

## 25. PLANKTONIC FORAMINIFERAL ASSEMBLAGES AND PALEOCEANOGRAPHIC CHANGE IN THE TRANS-TROPICAL PACIFIC OCEAN: A COMPARISON OF WEST (LEG 130) AND EAST (LEG 138), LATEST MIOCENE TO PLEISTOCENE<sup>1</sup>

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### ABSTRACT

Cores from four Ocean Drilling Program (ODP) sites were examined for planktonic foraminifers. One sample per core (from core-catchers in Holes 806B and 807B and from Section 4 in Holes 847B and 852B) was examined through the interval representing the last 5.8 m.y. Sites 806 (0°19.1'N; 159°21.7'E) and 847 (0°12.1'N; 95°19.2'W) are beneath the equatorial divergence zone. Sites 807 (3°36.4'N; 156°37.5'E) and 852 (5°19.6'N; 110°4.6'W) are located north of the equator in the convergence zone created by the interaction of the westward-flowing South Equatorial Current (SEC) and the eastward-flowing North Equatorial Countercurrent (NECC). Specimens were identified to species and then grouped according to depth habitat and trophic level. Species richness and diversity were also calculated.

Tropical neogloboquadrinids have been more abundant in the eastern than in the western equatorial Pacific Ocean throughout the last 5.8 m.y. During the mid-Pliocene (3.8–3.2 Ma), their abundance increased at all sites, while during the Pleistocene (after ~1.6 Ma), they expanded in the east and declined in the west. This suggests an increase in surface-water productivity across the Pacific Ocean during the closing of the Central American seaway and an exacerbation of the productivity asymmetry between the eastern and western equatorial regions during the Pleistocene. This faunal evidence agrees with eolian grain-size data (Hovan, this volume) and diatom flux data (Iwai, this volume), which suggest increases in tradewind strength in the eastern equatorial Pacific that centered around 3.5 and 0.5 Ma.

The present longitudinal zonation of thermocline dwelling species, a response to the piling of warm surface water in the western equatorial region of the Pacific, seems to have developed after 2.4 Ma, not directly after the closing of the Panama seaway (3.2 Ma). Apparently, after 2.4 Ma, the piling warm water in the west overwhelmed the upwelling of nutrients into the photic zone in that region, creating the oceanographic asymmetry that exists in the modern tropical Pacific and is reflected in the microfossil record.

In the upper Miocene and lower Pliocene sediments, the ratio of thermocline-dwelling species to mixed-layer dwellers is 60%:40%. During the mid-Pliocene, the western sites became 40% thermocline and 60% mixed-layer dwellers. Subsequent to ~2.4 Ma, the asymmetry increased to 20%:80% in the west and the reverse in the east. This documents the gradual thickening of the warm-water layer piled up in the western tropical Pacific over the last 5.8 m.y. and reveals two "steps" in the biotic trend that can be associated with specific events in the physical environment.

### INTRODUCTION

Sediments representing the last 5.8 m.y. were examined at four ODP sites on opposite ends of the equatorial Pacific Ocean circulation system (Fig. 1). Two cores in the western equatorial Pacific were drilled at Sites 806 and 807 during Leg 130 to the Ontong Java Plateau (Kroenke, Berger, Janecek, et al., 1991) and the two in the eastern equatorial Pacific were at Sites 847 and 852, drilled during Leg 138 (Mayer, Pisias, Janecek, et al., 1992). Planktonic foraminifers were counted and identified to species in one sample per core. The relative abundance of each species was calculated. The most common species and species grouped on the basis of depth habitat and trophic level are presented in time-series for all four sections. Temporal resolution in this study is relatively coarse. The interval between samples in Hole 806B is 273 k.y., in Hole 807B, 316 k.y., that in Hole 847B, 240 k.y., and that in Hole 852, 750 k.y.

The sites were selected for their oceanographic positions (see Table 1). Though on opposite sides of the tropical Pacific, both Sites 807 (3°36.4'N; 156°37.5'E) and 852 (5°19.6'N; 110°4.6'W) have been drifting into the convergence zone between the westward-flowing SEC and the eastward-flowing NECC. Likewise, Sites 806 (0°19.1'N; 159°21.7'E) and 847 (0°12.1'N; 95°19.2'W) are separated by the entire expanse of the Pacific, but both are beneath the equatorial divergence zone created by the sign change of the Coriolis force

as the southeast trade winds blow across the equator. Both of these sites have been beneath the divergence zone for the past 5.8 m.y., but the Equatorial Undercurrent (EUC) has risen in the water column since the late Miocene (Kennett et al., 1985).

The purpose of this study was to look for changes in the abundances of planktonic foraminifer species that occur in stratigraphic intervals associated with the closing of the Central American seaway between 3.8 and 3.2 Ma (Keigwin, 1978; 1982) and the intensification of Northern Hemisphere glaciation after 2.5 Ma. Northern Hemisphere glaciation began ~3.1 Ma, when continental-sized ice sheets began to grow and shrink in North America and Eurasia (Raymo et al., 1989). After 2.5 Ma,  $\delta^{18}\text{O}$  variations indicate the inception of large-scale glaciation in the Northern Hemisphere (Shackleton et al., 1984; Jansen et al., 1988; Jansen et al., 1993), with ice sheets, on average, at least half the size of those during the late Pleistocene (Raymo et al., 1989; see Fig. 2). The response of the faunal assemblages to the oceanographic consequences of these events is dictated by the ecologies of individual species. In the eastern equatorial Pacific, where the thermocline has been lifted higher into the photic zone by upwelling, species that live in the thermocline are expected to form a larger portion of the faunal assemblage in response to the hydrographic change. In the western equatorial Pacific, as the mixed layer thickens because of the "piling-up" of warm surface water by the trade winds, the species of planktonic foraminifer that dwell in the mixed layer are expected to increase their relative abundance in the faunal assemblage consequent to that hydrographic phenomenon.

Other proxy indicators of oceanographic change during the Central American seaway closing and the Northern Hemisphere intensification of glaciation intervals suggest that these were times of cooler

<sup>1</sup> Pisias, N.G., Mayer, L.A., Janecek, T.R., Palmer-Julson, A., and van Andel, T.H. (Eds.), 1995. *Proc. ODP, Sci. Results*, 138: College Station, TX (Ocean Drilling Program).

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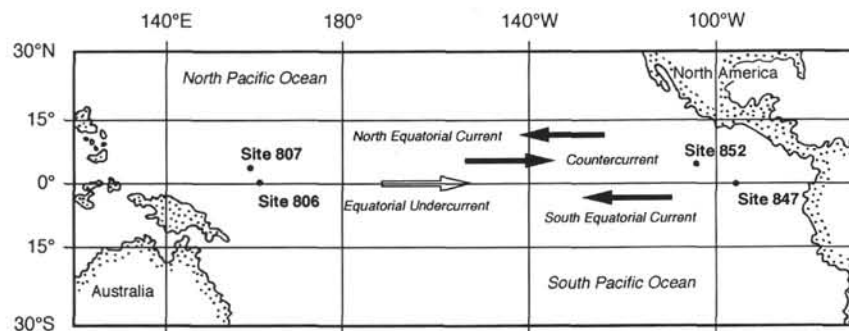


Figure 1. The equatorial circulation system of the Pacific Ocean and the positions of the study sites within it.

### Correlation of Biotic and Environmental Events

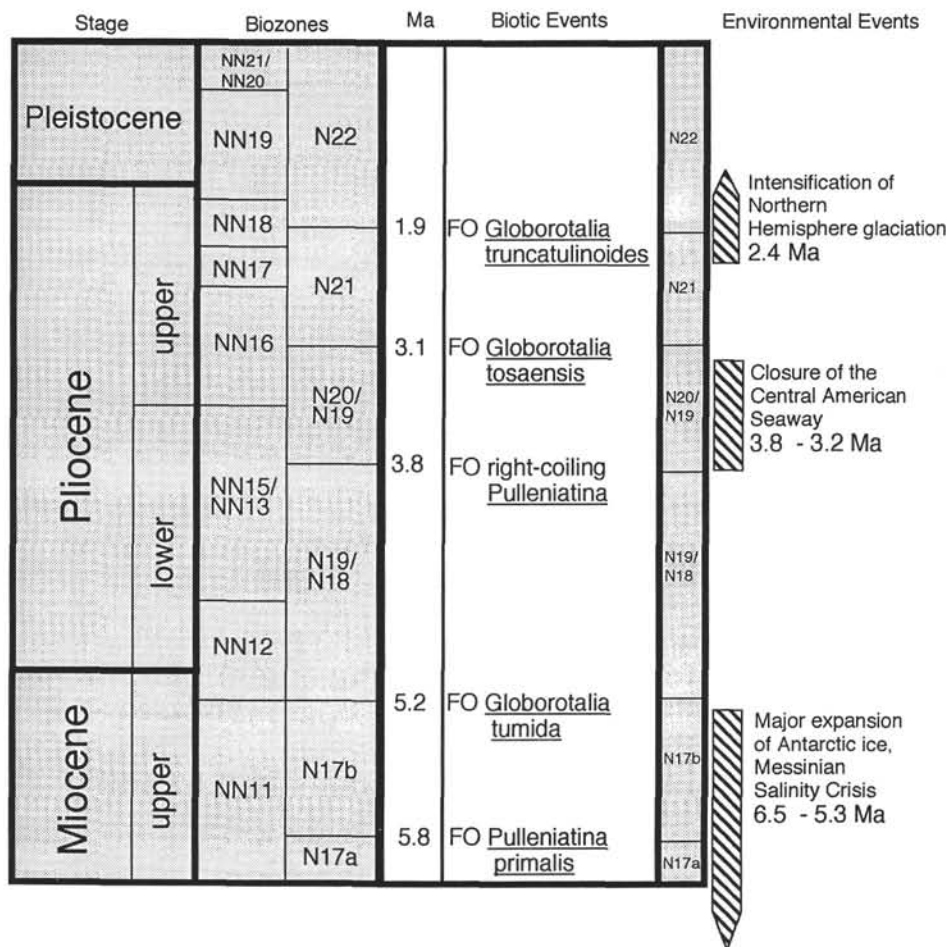


Figure 2. Foraminiferal datums are from Berggren et al. (1985). Correspondence of nannofossil zonation and foraminiferal zonation is for Site 806, as worked out by Takayama and Leckie for the *Scientific Results* volume of Leg 130 (1993). Foraminiferal zonation is from Chaisson and Leckie (1993) for Site 806.

sea-surface temperatures, increased wind strength, and increased upwelling and downwelling. The  $\delta^{18}\text{O}$  isotope record (Shackleton and Opdyke, 1977; Keigwin, 1978; 1979; 1982; Thunell and Williams, 1983; Jansen et al., 1993; Prentice et al., 1993) preserves a temperature and ice volume signal. Eolian dust particle flux (Hovan, this volume) records tradewind strength in the eastern equatorial Pacific,

while diatom flux at Site 852 is a measure of productivity and suggests downwelling strength in the eastern equatorial Pacific (Iwai, this volume). The faunal record of planktonic foraminifers does not contradict any of these indicators and should help to clarify the history of the upper water column as we develop a better understanding of the ecology of modern planktonic foraminifers.

Global climate during the Cenozoic was marked by step-like transitions from one stable climate regime to another (Berggren, 1972; Savin et al., 1975; Shackleton and Kennett, 1975; Kennett and Shackleton, 1976; Kennett, 1977; Vincent et al., 1980; Thunell and Williams, 1983; Berger et al., 1993). The onset of Northern Hemisphere glaciation during the middle to late Pliocene constituted the last in a series of descending "steps" as Cenozoic paleoclimate and paleoceanography cooled (Berggren, 1972; Shackleton and Kennett, 1975; Shackleton and Opdyke, 1977; Vincent et al., 1980; Thunell and Williams, 1983). Steepening of the equator-to-pole temperature gradients (Thunell and Belyea, 1982) followed the closing of the Central American seaway (3.8–3.2 Ma; Keigwin, 1978), while initiation of bipolar cooling intensified atmospheric-oceanic circulation due to intensification of major wind systems during glacial episodes. This led to more pronounced equatorial divergence and greater surface productivity in the equatorial regions (Arrhenius, 1952; Prell et al., 1976; Pederson, 1983; Gupta and Srinivasan, 1990). Janacek (1985) found a dramatic increase in eolian particles in the North Pacific during the seaway-closing interval and attributed their presence to intensified atmospheric circulation associated with the onset of Northern Hemisphere glaciation. Hovan (this volume) has found a coarsening of eolian particles at Sites 848, 849, and 843 through the seaway-closing interval, and Iwai (this volume) has found a sharp decline in diatom flux at Site 852. Both of these proxies indicate an increase in tradewind strength during the middle Pliocene (increased convergence at Site 852 would move diatoms down out of the photic zone).

