50	39	52	45	52	52	59	50	49	48	58	66
Pliocene–Pleistocene	1	4	3	7	4	5	1	3	4	0	0	0
Mixed-layer dwellers	65	68	60	59	67	54	52	60	53	78	69	56
Thermocline dwellers	33	31	38	39	33	45	48	40	46	21	31	43
<i>Globigerinoides ruber</i> group	28	24	19	23	30	21	15	21	19	27	33	26
<i>Globigerinoides sacculifer</i> group	11	20	14	13	19	18	22	27	25	39	28	17
Surface phytoplanktivores	24	24	27	22	17	15	14	11	8	11	7	13
Pulleniatinids	0	0	0	0	1	0	0	0	0	0	0	0
Neogene globoturborotalitids	6	6	4	5	6	14	17	14	8	4	9	16
Thermocline globoturborotalitids	9	8	10	5	7	9	15	12	15	10	10	2
Tropical neogloboquadrinids	7	11	17	19	12	17	7	8	12	0	0	8

and *Globoconella triangula*) make minor, sporadic appearances. Thermocline globorotaliids compose ~15% of the assemblage in peaks centered at 4.99 and 2.49 Ma, and 20% at 0.47 Ma, the latter corresponding to a peak in tropical neogloboquadrinid abundance (Fig. 4C; Table 6). Menardellid taxa make up the largest portion of the above-mentioned peaks. Between 2.24 and 1.52 Ma, when menardellid globorotaliids are very rare or absent, *Globorotalia tumida* appears in its greatest numbers (up to 5% of the assemblage).

Isotope work by Keller (1985) has identified *Globoturborotalita woodi* and *Globoturborotalita nepenthes* as “intermediate” dwellers. In the nomenclature of Savin and Douglas (1973), “intermediate” refers to species associated with the seasonal thermocline. The numbers of *G. woodi* and *G. apertura* fluctuate in concert at Site 925 and at sites in the tropical Pacific (Chaisson, 1995), and they intergrade morphologically (Chaisson and Leckie, 1993). *G. apertura* is treated here as a thermocline dweller. Lourens et al. (1992) regard it as a mixed-layer dweller based on its putative phylogenetic relationship to *G. rubescens*. That its chambers are generally more inflated than those of *G. woodi* lends credence to this argument (Hecht and Savin, 1972), but it will remain in its present category awaiting supporting isotopic evidence. *G. woodi* is always more common than any other globoturborotalitid at Site 925. Globoturborotalitid abundance oscillates between 15% and 5% between 6.14 and 2.24 Ma (Fig 7D; Table 6). There is a broad paracme between 4.19 and 3.25 Ma, followed by a sharp recovery to 25% at 2.77 Ma. The overall pattern is quite similar to that observed at Ocean Drilling Program (ODP) Site 806 in the western equatorial Pacific (Chaisson, 1995).

A peak in Neogene globoturborotalitid numbers (15%) at 4.71 Ma is coupled with an absence at Site 925 of tropical neogloboquadrinids large enough for isotopic analysis. The pronounced decrease in globoturborotalitid abundance between 4.19 and 3.25 Ma is centered around the minimum in *Globigerinoides sacculifer* $\delta^{18}\text{O}$ values. This Neogene group declines to extinction when *G. sacculifer* and *N. dutertrei* $\delta^{18}\text{O}$ values make their positive shift between 2.49 and 2.24 Ma.

The various pulleniatinids morphotypes do not show good stratigraphic integrity at ODP Site 925 as they do in the western equatorial

Pacific (Bolli and Saunders, 1985; Chaisson and Leckie, 1993). In the early and middle Pliocene, the pulleniatinid group is represented only by three left-coiling specimens *Pulleniatina primalis* at 4.14 Ma in this study. Biostratigraphic work (Curry, Shackleton, Richter, et al., 1995) has shown that it occurs sporadically in low numbers up to the “Atlantic disappearance” at 3.5 Ma and reappears in the late Pliocene at 2.3 Ma, (Saito, 1976; Keigwin, 1982; Bolli and Saunders, 1985; Curry, Shackleton, Richter, et al., 1995) largely composed of *P. obliquiloculata* with rare specimens of *P. primalis*. The period of peak abundance of the pulleniatinid group (2.11–1.12 Ma) corresponds to minima in the numbers of other thermocline-dwelling taxa (Fig. 7D; Table 6). Peaks in other thermocline dwellers are coincident with the absence of pulleniatinids at 0.70 and 0.52 Ma and the interval of greatest pulleniatinid abundance coincides with an interval of high *Globigerinoides* abundance. The pulleniatinid pattern of abundance is precisely the opposite of that of *Globigerinita glutinata*.

DISCUSSION

Late Miocene and Pliocene

Samples at Site 925 in which no tropical neogloboquadrinids of sufficient size for isotopic analysis were found (6.14 Ma), or no specimens at all were present (5.92 and 5.57 Ma; Figs. 3, 7B) correspond to periods of latest Miocene intensification of Antarctic glaciation between 6.1 and 5.9 Ma and centered at 5.6 Ma (Hodell and Kennett, 1986). The *Globigerinoides ruber* group constitutes about 30% of the assemblage in these three samples (Fig. 5C) and the *Globigerinoides sacculifer* group abundance increases steeply to 39% at 5.57 Ma (Fig. 5D). In the modern ocean, increased numbers of *Globigerinoides ruber* are associated with oligotrophic conditions and increased numbers of *Neogloboquadrina dutertrei* are associated with eutrophic conditions (Bé, 1977; Hemleben et al., 1989; Ravelo et al., 1990). Faunal evidence, therefore, suggests that during the latest Miocene glacial periods, the thermocline at Site 925 in the western tropical Atlantic was deep in the photic zone. The cooling of the southern latitudes increased the pole-to-equator temperature gradient, strength-

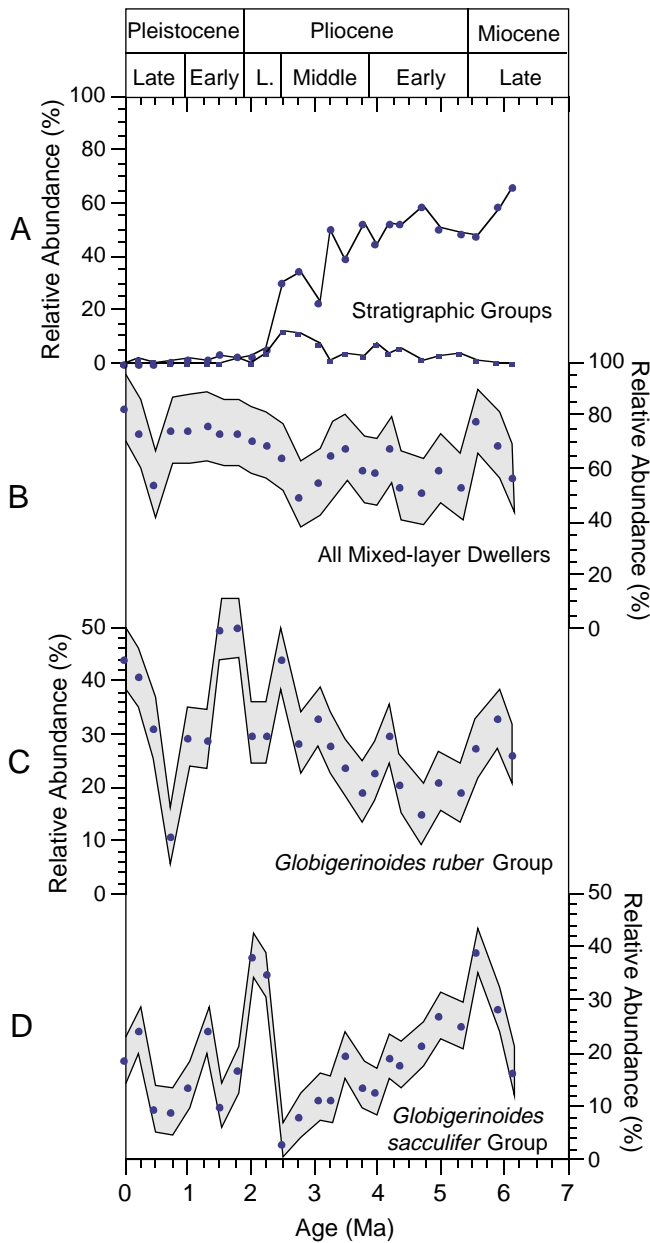


Figure 5. Relative abundance of stratigraphic groups, Miocene–Pliocene (circles) and Pliocene–Pleistocene (squares) (A), and mixed-layer dwelling groups (B, C, D). Gray areas represent two standard deviations, and are based on high-resolution data from Pliocene intervals in the Pacific (Chaisson, 1996).

ened wind fields, caused southeast tradewinds to “pile” warm surface water on the western side of the basin, and depressed the thermocline.