This study presents four coarse-resolution time-series of planktonic foraminifer assemblages in an attempt to detect in the faunal record oceanographic events that are indicated by other proxy records. The ecology of individual species was expected to determine their reactions to oceanographic change. Their reactions were interpreted in terms of changes in their relative abundance in the sediment assemblages. Species were grouped by depth habitat and trophic level. Changes in the proportions of these groups through time were interpreted as possible changes in surface-water hydrography. The last 6 m.y. has been a period of overall decline in the diversity of planktonic foraminifers (Kennett, 1986), but diversity, as measured by the Shannon-Wiener diversity index (Gibson and Buzas, 1973) at four tropical Pacific sites, did not decline drastically in the western equatorial region, and only in upper Pleistocene sediments has it declined appreciably in the east.

The effects of differential dissolution of carbonates on proportional representation of planktonic foraminiferal species in the sediment assemblage ("taphonocoenosis," Berger, 1973) will not be considered quantitatively in this study, but when dissolution may have been skewing relative proportions of species and mimicking oceanographic change was noted.

## BACKGROUND

The following section is a brief summary of the terrestrial and oceanic events of the last 5.8 m.y. as they have been detected in the stable isotope and faunal records.

By the late Miocene and earliest Pliocene, the West Antarctic ice sheet had become established (Ciesielski et al., 1982; Haq, 1984). During the latest Miocene, the Mediterranean was isolated ("the Messinian salinity crisis") by falling sea level, a consequence of the Antarctic ice volume increase (Shackleton and Kennett, 1975). The decrease in sea level that isolated the Mediterranean was associated with greater ocean fertility (Kennett et al., 1979), increased biogenic productivity, and high sediment accumulation rates (Davies et al., 1977).

Except for an episode of strong glaciation between 4.6 and 4.3 Ma (Jansen et al., 1993), the period from 5 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). High-latitude surface water seems to have warmed, while low-latitude water seems to have become relatively cool through this interval (Kennett and von

**Table 1. Location, depth, average sedimentation rate, temporal resolution, and position relative to ocean currents of Sites 806, 807, 847, and 852.**

Site	Latitude	Longitude	Water depth (m)	Average rate of sedimentation (m/m.y.)	Temporal resolution (k.y.)	Oceanographic setting
806	0°19.1'N	159°21.7'E	2523	0–3.4 Ma: 24 3.4–5.2 Ma: 52 5.2–5.8 Ma: 65	340 257 120	Equatorial divergence zone
807	3°36.4'N	156°37.5'E	2810	0–3.4 Ma: 21 3.4–5.8 Ma: 41	378 240	NECC and SEC boundary
847	0°12.1'N	95°19.2'W	3355	0–4.0 Ma: 30 4.0–5.8 Ma: 60	235 225	Equatorial divergence zone EUC and SEC juncture
852	5°19.6'N	110°4.6'W	3870	0–4 Ma: 12 4–5.8 Ma: 16	667 600	NECC and SEC boundary

Note: Data are from Mayer, Pisias, Janacek, et al. (1992).

der Borch, 1985). It was while the globe was in this climatic state that the tectonic uplift of the Isthmus of Panama occurred, which cut off the remaining low-latitude interoceanic connection (Berggren and Hollister, 1977; Thunell and Belyea, 1982).

The initiation of Northern Hemisphere cooling seems to have immediately 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. This interpretation agreed with an initial age estimate of 3.0 Ma for the first appearance of ice-rafted debris in North Atlantic sediments (Berggren, 1972; Poore, 1981). Reevaluation of biostratigraphy at North Atlantic DSDP Sites 111 and 116 caused Backman (1979) to date the first appearance of ice-rafted debris at ~2.5 Ma. Dowsett and Poore (1990), employing the GSF18 transfer function at DSDP Site 552 in the North Atlantic, found that the interval from 3.1 to 2.45 Ma showed a trend toward cooler sea-surface temperatures, with increasing amplitude changes around a declining mean. This trend was matched by increasingly heavy  $\delta^{18}\text{O}$  values through this interval. The coldest estimates coincided with unequivocal occurrence of ice-rafted debris at 2.45 Ma (Dowsett and Poore, 1990).

Other  $\delta^{18}\text{O}$  isotope studies, however, have found that ice-sheet growth was not a steady expansion from the 3.2-Ma enrichment (Jansen et al., 1993). Keigwin (1982) and Prell (1982) found subsequent lighter values in Caribbean and eastern equatorial Pacific cores. In the Mediterranean, Thunell and Williams (1983) noted that isotopic values at DSDP Site 132 increased 1 part per mil at about 3.3 to 3.2 Ma and then returned to values typical of the early Pliocene until 2.5 Ma. Variability in the  $\delta^{18}\text{O}$  isotopic record during this interval was greater than that of the early Pliocene, but smaller in amplitude than that of Pleistocene glacial/interglacial cycles.

Raymo et al. (1992) monitored the record of North Atlantic Deep Water (NADW) formation by estimating the  $\delta^{13}\text{C}$  gradient between the North Atlantic and the Pacific oceans. Their data complements the  $\delta^{18}\text{O}$  isotope evidence. Between 3 and 2 Ma, the production of NADW was always greater than has been estimated for late Pleistocene glacials. Global cooling has been associated with suppression of NADW production (Boyle and Keigwin, 1987). Thermohaline circulation played a critical part in modulating meridional heat transport and  $\text{CO}_2$  exchange between the deep ocean reservoir and the atmosphere. After 2.95 Ma, cold episodes began to be colder than the modern climate, but the warm intervals were also still significantly warmer (Raymo et al., 1992).

Before 2.8 Ma, no unambiguous cyclicity was apparent in the isotope records at the precessional or obliquity frequencies. After 2.75 Ma, a strong 41-k.y. period appeared (Raymo et al., 1992). Planktonic foraminifers in the Mediterranean changed from warm- to cool-water assemblages, and a turnover occurred in the benthic fauna (Thunell and Williams, 1983). At 2.5 Ma, a permanent enrichment of oxygen isotope values in North Atlantic DSDP cores marked what is probably the beginning of Northern Hemisphere ice volume build up



(Thunell and Williams, 1983; Raymo et al., 1989). Raymo et al. (1992) measured the  $\delta^{13}\text{C}$  gradient between the Atlantic and Pacific basins between 3 and 2 Ma and found that their South Atlantic site (DSDP Site 704) became more "Pacific-like" after 2.7 Ma, that is,  $^{13}\text{C}$ -rich NADW was beginning to have less of an influence than  $^{13}\text{C}$ -poor Antarctic Bottom Water (AABW). Northern Hemisphere ice-sheet development had begun to decrease NADW production.

## OCEANOGRAPHIC SETTING

The Pacific equatorial circulation system consists of three major surface currents and one subsurface one (Pickard and Emery, 1990). The westward-flowing North Equatorial Current (NEC) lies between about  $8^\circ$  and  $20^\circ\text{N}$  and will not be considered in this study. The westward-flowing South Equatorial Current (SEC) extends from about  $10^\circ\text{S}$  to  $3^\circ\text{N}$  in the west. The narrower, eastward-flowing North Equatorial Countercurrent (NECC) flows east between the equatorial currents ( $3^\circ$  to  $8^\circ\text{N}$ ) and above the thermocline in the western equatorial Pacific (Delcroix et al., 1987). This current transports relatively low-salinity water to the east ( $S < 34.5\text{‰}$ , Wyrtki, 1981; Delcroix et al., 1987). The southern border of the NECC is at about  $5^\circ\text{N}$  in the eastern equatorial Pacific (Wyrtki, 1981). The Equatorial Undercurrent (EUC) flows eastward below the surface, a geostrophic flow confined by the Coriolis force to between  $2^\circ\text{S}$  and  $2^\circ\text{N}$ . In the western equatorial Pacific, the EUC is usually centered 150 to 200 m below the surface at  $165^\circ\text{E}$  (Delcroix et al., 1987), and it rises with the thermocline across the Pacific, so that it may be only 30 to 50 m below the surface west of the Galapagos Islands (Wyrtki, 1981). This current system can be traced from near the Philippines in the west to the Gulf of Panama in the east, a distance of 15,000 km (Pickard and Emery, 1990; see Fig. 2).

In the modern ocean, a cool "tongue" of water extends from the Peru Current (PC) to  $180^\circ$ , created partly by advection and partly by divergence and upwelling along the equator. This tongue is best developed from August to October during the southern winter, when the southeast trade winds are at their strongest. The east-west temperature difference from the Galapagos to  $180^\circ$  during this period is  $8^\circ\text{C}$  (Wyrtki, 1981). West of  $180^\circ$ , the mixed layer is so thick ( $>100\text{ m}$ ) that upwelling is rarely seen at the surface. No upwelling can be observed above 140 m depth in a temperature section along  $165^\circ\text{E}$  (Delcroix et al., 1987). Satellite imagery gathered by the Coastal Zone Color Scanner on Nimbus-7 shows very low concentrations of chlorophyll at the surface along the equator over the Ontong Java Plateau during non-El Niño years, but higher concentrations extend to  $160^\circ\text{E}$  during El Niño years (see McClain et al., 1990 for explanation of imagery).

The equatorial circulation system began to resemble the modern one after the closing of the Indonesian seaway during the middle to late Miocene (Kennett et al., 1985). The EUC and NECC were established or greatly strengthened at that time, and the mixed layer began to thicken in the western equatorial region relative to the eastern. The piling occurs as the northeast and southeast trade winds blow surface water from east to west along the equator in the SEC, until it builds up against the collided Australian and Asian plates (the Indonesian archipelago). Consequently, the thermocline is deeper in the west than in the east. Global cooling through the late Neogene and Pleistocene increased tradewind strength and brought the thermocline nearer to the surface. With the closing of the Central American seaway, the thermocline shallowed more in the east and entered the photic zone (Kennett et al., 1985).

## METHODS

One sample per core was analyzed. In the western Pacific holes, core-catchers were used. In the eastern Pacific holes, a sample from the fourth section of each core was examined. A total 74 samples were examined.

Samples of approximately  $10\text{ cm}^3$  of sediment were soaked in a neutral mixture of dilute hydrogen peroxide and Calgon until they were disaggregated. Most samples disaggregated in less than 2 hr. The sediment then was washed through a  $63\text{-}\mu\text{m}$  screen and the  $>63\text{-}\mu\text{m}$  fraction was dried at  $-80^\circ$ – $-90^\circ\text{C}$ .

The  $>125\text{-}\mu\text{m}$  fraction has been divided with a microsplitter to provide a minimum of 300 specimens for species counts (see Appendix A). The taxonomies of Kennett and Srinivasan (1983) and Chaisson and Leckie (1993) were used. Foraminiferal preservation in Hole 852B was often poor, and it was sometimes impossible to get a full count (maximum: 309; minimum: 145; average: 267). Planktonic foraminiferal fragments, benthic foraminifers, and radiolarians were counted without being identified further.

The  $>125\text{-}\mu\text{m}$  fraction, rather than the  $>150\text{-}\mu\text{m}$  fraction, was counted to include as nearly as possible the full diversity of the living assemblage without identification of species becoming confounded by too many juvenile foraminifers. I hoped that inspection of a "smaller" fraction (i.e., smaller than the  $>150\text{-}\mu\text{m}$  fraction of CLIMAP, 1984 and that of PRISM, Dowsett and Poore, 1990) would produce a truer representation of the proportions of smaller species in the living assemblage and lessen the "no analog" phenomenon described by Hutson (1977). The count data of this study also are intended to be comparable to the sediment trap data of Deuser et al. (1981), Thunell et al. (1983), Thunell and Reynolds (1984), Deuser (1987), Reynolds and Thunell (1989), and Deuser and Ross (1989).