Warmer, interglacial conditions prevailed in Antarctica between 5.5 and 3.2 Ma (Hodell and Kennett, 1986; Jansen et al., 1993). The character of faunal and isotopic records at Site 925 changes to reflect the accompanying decrease in tradewind strength in the low latitudes from the late Miocene to early Pliocene. Three thermocline-dwelling groups increase to the abundance maxima between 5.57 and 3.78 Ma (Figs. 7B, C, D). The ML $\Delta\delta^{18}\text{O}$ record shows a steep decrease between 5.57 and 5.31 Ma. Smaller ML $\Delta\delta^{18}\text{O}$ values show that the temperature difference between *Globigerinoides sacculifer* and *Neogloboquadrina dutertrei* habitats decreased. Decreased advection of warm surface water to the western tropical Atlantic allowed the ther-

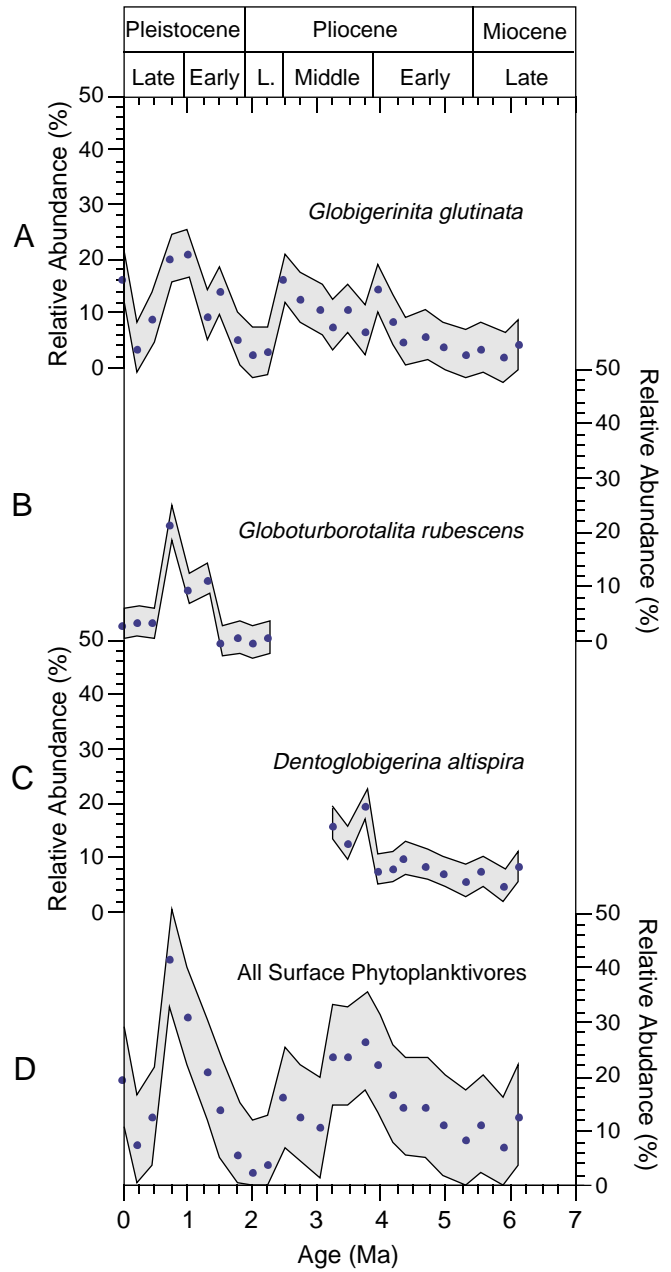


Figure 6. Relative abundance of the surface phytoplanktivores. The last group represents the sum of the previous three species. Gray areas as in Fig. 5.

mocline to shoal higher in the photic zone and decreased sea-surface temperatures (SST).