The  $>125\text{-}\mu\text{m}$  fraction also was examined so that the effect of dissolution on these assemblages could be quantitatively ascertained in a future study. Berger et al. (1982) noted that indexing fragmentation in the 125- to  $150\text{-}\mu\text{m}$  fraction is an excellent proxy for estimating the amount of dissolution that a sample has undergone. Coulbourn et al. (1980) counted the fine fraction (125- to  $150\text{-}\mu\text{m}$ ) of well-preserved samples and found good correspondence between sediment and surface-water distribution of assemblages. This is contrary to Bé and Hutson (1977), who also counted the  $>125\text{-}\mu\text{m}$  fraction.

## LITHOSTRATIGRAPHY

Site 806 was drilled in a water depth of 2520 m on the northeastern margin of the Ontong Java Plateau ( $0^\circ19.1'\text{N}$ ,  $159^\circ21.7'\text{E}$ ), approximately 125 km northeast of DSDP Sites 289/586 (Kroenke, Berger, Janecek, et al., 1991). Hole 806B cored the entire Neogene sequence (743.1 mbsf) to the Oligocene/Miocene boundary interval. The entire interval examined in this study lies within Subunit IA (0–339 mbsf).

Site 807 is located in 2810 m of water on the northern rim of the Ontong Java Plateau, roughly 475 km northwest of DSDP Sites 289/586. The sediments of the last 5.8 m. y. are included in Subunit IA of Unit I (0–968 mbsf), which includes Pleistocene to upper/middle Eocene sediments (Kroenke, Berger, Janecek, et al., 1991). Site 847 is located in 3355 m of water approximately 380 km west of the Galapagos Islands ( $0^\circ12.1'\text{N}$ ,  $95^\circ19.2'\text{W}$ ). There was continuous recovery from the Pleistocene through the upper Miocene sections (0.0–6.5 Ma) in Hole 847B. The entire sequence is described as a single unit (Mayer, Pisias, Janecek, et al., 1992).

Site 852 is located west of the East Pacific Rise and south of the Clipperton Seamounts ( $5^\circ19.6'\text{N}$ ,  $110^\circ4.6'\text{W}$ ) in 3870 m of water. The entire sedimentary sequence in this hole is classified as one unit. The sediments examined in this study are included in the upper two of three subdivisions of that unit.

## BIOSTRATIGRAPHY

The N zonation of Blow (1969), as emended by Srinivasan and Kennett (1981a, 1981b) and Chaisson and Leckie (1993), was followed at all sites.

One biostratigraphic problem was the demarcation of the lower boundary of Zone N19/N20 in the eastern holes. This boundary was



used by Chaisson and Leckie (1993) in Hole 806B on the Ontong Java Plateau and is defined by the coiling change of the genus *Pulleniatina* (Berggren et al., 1985). In the western holes, all *Pulleniatina* change from left- to right-coiling through a very short interval. In the eastern holes, the first appearance of right-coiling specimens is followed by an interval through which left- and right-coiling specimens coexist. Because left-coiling *Pulleniatina* do not disappear in N19/N20 in the eastern holes, the lower boundary of that zone was redefined as coincident with the first appearance and persistence of right-coiling specimens, rather than by the change from left- to right-coiling.

## PLANKTONIC FORAMINIFERAL ECOLOGY

### Depth Stratification

Depth stratification of species populations in the water column has been verified by numerous workers (e.g., Bé, 1960; Hecht and Savin, 1972; Douglas and Savin, 1978; Deuser et al., 1981; Fairbanks and Wiebe, 1980; Fairbanks et al., 1980, 1982; Keller, 1985; Deuser, 1987; Deuser and Ross, 1989; Gasperi and Kennett, 1992, 1993). Depth stratification of foraminifer species is related closely to thermohaline stratification. While a single species may inhabit different depth ranges in different regions, each species tends to occupy water with a restricted range of densities throughout the world (Emiliani, 1954; Hecht and Savin, 1972; Savin and Douglas, 1973). Savin and Douglas (1973) suggested that individual foraminifers are able to control their density by an osmo-regulatory mechanism and thereby maintain a particular depth habitat.

The correspondence with density has been noted in light of an apparently confounding relationship with temperature. Cifelli (1971) examined the shell building temperatures ( $^{18}\text{O}$  determined) and found that *Globorotalia menardii* tests were formed at 19°–20°C and those of *Globorotalia tumida* between 15° and 19°C, surprisingly cool for species restricted to the tropics and subtropics. He interpreted the values of these isotopic temperature estimates as a reflection of the occurrence of species' population maxima at different depths in a thermally stratified water column. He also decided that shell-building temperatures were different in the past for a given species. *Globigerinoides sacculifer* shows a 6°C range of flux (isotopic temperature equivalent) in Caribbean cores (Cifelli, 1971). In the modern ocean, shell-building temperatures for a given species vary from location to location. It seems less likely that the temperature preference of *Gs. sacculifer* changes and more likely that the temperature of its preferred habitat, defined by the availability of nutrients, food and other parameters, changed within an genetically determined tolerable range of density, preserved to the fossil record as an isotopic temperature proxy.

A general relationship exists between test morphology and depth habitat that can be correlated with oxygen isotopic values. Regardless of age or taxonomy, homeomorphic species tend to occupy similar isotopic ranks: spinose, globigerine forms are shallow dwelling, found above the thermocline, and are eurytopic with a broad adaptive range, while nonspinose globorotaliid forms occupy deeper habitat near or below the thermocline with more specialized, narrower adaptive ranges (Douglas and Savin, 1978; Leckie, 1989).

The abundance of individual species is determined not only by interaction with the physical environment, but also by interaction with species in overlapping, adjacent niches (Ricklefs, 1979). For this reason, the appearance, disappearance, or variation in abundance of a single species cannot be used as a bellwether indicator of change in the physical environment. This may be particularly true in the tropical oceans. In the low latitudes, planktonic foraminiferal diversity is high as a result of low seasonality and a water column that is density stratified year round. There tend to be two or three dominant species (>20%) and the rest of the assemblage is composed of rare species. Three groups of species are described: (1) mixed-layer dwellers ("surface dwellers" in the terminology of Douglas and Savin, 1978), (2) thermocline dwellers ("intermediate dwellers" per Douglas and Savin, 1978), and (3) deep dwellers, which show population

Table 2. Depth habitat groups.

Surface	Thermocline	Deep
<i>Beella praedigitata</i>	<i>Globigerina bulloides</i>	<i>Candeina nitida</i>
<i>Dentoglobigerina altispira</i>	<i>Globigerina nepenthes</i>	<i>Globoquadrina conglomerata</i>
<i>Globigerina falconensis</i>	<i>Globigerina woodi</i>	<i>Globoquadrina dehiscens</i>
<i>Globigerina quinqueloba</i>	<i>Globigerinella calida</i>	<i>Globoquadrina venezuelana</i>
<i>Globigerina rubescens</i>	<i>Globigerinoides conglobatus</i>	<i>Globorotalia crassaformis</i>
<i>Globigerinella aequilateralis</i>	<i>Globorotalia inflata</i>	<i>Globorotalia truncatulinoides</i>
<i>Globigerinita glutinata</i>	<i>Globorotalia limbata</i>	<i>Globorotaloides hexagona</i>
<i>Globigerinoides fistulosus</i>	<i>Globorotalia menardii</i>	<i>Streptochilus</i> spp.
<i>Globigerinoides obliquus</i>	<i>Globorotalia merotumida</i>	
<i>Globigerinoides ruber</i>	<i>Globorotalia plesiotumida</i>	
<i>Globigerinoides sacculifer</i>	<i>Globorotalia scitula</i>	
<i>Orbulina universa</i>	<i>Globorotalia theyeri</i>	
<i>Pulleniatina obliquiloculata</i>	<i>Globorotalia tumida</i>	
<i>Turborotalia humilis</i>	<i>Neoglobobulimina acostaensis</i>	
	<i>Neoglobobulimina dutertrei</i>	
	<i>Neoglobobulimina pachyderma</i>	
	<i>Sphaeroidinella dehiscens</i>	
	<i>Sphaeroidinellopsis seminulina</i>	
<i>Globigerinita uvula</i> <sup>a</sup>	<i>Globigerina apertura</i> <sup>a</sup>	<i>Globorotalia crassula</i> <sup>a</sup>
<i>Globigerinoides extremus</i> <sup>a</sup>	<i>Globigerinella obesa</i> <sup>a</sup>	<i>Globorotalia tosaensis</i> <sup>a</sup>
<i>Globigerinoides tenellus</i> <sup>a</sup>	<i>Globorotalia juana</i> <sup>a</sup>	<i>Globoquadrina baromoensis</i> <sup>a</sup>
<i>Pulleniatina primalis</i> <sup>a</sup>	<i>Globorotalia anfracta</i> <sup>a</sup>	
<i>Pulleniatina spectabilis</i> <sup>a</sup>	<i>Globorotalia cibaoensis</i> <sup>a</sup>	
<i>Tenuitellids</i> <sup>a</sup>	<i>Globorotalia margaritae</i> <sup>a</sup>	
	<i>Globorotalia miocenica</i> <sup>a</sup>	
	<i>Globorotalia puncticulata</i> <sup>a</sup>	
	<i>Globorotalia unguata</i> <sup>a</sup>	
	<i>Sphaeroidinellopsis kochi</i> <sup>a</sup>	
	<i>Sphaeroidinellopsis paenedehiscens</i> <sup>a</sup>	

Notes: "Surface" corresponds to the mixed layer, "thermocline" is self explanatory, and "deep" refers to the part of water column below the thermocline (see Douglas and Savin, 1978; Keller, 1985).

<sup>a</sup>Depth habitats of these species have not been identified. Tentative assignments are based on phylogenetic relationship to species of known habitat and/or based on "morphologic category" (see Douglas and Savin, 1978). These species have not been assigned depth habitats on the basis of capture in net tows or isotopic ranking.

maxima below the thermocline. (Douglas and Savin [1978] and Keller [1985] further divide the intermediate group into upper and lower subgroups; see Table 2.)

### Trophic Level

Fairbanks et al. (1982) and Fairbanks and Wiebe (1980) demonstrated the association of various species with the deep chlorophyll maximum (DCM) found at the depth in the photic zone coincident with the top of the thermocline. The two limiting resources that control vertical distribution of planktonic foraminifers, either directly or indirectly, are light and the availability of nutrients. The interaction of light and nutrient levels controls the distribution of both phytoplankton and other zooplankton densities (Mann and Lazier, 1991). These biota are the food supply of the planktonic foraminifers and the density of the prey directly affects that of the predator.

In feeding experiments (Hemleben and Spindler, 1983) and by examination of the food vacuoles of captured foraminifers (Bé et al., 1977; Anderson et al., 1979; Bé, 1982), it was noted that these organisms do not feed on particular species. Rather, the diet of a species of planktonic Foraminifera includes distinct proportions of phytoplankton and zooplankton. *Hastigerina pelagica* is the most zooplanktivorous species (Anderson et al., 1979), but it is rarely preserved to the sediment and is unimportant in paleoecologic analysis. *Globigerinoides sacculifer* is the next most entirely zooplanktivorous species, but it does include diatoms in its diet (Anderson et al., 1979; Spindler et al., 1984). Other spinose species that have been investigated have shown varying appetites in terms of prey variety and the proportion of their diet that is zooplankton (Spindler et al., 1984). Nonspinose species accept pieces of zooplankton protoplasm (Anderson et al., 1977), but do not seem able to capture live prey (Spindler et al., 1984). They are, strictly speaking, detritivores (*sensu* Ricklefs, 1979). Spinose species consume more copepods, while nonspinose species consume more phytoplankton, and within the *Globigerinoides* group, the diet of *Gs. sacculifer* includes more zooplankton than does that of *Gs. ruber* (Spindler et al., 1984; Hemleben and Spindler, 1983). Because

planktonic foraminifers feed passively, ensnaring acceptable prey as it drifts by, the spatial variation in the densities of phytoplankton and other zooplankton populations may be an important factor influencing the relative abundance of various foraminiferal species.

Table 3 shows tentative trophic-level assignments for each species. Nonspinose planktonic foraminifers capture phytoplankton and most spinose planktonic foraminifers prey on both zooplankton and phytoplankton (Bé et al., 1977; Hemleben and Spindler, 1983; Spindler et al., 1984). Specialized exceptions to this rule include *Globigerina bulloides*, a spinose species adapted to productive areas of the oceans (Hecht, 1976; Duplessy et al., 1981), but generally this rule holds. The sediments examined in the course of this study are all less than 6 m.y. old and contain no taxa of ambiguous assignment with regard to spinosity. All species (with the exception of *Dentoglobigerina altispira*) are members of extant genera (see Table 3 for trophic-level assignment for each species)

## Diversity

The past 6 m.y. generally has been a period of decline in species diversity for planktonic foraminifers (Kennett, 1986; Wei and Kennett, 1986). This is plainly visible when looking at a plot of species richness through the entire Neogene section (Chaisson and Leckie, 1993, for Site 806), but difficult to see when looking at sediments of only the last 5.8 m.y. Species richness (a count of the number of species without regard to their abundance) decreased sharply in the global ocean during the Messinian (Wei and Kennett, 1986). At Site 806, Messinian richness levels were approximately equal to those to which they would later fall in the Pleistocene (Chaisson and Leckie, 1993).

True measure of diversity takes into account the weight of each species' contribution toward the species richness number. Diversity, then, is not only the number of species present, but also how abundant each of them is in a given sample. The Shannon-Wiener index  $[H(S)]$  is a popular measure of diversity:  $H(S) = -\sum p_i \ln p_i$ , where  $p_i$  is the proportion of the  $i$ th species (Gibson and Buzas, 1973). The value of  $H(S)$  is greater when all species present are equally common; this is considered maximum equitability. The greater the number of equally common species, the higher the diversity.

Leckie (1989) showed, using sediment trap data from two sites in the Pacific, that where the thermocline is weaker and deep in the photic zone, surface-dwelling *Globigerinoides* are abundant and thermocline-dwelling *Globorotalia* and *Neoglobobulimina* are rare. Where the thermocline is steeper and high in the photic zone, members of these three genera show equitable abundance (i.e., diversity is higher). One assumes, by virtue of the uniformitarian principle, that this relationship existed in the past as it does in the present and that increased diversity at a given site suggests the more equitable distribution of depth habitat within the photic zone. Raising the thermocline (more exactly, the pycnocline) in the photic zone is one mechanism for increasing diversity.

## RESULTS

### *Globigerina*

The relative frequencies of three *Globigerina* species decreased toward the middle Pliocene sections at all four sites. *Globigerina nepenthes* is never a dominant constituent of the assemblage at any of the sites at any point in the sections; it rarely accounts for >5% of the >125- $\mu$ m fraction (see Fig. 3). *Globigerina nepenthes* is most common in the upper Miocene (Zone N17b) at all sites except Site 807, and it tapers quickly upsection through the lower Pliocene. On the basis of isotopic evidence, Keller (1985) defined this species as an upper intermediate water dweller. In the terminology of Douglas and Savin (1978), "upper intermediate" denotes the portion of the water column just below the mixed layer and "above" the thermocline, the usual position of the nutricline where one exists (Fairbanks and Wiebe, 1980; Fairbanks et al., 1980, 1982). *G. nepenthes* disappeared

Table 3. Spinosity and trophic level.

Nonspinose and/or Herbivorous	
<i>Candeina nitida</i>	<i>Globorotalia plesiotumida</i>
<i>Dentoglobigerina altispira</i>	<i>Globorotalia puncticulata</i>
<i>Globigerina bulloides</i> <sup>a</sup>	<i>Globorotalia scitula</i>
<i>Globigerina quinqueloba</i>	<i>Globorotalia theyeri</i>
<i>Globigerinita glutinata</i> <sup>a</sup>	<i>Globorotalia tosaensis</i>
<i>Globigerinita uvula</i>	<i>Globorotalia truncatulinoides</i> <sup>a</sup>
<i>Globoquadrina barroemouensis</i>	<i>Globorotalia tumida</i> <sup>a</sup>
<i>Globoquadrina conglomerata</i>	<i>Globorotalia unguata</i>
<i>Globoquadrina dehiscens</i>	<i>Globorotaloides hexagona</i>
<i>Globoquadrina venezuelana</i>	<i>Neoglobobulimina acostaensis</i>
<i>Globorotalia anfracta</i>	<i>Neoglobobulimina dutertrei</i> <sup>a</sup>
<i>Globorotalia cibaoensis</i>	<i>Neoglobobulimina humerosa</i>
<i>Globorotalia crassaformis</i>	<i>Neoglobobulimina pachyderma</i>
<i>Globorotalia crassa</i>	<i>Sphaeroidinella dehiscens</i>
<i>Globorotalia inflata</i>	<i>Sphaeroidinella kochi</i>
<i>Globorotalia juanai</i>	<i>Sphaeroidinella paenedehiscens</i>
<i>Globorotalia margaritae</i>	<i>Sphaeroidinella seminulina</i>
<i>Globorotalia merotumida</i>	<i>Streptochilus</i> spp.
<i>Globorotalia miocenica</i>	Tenuitellids
Spinose and/or Omnivorous	
<i>Beella praedigitata</i>	<i>Globigerinoides fistulosus</i>
<i>Globigerina apertura</i>	<i>Globigerinoides obliquus</i>
<i>Globigerina falconensis</i>	<i>Globigerinoides ruber</i> <sup>a</sup>
<i>Globigerina nepenthes</i>	<i>Globigerinoides sacculifer</i> <sup>a</sup>
<i>Globigerina rubescens</i>	<i>Globigerinoides tenellus</i>
<i>Globigerina woodi</i>	<i>Globorotalia limbata</i>
<i>Globigerinella aequilateralis</i> <sup>a</sup>	<i>Globorotalia menardi</i> <sup>a</sup>
<i>Globigerinella calida</i>	<i>Orbulina universa</i> <sup>a</sup>
<i>Globigerinella obesa</i>	<i>Pulleniatina obliquiloculata</i> <sup>a</sup>
<i>Globigerinoides conglobatus</i>	<i>Pulleniatina primalis</i>
<i>Globigerinoides extremus</i>	<i>Pulleniatina spectabilis</i>
	<i>Turborotalita humilis</i>

Notes: Assignment to a "trophic level" was based on the predominant component of a species' diet. Species that feed largely on diatoms and dinoflagellates are referred to as "herbivorous," and species that feed largely on copepods and other zooplankton are referred to as "omnivorous."

<sup>a</sup>These species have been observed feeding or the contents of their food vacuoles have been examined. Apparently, nearly all planktonic foraminifers are omnivorous to some extent (Bé et al., 1977), and trophic assignments are based on what seems to be the largest portion of a species' diet. Other assignments are made on the basis of spinosity and its general correlation with trophic level (Hemleben and Spindler, 1983).

at the western sites at the top of Zone N18/N19, but persists into Zone N19/N20 at the eastern sites. The age of sediments in Zone N19/N20 corresponds to the time of the creation of the Central American land bridge (see Fig. 2).

*Globigerina woodi* has been conditionally ranked as a "lower intermediate" water dweller by Keller (1985). It is a dominant species at the western sites and a minor constituent of the eastern assemblages (see Fig. 4). Nearly one-half of all planktonic foraminifers counted at Site 807 at the top of the Miocene section were identified as *G. woodi*. In Zone N19/N20, *G. woodi* became rare in the west, decreasing to numbers equal to those typically found in the eastern equatorial Pacific. The overall temporal pattern of abundance when viewed geographically can be described as a switch from asymmetrical abundances in the east and west before 3.5 Ma to a symmetrical and reduced abundances following 3.5 Ma.

*Globigerina apertura* descended from *G. woodi* (Kennett and Srinivasan, 1983), but it shows an inverse temporal pattern of abundance at the western sites where, like its ancestor, it is an abundant species (see Fig. 5). For a discussion on distinguishing *G. woodi* and *G. apertura*, see Chaisson and Leckie (1993). Whereas *G. woodi* declines through the lower Pliocene, *G. apertura* increases through the same interval. Both species, however, decrease to a minimum through Zone N19/N20. Unlike *G. woodi*, however, *G. apertura* recovers above 3.5 Ma, but not to its pre-Zone 19/20 numbers, before tapering to extinction in Zone N22.

*Globigerina rubescens* appears in the middle Pliocene section. At the western sites, it first appears in Zone N19/N20 and at the eastern sites, during Zone N21 (see Fig. 6). By the upper Pliocene, it is distinctly more common (by an order of magnitude) in the west. The equatorial sites (806 and 847) at either end of the ocean show a similar pattern: gradual increase in representation to an apex in the middle

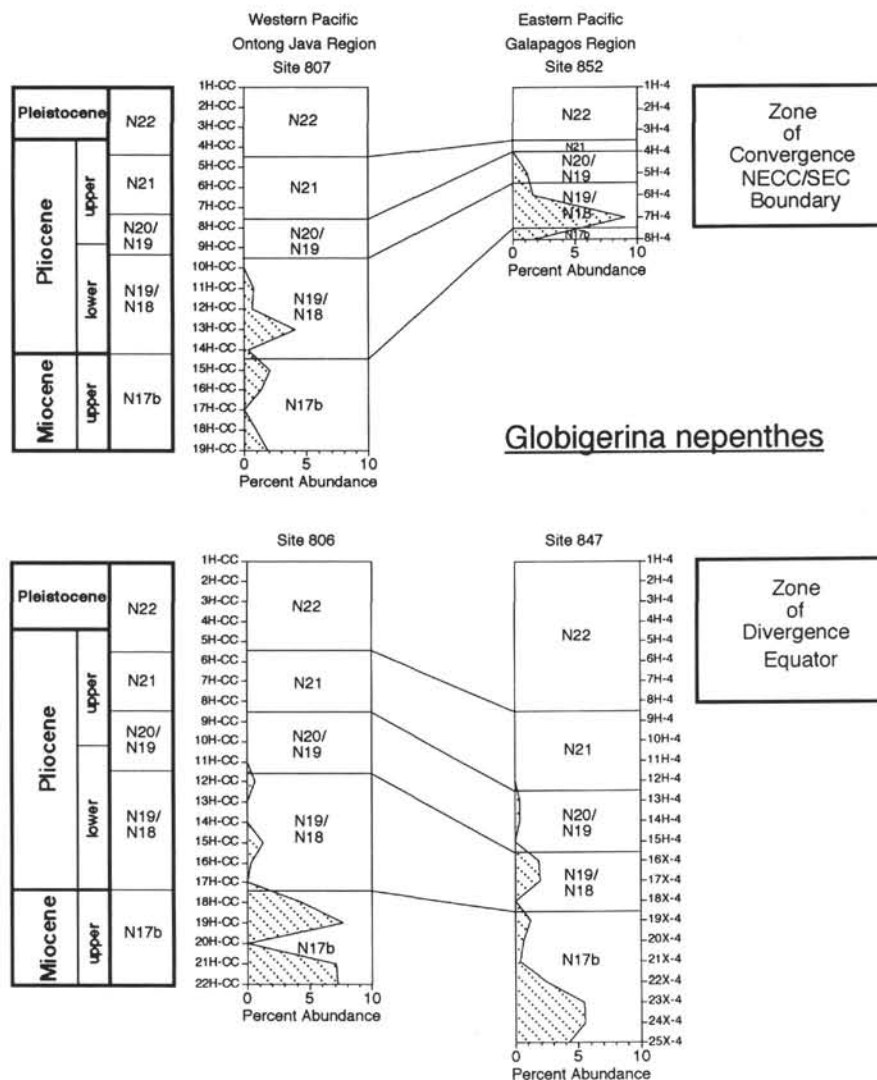


Figure 3. Relative abundance of *Globigerina nepenthes* in cores from Sites 806, 807, 847, and 852. Top row represents the two sites beneath the convergence zone between the SEC and the NECC. Bottom row represents the two sites beneath the equatorial divergence zone. Left column represents the sites in the western equatorial Pacific; right column represents the sites in the eastern equatorial Pacific.

Pleistocene and then decrease to the top of the section. The convergence zone sites (807 and 852) are difficult to compare. Dissolution removes this susceptible species at Site 852 from all samples, except the topmost. *Globigerinita glutinata* and *Globigerinoides sacculifer*, two other surface-dwelling, solution-susceptible species, also show increases in numbers from Sections 138-852-2H-4 to -1H-4. At Site 807 in the western Pacific, *G. rubescens* becomes steadily more common from its initial appearance to the top of the section. It is possible that solution hides this pattern at Site 852 until test production outpaces test destruction in the topmost sample.