Eolian dust records indicate that the late Miocene to early Pliocene was a period of declining tradewind strength. In the western (Krissek and Janecek, 1993) and eastern (Hovan, 1995) equatorial Pacific, grain size of eolian material decreased between 5.5 and 4.0 Ma. In the eastern tropical Atlantic (Tiedemann et al., 1989, 1994), dust flux reached a minimum value for the Pliocene at approximately 4.0 Ma.

Jansen et al. (1993) attributed a positive drift in *Globigerinoides sacculifer* $\delta^{18}\text{O}$ after 3.7 Ma at Site 806 in the western equatorial Pacific to the growth of Northern Hemisphere ice sheets. The $\delta^{18}\text{O}$ records of both *G. sacculifer* and *N. dutertrei* (Fig. 2) also show a strong positive drift at Site 925 after 3.78 Ma, recording the global

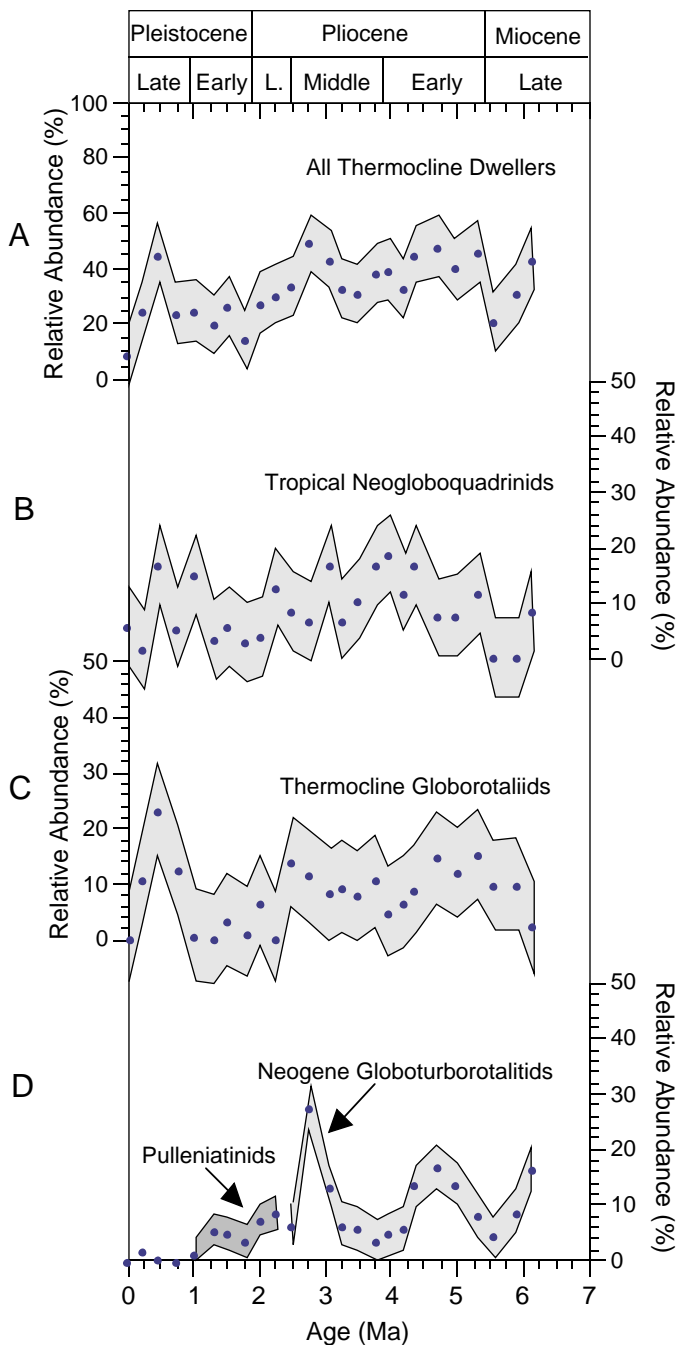


Figure 7. Relative abundance of thermocline dwelling faunal groups. Gray areas as in Fig. 5.

trend noted by Jansen et al. (1993). A trend in upper water-column conditions at Site 925 is revealed by the increase of ML $\Delta\delta^{18}\text{O}$ values between 4.19 and 1.80 Ma, which represents a growing temperature difference between *G. sacculifer* and *N. dutertrei* habitats.