### *Globigerinoides*

Three species of this genus appear in significant numbers. *Globigerinoides obliquus* is present in low numbers from the bottom of all of the sections into the upper Pliocene (see Fig. 7). In the western sections, it reaches a maximum in Zone N19/N20, but never accounts for more than 7% of the assemblage (Site 806). Through the upper Pliocene, *Gs. obliquus* and *Globigerinoides ruber* have a reciprocal relationship (see Fig. 8). By the uppermost Pliocene at Site 807, *Gs. ruber* accounted for between 25% and 30% of the assemblage before

gradually declining to approximately 15% at the top of the section. At Site 806, this species increases slowly, but steadily, through the upper Pliocene and averages around 15% through the Pleistocene before declining abruptly to 5% of the assemblage at the top of the section. At the eastern sites, *Gs. ruber* is less common, but shows similar trends (*Gs. ruber* appears as *Gs. obliquus* disappears) and reaches a maximum directly above the extinction of the latter species. This coupled extinction and expansion is coincident with the intensification of Northern Hemisphere glaciation (~2.5 Ma).

*Globigerinoides sacculifer* is present throughout, but only occasionally accounts for more than 10% of the assemblages (see Fig. 9). The three morphotypes in the "sacculifer plexus" delineated by Kennett and Srinivasan (1983) are considered ecophenotypes of *Gs. sacculifer* here. The nonsaccate morphotype ("*Globigerinoides triloba*") generally is more abundant throughout. *Gs. sacculifer* generally is more abundant at the convergence zone sites than at the sites in the equatorial divergence zone (see Fig. 10). Abundance of specimens with and without the saclike final chamber generally fluctuate in synchrony throughout the sections, as they do when examined at higher resolution through the Pleistocene in the equatorial Pacific (Thompson, 1976).



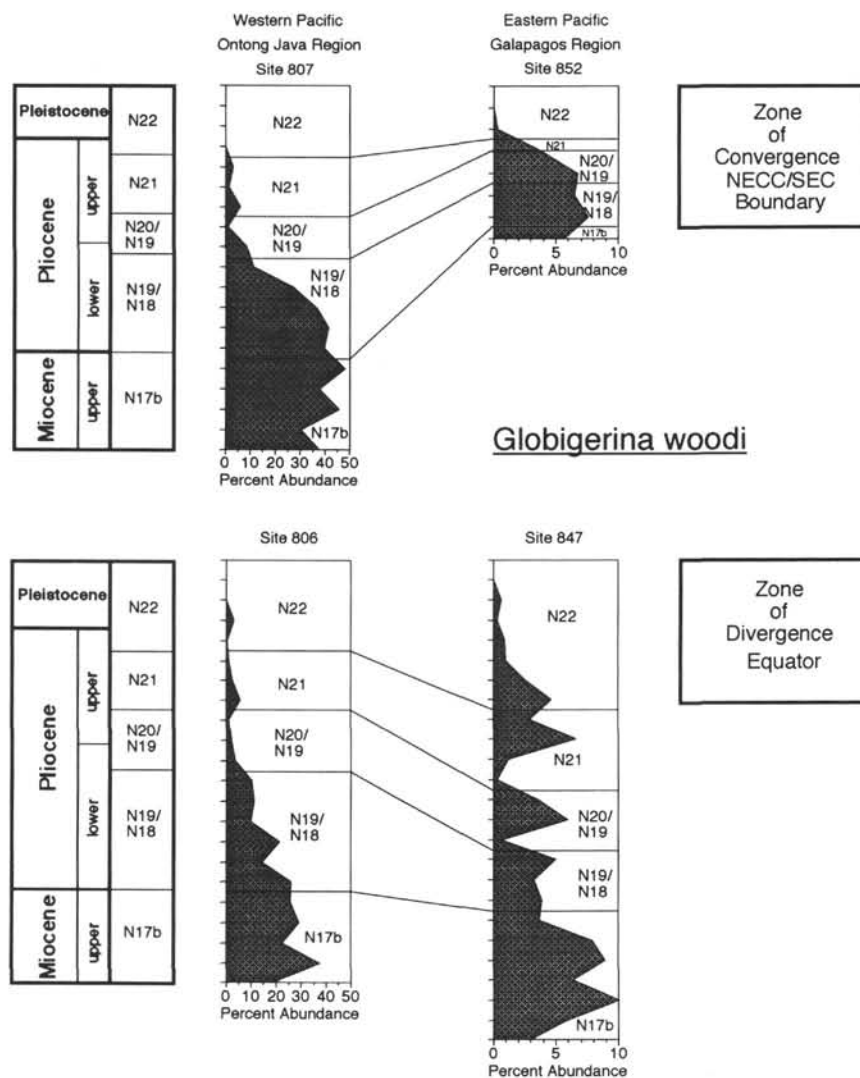


Figure 4. Relative abundance of *Globigerina woodi* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3. Abundance axes have been expanded to 50% at the western sites.

### *Globigerinita glutinata*

*Globigerinita glutinata* is a small species and use of the >125- $\mu$ m fraction, rather than the more widely used >150- $\mu$ m fraction, causes this species to become a significant part of the measured sediment assemblage. It is present in every sample at all four sites, usually making up at least 15% of the assemblage (see Fig. 11). In the two convergence zone sites, it is present in steady numbers from the upper Miocene to the mid-Pliocene. In the east (Site 852), it declines through the upper Pliocene (N19/N20), nearly disappearing in the Pleistocene (N22), before recovering in the topmost sample to approximately 10% of the assemblage. In the west (at Site 807), the decline begins at the N21/N22 boundary with a similar recovery in the topmost sample. As with *Globigerina rubescens*, the numbers of this solution-susceptible species are reduced in the east relative to the west, but the pattern of relative abundance through the section is similar.

The equatorial sites present a more complicated picture. In the west (Site 806), *Globigerinita glutinata* forms an increasingly large portion of the sediment assemblage from the bottom of the Pliocene to the middle Pliocene, where in one sample it constitutes 50% of the foraminifers counted. It then declines to approximately 30% in the upper Pliocene (middle N21), before recovering to 40% in

the Pleistocene. In the east (Site 847), this species shows broad peaks in the upper Miocene, middle Pliocene, and uppermost Pliocene-lower Pleistocene.

### *Globorotalia tumida*

The first occurrence of this species marks the boundary between Zones N17b and N18/N19 (Miocene/Pliocene boundary). It is rare at every site but Site 852, where its relative abundance is swollen by dissolution of other species, particularly in the upper Pliocene and the lower Pleistocene (see Fig. 12). Even in Hole 852B, it was rare near its first appearance. Although found in Section 138-852B-7H-4 in the course of doing biostratigraphy, no specimens were seen during the population count. All of the abundance peaks of this species are probably exaggerated to some degree by carbonate dissolution; this is one of the most solution-resistant species of planktonic foraminifer (Berger, 1970).

The compression of Zone N21 (no samples were observed to be completely within this zone) at Site 852 is accompanied by an increase in the abundance of *Gr. tumida* to 25% of the assemblage. This is a good indication that this peak corresponds to a series of dissolution events, rather than to any surface hydrographic phenomenon. At the

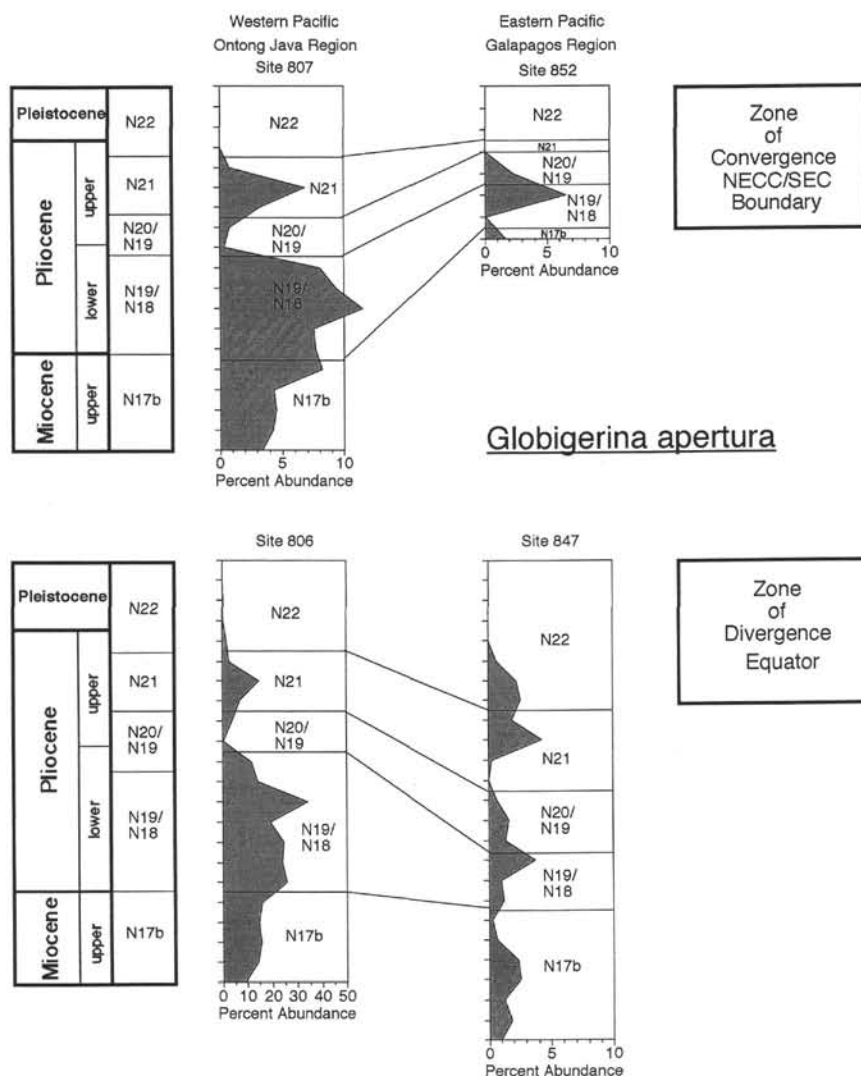


Figure 5. Relative abundance of *Globigerina aperture* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3. Abundance axes have been expanded to 50% at the western sites.

shallower equatorial Site 847, preservation is better and the "peak" at Site 852 resolves into two smaller peaks immediately above and below Zone N21. In the western Pacific at Site 806, where preservation is very good, three sharp peaks appear through the same interval. At Site 807, a broad peak in abundances of *Gr. tumida* begins in upper Zone N19/N18 and ends abruptly in middle Zone N21. Were these peaks created only by dissolution, then solution-susceptible species would be expected to decline in all samples where *Gr. tumida* showed sharp increases. In Sample 130-806B-9H-CC, *Gr. tumida* reaches its maximum value in the section. In this sample, the relatively more solution-susceptible *Globigerinita glutinata* declines abruptly, but the even more susceptible *Globigerinoides sacculifer* attains a maximum. *Pulleniatina primalis*, another solution-resistant species, would be expected to show gains in this sample were the increase of *Gr. tumida* merely an artifact of dissolution. In fact, the record shows no significant change in the abundance of this species.

The coarseness of the temporal resolution in this study and the general scarcity of *Globorotalia tumida* prevents identification of a clear relationship between its abundance pattern and dissolution or oceanographic history. At Sites 806, 807, and 852, the species fluctuates most widely through the Pliocene and then levels off in the Pleistocene. At Site 847, it does not level off in the Pleistocene.

### *Globorotalia menardii*

In agreement with the observations of Ericson et al. (1964), a shift from largely right-coiling specimens to largely left-coiling specimens occurs above the Pliocene/Pleistocene boundary at all sites except Site 806, where very few *Globorotalia menardii* and only one left-coiling specimen were found in the Pliocene and the Pleistocene portions of the section (see Figs. 13 and 14). An almost complete absence of left-coiling *Gr. menardii* can be observed at the equatorial Sites 806 and 847 through the lower Pliocene, while at the convergence zone, Sites 807 and 852, this is the dominant morphotype through this interval.

### Neogloboquadrinids

The temporal and geographic changes in the abundance of *Neogloboquadrina acostaensis* echo the changes in coiling direction of *Globorotalia menardii*; a tendency exists for the pairs of sites in the same hydrographic realm to resemble one another more than pairs of sites on the same side of the ocean.