Between 3.49 Ma and 2.00 Ma, ML $\Delta\delta^{13}\text{C}$ values declined (Fig. 4C), indicating that the $\delta^{13}\text{C}$ gradient in the upper water column was declining through this interval. The larger part of the change in the ML $\Delta\delta^{13}\text{C}$ record is due to the decline in *G. sacculifer* $\delta^{13}\text{C}$ values (Fig. 3). There is no significant trend in the global carbon budget through this interval (Mix et al., 1995), and the decline in surface

$\delta^{13}\text{C}$ values is likely due to a decrease in productivity at Site 925, which is also suggested by the overall decline in both tropical neogloboquadrinid and surface phytoplanktivore abundance (Fig. 7B), and the large increase in the *Globigerinoides ruber* group abundance (Fig. 5C) after the early Pliocene. Through this interval, the abundance of Miocene species at Site 925 declines from approximately 50% of the assemblage to near absence. The decline of this group in the equatorial Pacific (Sites 806 and 847) began after 4.5 Ma (Chaisson, 1996). Conditions favorable to species that evolved in the Miocene were evidently favorable into the middle Pliocene in the western tropical Atlantic. The nature of those conditions is unknown, although the general correlation with the ML $\Delta\delta^{13}\text{C}$ record at Site 925 suggests that nutrient distribution in the upper water column may have been a factor.

TH $\Delta\delta^{18}\text{O}$ and TH $\Delta\delta^{13}\text{C}$ records provide further evidence of surface warming and increasing oligotrophy at Site 925 through the mid- and late Pliocene. *Truncorotalia crassaformis* $\delta^{18}\text{O}$ values generally decreased between 3.78 and 2.24 Ma, in spite of a global trend toward increased $\delta^{18}\text{O}$ values. TH $\Delta\delta^{18}\text{O}$ values declined sharply as *N. dutertrei* and *T. crassaformis* habitats converged. In the equatorial Atlantic, *T. crassaformis* is found between 150 and 200 m depth in association with the oxygen minimum zone (OMZ; Jones, 1967). Declining surface productivity and thickening of the mixed layer would have the effect of weakening the OMZ and depressing a warmer portion of the thermocline into *T. crassaformis* habitat. The absence of this species in samples at 2.00 and 1.80 Ma probably records the culmination of this trend. This interpretation is supported by the high numbers of both *Globigerinoides* groups in these samples (Figs. 5C, D). The maximum in pulleniatinid numbers at 2.24 Ma is another indication of oligotrophic conditions at Site 925. This group is most abundant in the deep, nutrient-poor thermocline waters of the western equatorial Pacific (Parker and Berger, 1971; Kennett et al., 1985; Whitman and Berger, 1993).

Late Pliocene and Pleistocene

The low resolution of sampling in this study prevents detailed interpretation of a relationship between faunal and isotopic evidence and upper water-column hydrography. However, some general observations are possible. The large late Pliocene increase in *Truncorotalia crassaformis* $\delta^{18}\text{O}$ values (also noted by Spencer-Cervato, pers. comm., 1995) in the southwest Pacific suggests either a genetic change in this species or substantial cooling of upper intermediate water at this time. Further investigation is necessary before conclusions can be drawn. ML $\Delta\delta^{18}\text{O}$ values remained elevated until the latest Pleistocene (0.22 and 0.01 Ma). Unlike the early Pliocene decrease in ML $\Delta\delta^{18}\text{O}$ values, this event is coupled with a decrease in thermocline-dweller abundance (Figs. 4C, 7A, 7B, 7C). Faunal and isotopic evidence suggest an increase in downwelling and a warming of sub-surface water rather than shoaling of the thermocline and cooling of surface water.

Downwelling is also suggested by the sharp increase in TH $\Delta\delta^{13}\text{C}$ in the latest Pleistocene at Site 925. The $\delta^{13}\text{C}$ gradient was steepest between *Globigerinoides sacculifer* and *Neogloboquadrina dutertrei* habitat in the Pliocene of Site 925 (Fig. 4C), averaging nearly 1.5‰ in the early Pliocene. The decline of ML $\Delta\delta^{13}\text{C}$ and the rise of TH $\Delta\delta^{13}\text{C}$ suggests a downward movement of the $\delta^{13}\text{C}$ gradient through the Pliocene into the Pleistocene at Site 925. Downwelling of surface water relatively rich in ^{13}C has the effect of making *G. sacculifer* and *N. dutertrei* $\delta^{13}\text{C}$ values more similar, and *N. dutertrei* and *Truncorotalia crassaformis* $\delta^{13}\text{C}$ values more dissimilar (Fig. 3).

The large sampling interval used for this study attaches too much uncertainty to the faunal and isotopic values to make regression analysis informative. Therefore, the isotopic values are divided into three classes, and threshold abundances are recognized for each faunal group. The interrelationships between the abundance fluctuations

of the faunal groups and the values of the isotopic difference curves are summarized in Table 7. Table 7 suggests that variations in the thermal gradient implied by the $\delta^{18}\text{O}$ gradients in the mixed layer (ML $\Delta\delta^{18}\text{O}$) and thermocline (TH $\Delta\delta^{18}\text{O}$) can be reliably associated with high numbers (i.e., favorable environmental conditions and consequent reproductive success) of these faunal groups. The descriptions of tradewind and convergence strength, SST and strength, depth, and variability of the seasonal thermocline in Table 8 are based on inferences drawn from the associations of faunal and isotopic values presented in Table 7. In Table 8, increasing ML $\Delta\delta^{18}\text{O}$ values (top to bottom) are associated with warmer SSTs and stronger tradewinds. Increasing TH $\Delta\delta^{18}\text{O}$ values (left to right) are associated with a stronger and more seasonally variable thermocline. These paleoenvironmental deductions are applied only to Site 925, where increased tradewinds advect surface water, warm SSTs, and depress the thermocline. At sites on the eastern side of the equatorial Atlantic, in-

creased tradewinds would be expected to cool SSTs and shoal the thermocline.

In the modern ocean, Site 925 is on the edge of a weak upwelling zone during the boreal summer and is beneath downwelling for the rest of the year (Hastenrath and Lamb, 1977; Molinari and Johns, 1994). Faunal data suggest that upwelling was never strong at Site 925 during the last 6 m.y.; tropical neogloboquadrinids never account for more than 20% of the assemblage. Rather, downwelling was at a minimum in the early Pliocene and gradually increased in strength and duration into the Pleistocene. Hastenrath (1985) noted that the SST maximum in the tropical Atlantic coincides with the convergence maximum. Increasingly large values of ML $\Delta\delta^{18}\text{O}$ between the early Pliocene and early Pleistocene are coupled with decreases in the abundance of thermocline-dwelling fauna. These coinciding trends argue for increasing SST due to southward migration of the average position of the ITCZ (Fig. 8).

Table 7. Relating faunal abundance and isotopic gradients.

		Thermocline		
		Small	Moderate	Large
Mixed layer	Small	Dominant faunal groups		
		<i>Globigerinoides sacculifer</i> group * Neogene globoturborotalitids Thermocline globorotaliids	<i>Globigerinoides sacculifer</i> group * Thermocline globorotaliids	<i>Globigerinoides ruber</i> group * Thermocline globorotaliids
	Moderate	<i>Globoturborotalita rubescens</i> <i>Globigerinita glutinata</i> * Neogene globoturborotalitids Pulleniatinids	<i>Dentoglobigermia altispira</i> <i>Globigerinita glutinata</i> * Tropical neogloboquadrinids	<i>Globigerinoides ruber</i> group <i>Globigerinita glutinata</i> * Tropical neogloboquadrinids
Large	?	<i>Globigerinita glutinata</i> * Tropical neogloboquadrinids	<i>Globigerinoides ruber</i> group <i>Globigerinita glutinata</i> * Tropical neogloboquadrinids <i>Menardella menardii</i>	

Note: Faunal groups are considered to be dominant at varying levels: >30% for the *Globigerinoides ruber* group, >20% for the *Globigerinoides sacculifer* group, and >15% for all other groups, except for the thermocline globorotaliids (>10%) and the pulleniatinids (>5%). Mixed-layer groups are above the asterisk and thermocline-dwelling groups below.