In the eastern equatorial Pacific, *Neogloboquadrina acostaensis* is a dominant species in the sediment assemblage in the upper Mio-

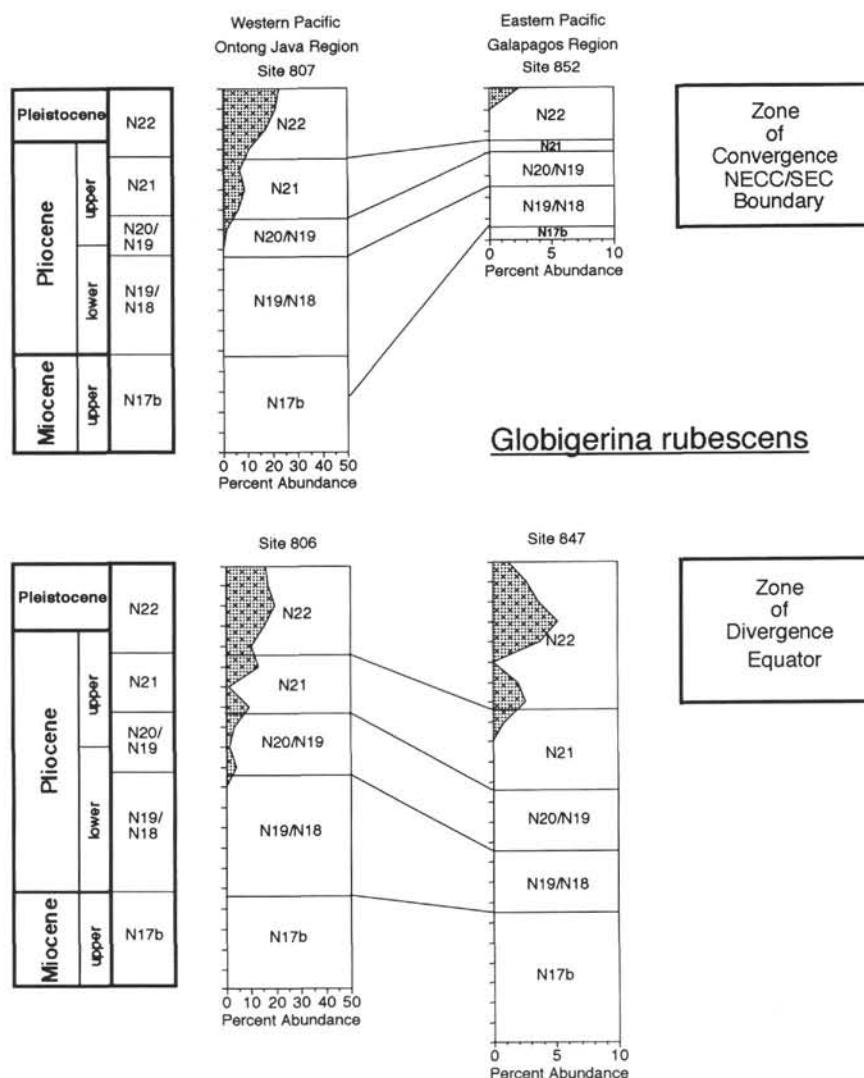


Figure 6. Relative abundance of *Globigerina rubescens* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3. Abundance axes have been expanded to 50% at the western sites.

cene and much of the Pliocene (see Fig. 15). Its abundance pattern at Site 847 resembles that of Site 806, except that the numbers are greater by an order of magnitude in the east. At both equatorial sites, this species makes a recovery in the middle Pliocene before disappearing in the upper Pliocene. This resembles the pattern expressed by *Globigerina woodi*, but *G. woodi* persists farther upsection.

The peak in abundance at the bottom of Zone N21 in Hole 807B may be correlated with the increase in abundance observed at Site 852 in the bottom of Zone N21. Zone N22 is truncated in Hole 852B, and the top of this peak may be missing. At both convergence zone sites, *N. acostaensis* seems to peak in the upper Pliocene, rather than during the mid-Pliocene (~3.5 Ma), as it does at the equatorial sites, although the "peak" at Site 806 is merely a small revival to ~2% of the assemblage from near disappearance.

*Neogloboquadrina humerosa* and *Neogloboquadrina dutertrei* were not distinguished in this study (see Fig. 16). Large, five-chambered neogloboquadrinids appear in the upper Miocene at all the sites except Site 852. They are rare everywhere in the upper Miocene and were probably removed by solution at Site 852.

A definite asymmetry in the abundance of *Neogloboquadrina dutertrei* develops between the eastern and western sites in the upper Pliocene. In the west, the numbers of *N. dutertrei* decline toward the top of the section, with one reversal of this trend at the bottom of Zone

N22. Throughout the sections, *N. dutertrei* is more abundant at Site 807 than at Site 806. At the eastern sites, the numbers of *N. dutertrei* steadily expand toward the top of the sections. It is a dominant species in the eastern sediment assemblages through the uppermost Pliocene and Pleistocene.

### Pulleniatinids

The change in the coiling direction of *Pulleniatina* tests that has been used as a biostratigraphic marker (Berggren, 1973; Chaisson and Leckie, 1993) does not seem to be everywhere identical in character (see Fig. 17). In Hole 806B, the transition upsection from a left- to a right-coiling population was rapid (Chaisson and Leckie, 1993). Chaisson and Leckie (1993) examined one sample per section in this hole, and the population of *Pulleniatina primalis* went from all left- to all right-coiling from one sample to the next. Only core-catcher samples have been examined so far in Hole 807B, and both left- and right-coiling specimens appear in Sample 130-807B-9H-CC. In the eastern holes, only one sample per core has been examined, but the first occurrence of right-coiling *Pulleniatina* is in lower Zone N21 in Hole 847B and lower Zone N22 in Hole 852B. In the eastern holes, left-coiling specimens persist to mid-N22 (138-847B-5H-4) in Hole 847B and to the top of the section in Hole 852B.



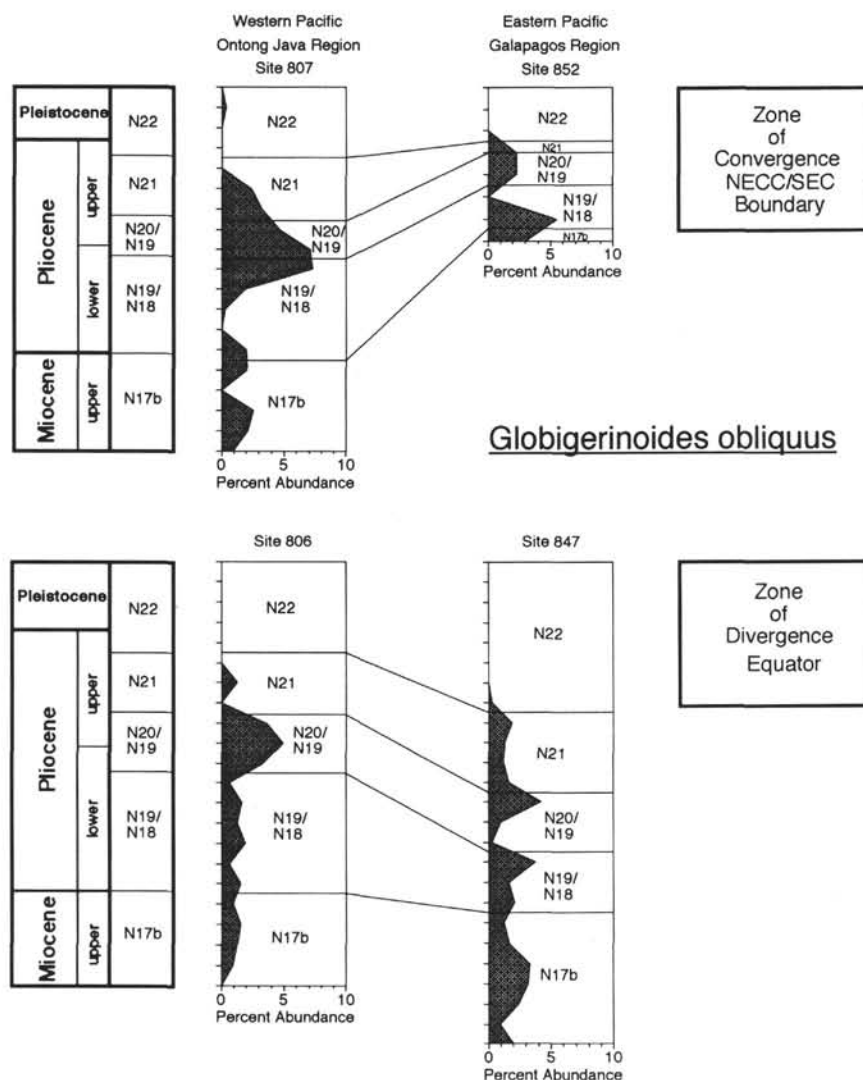


Figure 7. Relative abundance of *Globigerinoides obliquus* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3.

The transition from left- to right-coiling populations of *Pulleniatina primalis* at the western sites is at approximately 3.8 Ma, and the disappearance of the species in the west occurs at approximately 2.5 Ma, where it was completely replaced by *Pulleniatina obliquiloculata* (see Appendix A). *P. primalis* persists farther upsection in the east, and the first occurrence of right-coiling specimens is upsection of the interval associated with the closing of the seaway. *Pulleniatina obliquiloculata* (with the apertural lip wrapping around to the spiral side) does not appear until Zone N22 in the east. Scattered specimens of “obliquiloculata-type” pulleniatinids in Hole 806B first appear in the upper Pliocene, but do not outnumber the “primalis-type” until the upper Pliocene (Zone N21). In Hole 807B, the two forms are present in roughly equal (low) numbers in Zone N19/N20 and lower Zone N21.

## ECOLOGICAL GROUPS

### Depth Habitat

At the base of all four sections examined in this study, the mixed-layer group makes up approximately 40% of the sediment assemblage, the thermocline-dwelling group makes up most of the remaining 60%, and the deep-dwelling taxa usually amount to roughly 5% of the total (see Fig. 18). These proportions are maintained at all sites through

Zone N17b (uppermost Miocene) and much of Zone N19/N18 (lower Pliocene). An abrupt change occurs at both of the western sites in upper Zone N19/N18. In the western tropical Pacific, the proportions reverse, with the mixed-layer group amounting to 60% of the sediment and the thermocline-dwelling group defining most of the remaining 40%. This change in population structure began at the same time that the Central American seaway began to close (~3.8 Ma).

In the interval associated with the intensification of Northern Hemisphere glaciation at the top of Zone N21, the trend is exacerbated. The increase in the proportion of mixed-layer dwellers at this point in the western sections is more dramatic at Site 807, where the thermocline dwellers had maintained a slightly greater presence through the upper Pliocene section than they had at Site 806.

The deep dwellers (primarily *Globoquadrina conglomerata* and *Globorotaloides hexagona*) in Hole 806B account for a steady 5% of the sediment assemblage through Zone N22. The mixed-layer group makes up about 70% of the assemblage at the bottom of Zone N22 and then steadily expands at the expense of the thermocline-dwelling group until, in Sample 138-806B-1H-CC, the mixed-layer species represent >80% of the assemblage. In Hole 807B, the mixed-layer group accounts for about 80% of the sediment assemblage at the bottom of Zone N22, then decreases to about 75% and maintains that level to the top of the section.