Table 8. Interpreting climatic and oceanographic conditions.

		Thermocline		
		Small	Moderate	Large
Mixed layer	Small	Tradewinds weak (NE < SE) Cooler SST Convergence weak Weak, deep seasonal thermocline	Tradewinds weak (NE < SE) Cooler SST Convergence weak Stronger, deep seasonal thermocline	Tradewinds weak (NE < SE) Cooler SST Convergence weak Seasonally variable strong thermocline
	Moderate	Tradewinds weak (NE < SE) Warmer SST Weaker seasonal thermocline; base of photic zone	Tradewinds moderate (NE = SE) Warmer SST Moderately variable seasonal thermocline; base of photic zone	Tradewinds moderate (NE = SE) Warmer SST Highly variable seasonal thermocline; base of photic zone
	Large	Tradewinds strong Warmest SST Weaker seasonal thermocline; base of photic zone	Tradewinds strong Warmest SST Moderately variable seasonal thermocline; base of photic zone	Tradewinds strong Warmest SST Highly variable seasonal thermocline; base of photic zone

CONCLUSIONS

Planktonic foraminifer counts from undissolved sediments preserve a record of the relative reproductive success of each species. Isotopic measurements of multiple species document the isotopic gradients that are associated with the abundances in those samples. If these isotopic gradients are interpreted as thermal ($\Delta\delta^{18}\text{O}$) and nutrient ($\Delta\delta^{13}\text{C}$) gradients within the euphotic zone, then an association can be made between the reproductive success of certain species, or groups of species, and a particular physical environment. Many studies in the modern ocean that link the distribution of assemblages with the extent of particular water masses (e.g., Bé and Tolderlund, 1971; CLIMAP, 1981) have laid the groundwork for interpreting this relationship in the geologic past.

Small $\delta^{18}\text{O}$ gradients in the mixed layer (ML $\Delta\delta^{18}\text{O}$) are associated with high numbers of *Globigerinoides* species, while larger gradi-

ents are associated with high numbers of surface phytoplanktivores (Tables 4, 5). This concurs with what is observed in the modern ocean (e.g., Bé and Tolderlund, 1971); *Globigerinoides* spp. favor a less thermally stratified mixed layer. Larger gradients between the top of the seasonal thermocline and sub-thermocline water (TH $\Delta\delta^{18}\text{O}$) are associated with larger numbers of the *G. ruber* group. In the modern ocean, *G. ruber* is more common at subtropical latitudes than is *G. sacculifer* (Bé, 1977), suggesting that it tolerates more seasonal change in the water column. Larger values of TH $\Delta\delta^{18}\text{O}$ may, therefore, be indicative of greater seasonal change in the structure of the water column at Site 925. This conclusion is complemented by the association of larger numbers of pulleniatinids with small values of TH $\Delta\delta^{18}\text{O}$. In the modern ocean, this thermocline-dwelling group is most common in the western equatorial Pacific, an area of minimal seasonality (Parker and Berger, 1971). By contrast, the greatest number of tropical neogloboquadrinids are associated with moderate to large values of ML and TH $\Delta\delta^{18}\text{O}$ at Site 925, that is, with the most thermal stratification of the euphotic zone. This pattern agrees with the biogeography of *Neogloboquadrina dutertrei* in the modern ocean, where it is more common in the eastern tropical regions and along eastern boundary currents (Bé, 1977; Parker and Berger, 1971), where there is seasonal or persistent upwelling.

When viewed in time series (Figs. 4–8), the above connections between planktonic foraminifer ecology and the structure of the upper water column suggest that during the last 6 m.y. at Site 925, the thermocline shoaled to its shallowest levels near the early to mid-Pliocene boundary (3.8 Ma). Numbers of tropical neogloboquadrinids are highest through this interval, but do not exceed 20% of the assemblage, which is similar to their representation in a core top from V29-144 in the eastern tropical Atlantic, where they calcify between 25 and 75 m (Ravelo and Fairbanks, 1992). Mix et al. (1995) show a $\sim 1.5\text{‰}$ increase in benthic $\delta^{18}\text{O}$ values between the mid-Pliocene and the Pleistocene at Site 849. This range is approximated by the $\delta^{18}\text{O}$ values of *Neogloboquadrina dutertrei* through the comparable interval at Site 925, while the change in *Globigerinoides sacculifer* values is smaller. This suggests that at Site 925 the increase in *G. sacculifer* $\delta^{18}\text{O}$ due to the increase in ice volume between the Pliocene and Pleistocene was off-set by a regional increase in SST. The increase in ML $\Delta\delta^{18}\text{O}$ at Site 925 is therefore interpreted as largely due to an increase in SST. This evidence is coupled with an overall increase in the abundance of mixed-layer dwellers, driven by a very large increase in the number of *G. ruber* in the sediments after 2 Ma.

The faunal and isotopic data in this study suggest that the thermocline in this region (4°N , 43°W) has been gradually depressed since ~ 4 Ma, and that SST has gradually increased. We conclude that the cause for these oceanographic changes was the southward movement of the winter position of the ITCZ, and the downwelling and SST maximum that characterize the surface ocean below this atmospheric feature. This southward movement was a result of the progressive cooling of the northern hemisphere between the Pliocene and Pleistocene.

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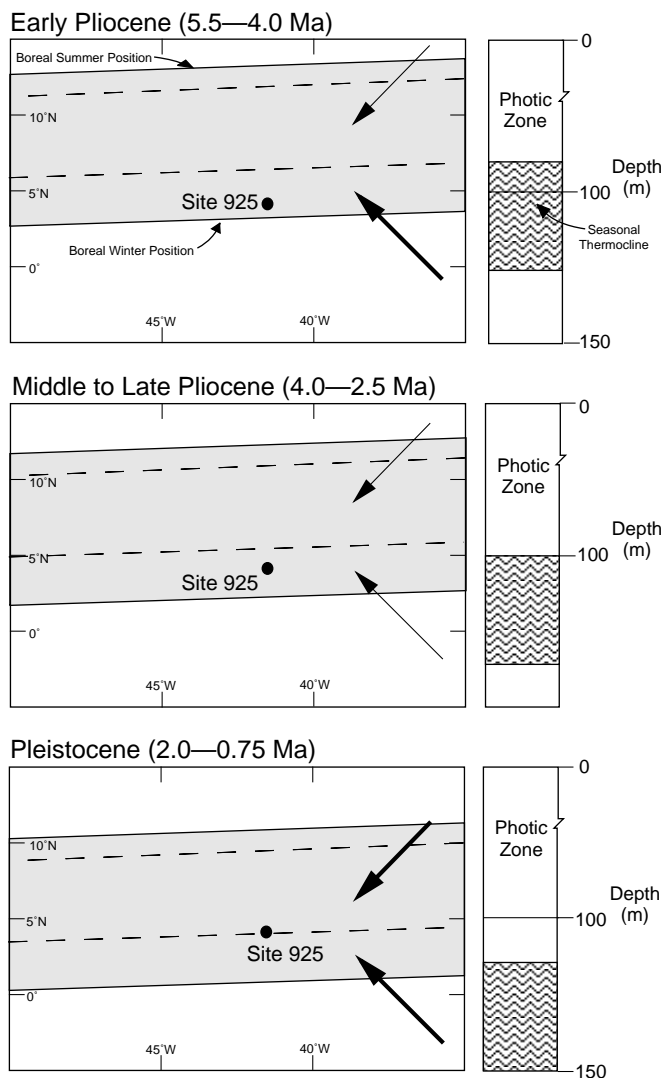


Figure 8. Three stages of paleoceanographic development at Site 925 in the western tropical Atlantic. The area between the extreme northern and southern positions of the intertropical convergence zone (ITCZ) is shaded. The dashed lines indicate the zone of maximum convergence. Large arrows indicate tradewind direction. The weight of the arrow represents wind strength. The concurrent position of the seasonal thermocline is indicated in the accompanying figures on the right. The uppermost portion of the thermocline ($\sim 20^\circ$ – 15°C) is shown as dark shading.

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