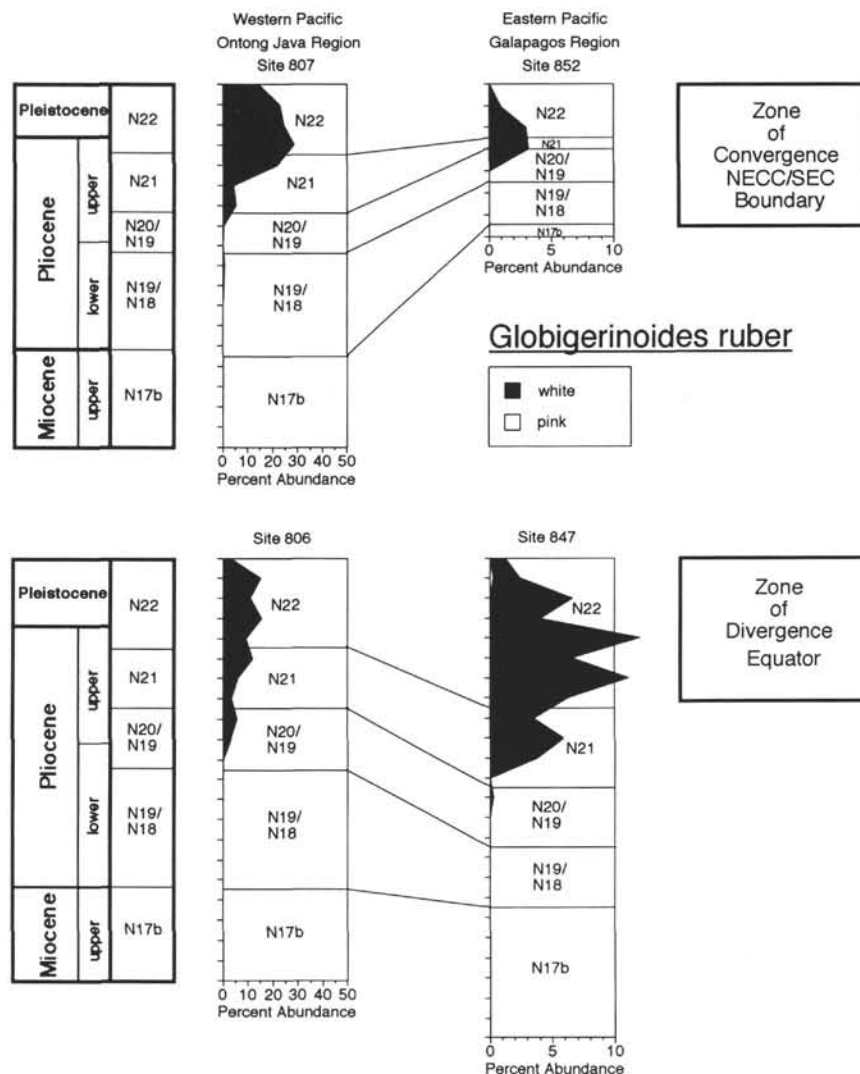


Figure 8. Relative abundance of *Globigerinoides ruber* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3. Abundance axes have been expanded to 50% at the western sites.

By contrast, the eastern sites show no pronounced changes in proportions of the different depth groups through the mid-Pliocene (3.8–3.2 Ma). No permanent mid-Pliocene shift at Site 847 is comparable to the one at Site 806. The pattern in Hole 852B is a temporally coarser, compressed version of the one in Hole 847B. The 60% mixed-layer group/40% thermocline group proportionality is maintained in Hole 847B until approximately 2.5 Ma, after which the thermocline group briefly decreased, but then expanded steadily toward predominance at the top of the section.

### Spinosity and “Trophic Level”

Here, planktonic foraminiferal species that have been shown to capture live prey will be referred to as omnivores, while species that feed primarily on living phytoplankton and zooplankton detritus will be referred to as herbivores. An extinct species will be assumed to share the same trophic level with modern members of its genus (with known diet) unless evidence to the contrary exists based on isotopic information or biogeographic distribution.

A pronounced difference can be seen between the eastern and western equatorial sites with reference to the proportions of each trophic level in the sediment assemblages (see Fig. 19). The omnivores (spinose species) are far more important in the western holes,

constituting between 40% and 60% of the assemblages in all samples except through one interval. Through the middle Pliocene (3.8 to 3.2 Ma) at Sites 806 and 807, a definite and surprisingly symmetrical (up and down section) expansion and contraction of the herbivorous (nonspinose) species is found, so that at Zone mid-N19/N20, they account for approximately 75% of all foraminifers counted. Hole 807B is the one most completely dominated by omnivores above and below this interval: they usually make up approximately 60% of the sediment assemblage.

Omnivorous species in Hole 847B rarely make up more than 20% of a sediment assemblage. No definite excursions by either trophic group occurred during the middle Pliocene. In Hole 852B, the omnivores are more numerous, not for any ecological reason, but because *Pulleniatina obliquiloculata* is overrepresented because of its resistance to carbonate dissolution. However, in spite of enhancement by dissolution, the omnivores make up more than 30% of the assemblage in only one sample in Hole 852B.

### Diversity

The general trend in species richness at the western sites is one of gradual increase through the Pliocene (recovery from the latest Miocene plunge) ending abruptly in the uppermost Pliocene (see Fig. 20).

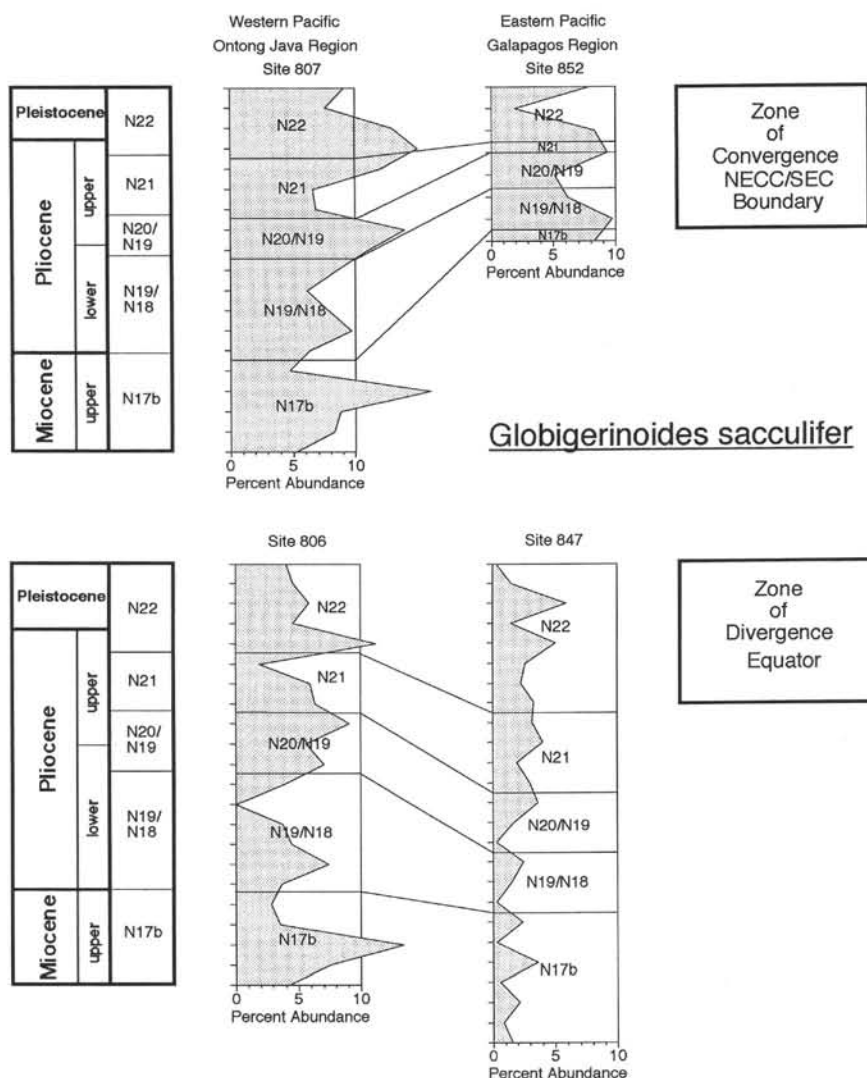


Figure 9. Relative abundance of *Globigerinoides sacculifer* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3.

Richness is generally greater at Site 806 than at Site 807 throughout. The peak values in the uppermost Pliocene are 28 species at Site 806 and 24 species at Site 807. The average species richness throughout the last 5.8 m.y. is 23 species at Site 806 and 19 species at Site 807.

The sites in the eastern equatorial Pacific exhibit the same trend in species richness as the western sites, but less clearly. The average species richness at Site 847 throughout the past 5.8 m.y. is equal to that of Site 806. Even when averaged over the entire depth of each section, the sites in the zone of divergence on the equator have a higher species richness than those in the zone of convergence on the boundary (~23 vs. ~20).

The Shannon-Wiener diversity index for the entire assemblage at each site shows trends similar to those seen in the species richness curves (see Fig. 21). The  $H(S)$  of Site 852 is high, probably because differential carbonate dissolution has removed many of the rarer species to leave resistant species to become more equitably abundant by default.

The diversity index of depth habitat groups restates the trends seen in Figure 18 (which shows their percent abundance change). Diversity of depth habitat groups declines steadily at the western sites through the last 5.8 m.y. It also declines steadily at Site 852 in the east, although the role that dissolution has in this trend is uncertain. Little change in depth habitat diversity at Site 847 takes place until the

mid-Pleistocene (Zone N22). In contrast to the depth habitat group diversity, overall diversity at the western sites changes little throughout the section at the western sites, indicating that within-group diversity of the mixed-layer group increases as its proportion of the entire assemblage increases. At the eastern sites, the depth habitat diversity curves and the whole assemblage diversity track each other, indicating that as the thermocline dwellers expand their proportion of the assemblage, they do not diversify.

## DISCUSSION

### *Globigerina*

*G. nepenthes* and *G. woodi* are intermediate-depth dwellers (Keller, 1985), while the niche of *G. apertura* is not known. *Globigerina nepenthes*, lighter isotopically, may have been a specialized descendant of the opportunistic *G. woodi* that adapted to a narrower portion of the photic zone, perhaps a weak nutricline at the top of a deep thermocline. The closing of the Central American seaway was associated with increased build-up of warm surface water in the western equatorial Pacific. As the source of upwelled water became more nutrient-poor, the food supply of *G. nepenthes* decreased and so did its numbers. Intensified gyre circulation would advect nutrient-rich water from the temperate water masses into the eastern equatorial



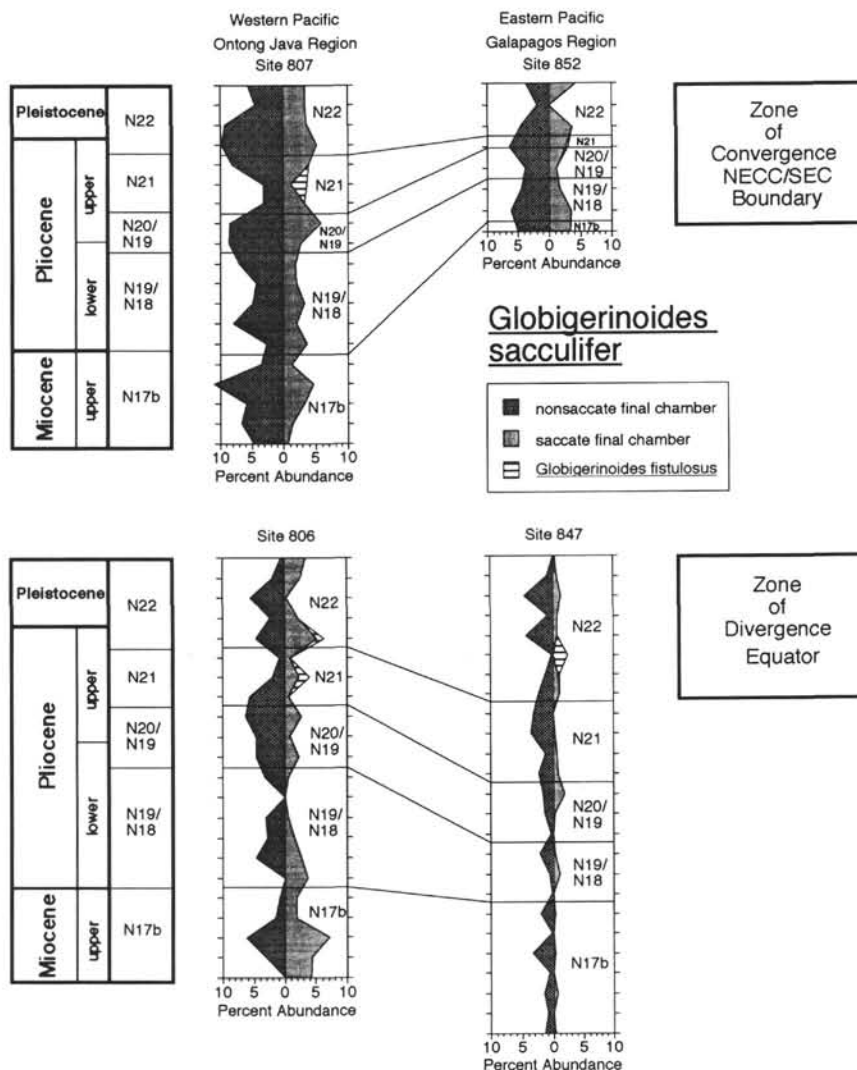


Figure 10. Relative abundance of *Globigerinoides sacculifer* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3, but with a central axis dividing the abundance of nonsaccate specimens from that of saccate specimens (both simple sac forms and *Gs. fistulosus*).

Pacific, permitting *G. nepenthes* to survive there until increasing seasonality of that water led to its extinction.

Usually identified as a temperate to warm subtropical species (Kennett and Srinivasan, 1983; Kennett et al., 1985), *Globigerina woodi* was probably found in large numbers in the western equatorial holes because the >125- $\mu$ m fraction was counted. Specimens found outside the optimal habitat of a species are often small (Hecht, 1976). *G. woodi* seems to be the oligotrophic ecologic equivalent of the *Neoglobobadrina* genus. It is more common in the west, especially in the upper Miocene and lower Pliocene sections of Hole 807B. Site 807 was off the equator and moving toward the convergence zone during the late Miocene, having crossed the equator during the middle Miocene (Berger et al., 1993).

During the mid-Pliocene Central American seaway-closing interval, *Globigerina woodi* percentages in Ontong Java Plateau holes declined and became equal to those typically found in the eastern equatorial Pacific. The increase in the thickness of the mixed layer following the seaway closing may have submerged *G. woodi*'s niche below the photic zone, diminishing its food supply and, therefore, its numbers. The "intermediate" (*sensu* Douglas and Savin, 1978) water-dwelling *G. woodi* disappeared, most likely because its niche did so. Its habitat was probably deep in the photic zone in tropical oligotrophic

waters. After the seaway closing, *G. woodi* was replaced by *Neoglobobadrina dutertrei*, a more purely herbivorous species (Spindler et al., 1984) than are *Globigerina*. Modern *Globigerina* typically require a mixture of phytoplankton and zooplankton in their diet (Spindler et al., 1984). The subgenus *Zeaglobigerina*, which includes *G. woodi*, *G. apertura*, and *G. nepenthes*, does not appear to have been spinose (Kennett and Srinivasan, 1983). Spines seem to be necessary for capturing live zooplankton.

Lourens et al. (1992) considered *G. apertura* to be a surface dweller because it is ancestral to *G. rubescens*. *Globigerina apertura* tends to be more inflated than its ancestor, *G. woodi* (Kennett and Srinivasan, 1983) and, consequently, to have less chamber overlap. This morphology suggests that it may have inhabited shallower depths. This suggestion is not contradicted by the patterns of abundance shown by these two species in Holes 806 and 807. *G. apertura*'s decline in the middle Pliocene is abrupt and follows a period of expansion. For *G. woodi*, the consequences of the seaway closing seem merely to have hastened a gradual decline toward extinction.

*Globigerina rubescens*, a possible descendant of *G. woodi* through *G. decoraperta* (Kennett and Srinivasan, 1983), seems to have inaugurated a new era for the genus in the post-seaway Pacific. *G. rubescens* is a solution-susceptible (Berger, 1970) surface dweller

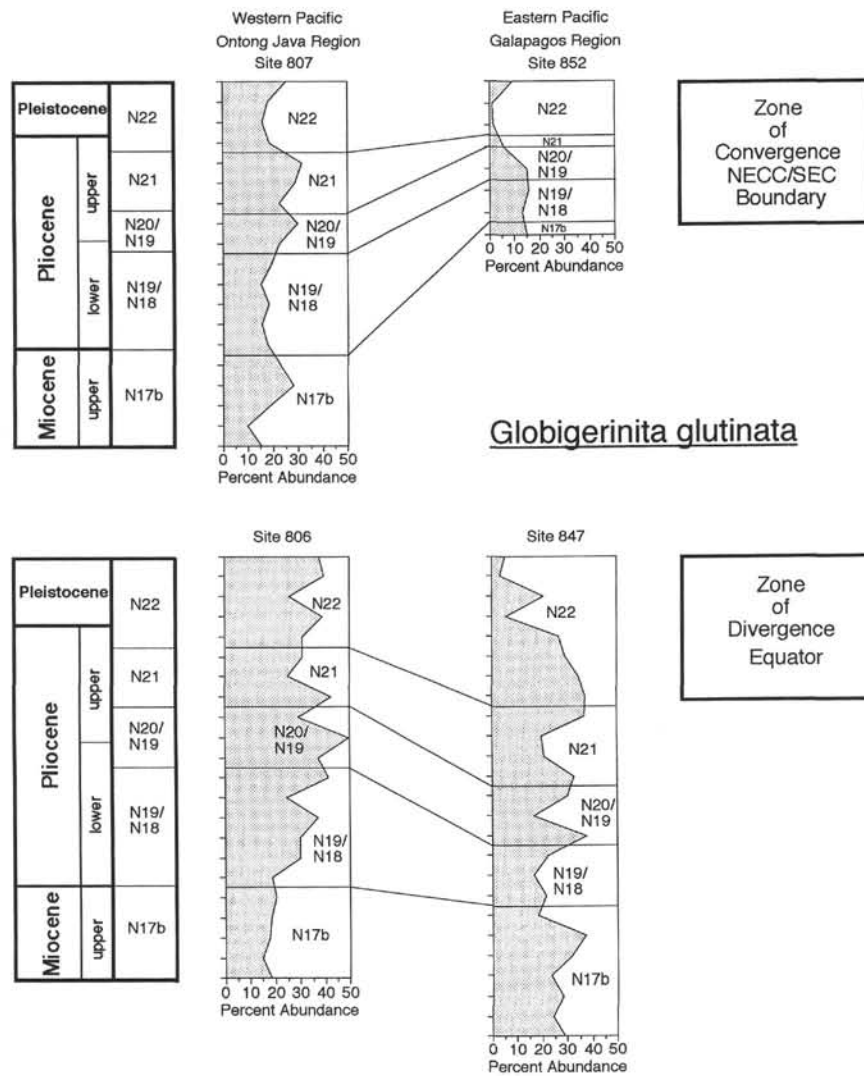


Figure 11. Relative abundance of *Globigerinita glutinata* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3. Abundance axes have been expanded to 50% at the western sites.

in the modern ocean (Hemleben et al., 1989). Its earlier appearance in the western equatorial regions may indicate that the deeper-dwelling "Miocene" globigerinids were declining through the Pliocene as result of thickening of the mixed layer over the Ontong Java Plateau. The period of expanding *G. rubescens* from the mid-Pliocene to the mid-Pleistocene, observed at all sites (except the very deep Site 852), corresponds well to the period between the beginning of Northern Hemisphere cooling (3.2 Ma), through the intensification of Northern Hemisphere glaciation (2.4 Ma) to the beginning of the dominance of the 100-k.y. period for glacial/interglacial cycles (0.9 Ma) observed in the  $\delta^{18}\text{O}$  record (Thunell and Williams, 1983).

The "Miocene" members of the *Globigerina* genus (*G. nepenthes*, *G. woodi*, *G. apertura*) were present in their greatest numbers in the western Pacific of the early Pliocene, but could not survive in the increasingly unstable late Pliocene. *G. rubescens* may have been more adapted to the climatic variability of the late Pliocene and early Pleistocene.

### *Globigerinoides*

*Globigerinoides ruber* frequently is described as the most solution-susceptible species of planktonic foraminifer (e.g., Berger, 1970). Comparisons among population counts done with sediments from ERDC

box cores from the Ontong Java Plateau reveal that the relative abundance of *Gs. ruber* in the surface sediments across the plateau is more strongly controlled by the depth of deposition than any physical environmental factor measured in the mixed layer (temperature, salinity, depth of mixed layer) (Chaisson, unpubl. data, 1992). One assumes that the homeomorphic *Globigerinoides obliquus* is as susceptible to dissolution as is *Gs. ruber*. This pair of species demonstrates a stratigraphic abundance pattern similar to that of *Globigerina apertura* and *G. rubescens*, as the older species decreases in abundance, the more recent one increases. However, *Gs. obliquus* and *G. apertura* show inverse patterns of abundance. The proportional representation of *Gs. obliquus* expands in Zone N19/N20 (the seaway-closing interval), while that of *G. apertura* contracts.

Note that *Gs. obliquus* increases at Site 852 through Zone N19/N20 in spite of the depth, while it declines at the more shallow Site 847. An oceanographic explanation may exist, such as a decrease in sea-surface temperature because of an increase in the influence of the Peru Current and/or a decrease in the depth of the mixed layer caused by increased upwelling. The data of Iwai (this volume) show a minimum in diatom flux in Hole 852B through the seaway-closing interval, certainly beneficial to species favoring oligotrophic waters. The eolian grain-size data of Hovan (this volume) for Sites 848, 849, and 853 indicate a sharp peak toward larger mean grain size, beginning from a low at ~4 Ma

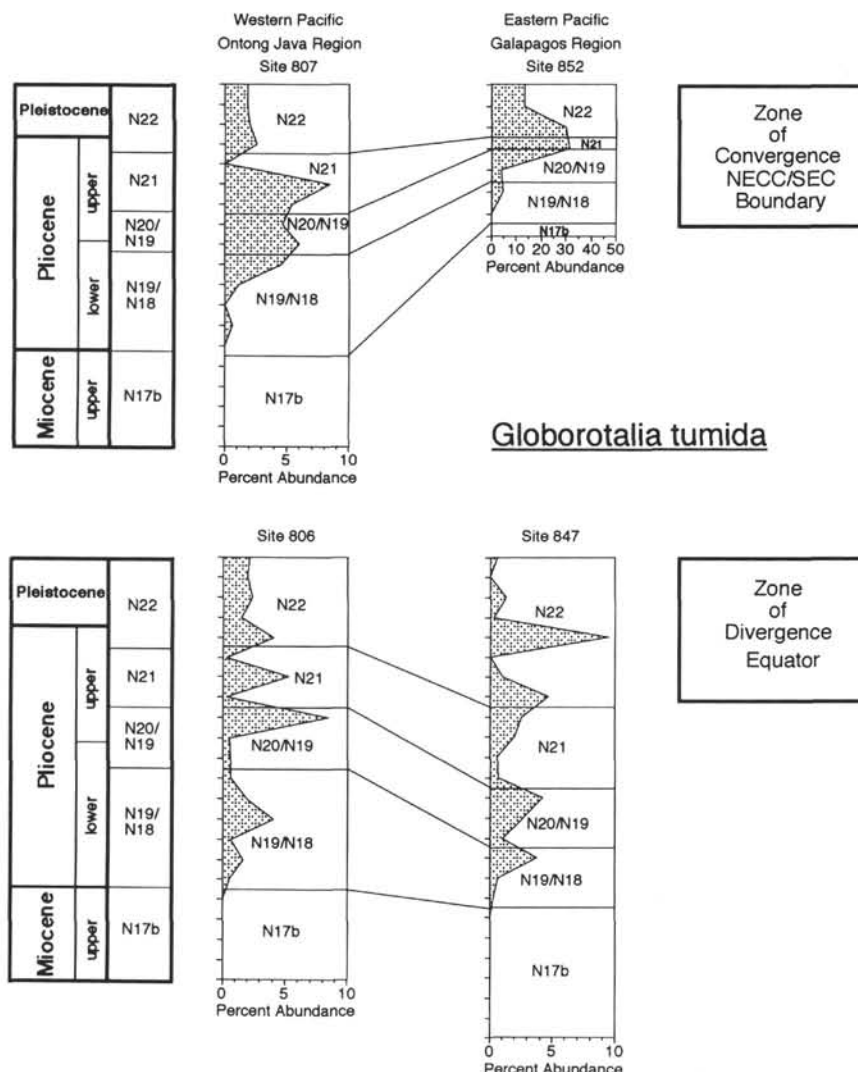


Figure 12. Relative abundance of *Globorotalia tumida* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3. Abundance axes are expanded to 50% at the Site 852.

and reaching a peak at ~3 Ma, strongly suggesting an increase in tradewind strength through the seaway-closing interval, consequently increasing equatorial divergence and decreasing the thickness of the mixed layer at the equator in the eastern equatorial Pacific, while it increased mixing in the zone of convergence.

By contrast, *Globigerinoides ruber* and *Globigerina rubescens* show similar patterns of abundance at all sites except Site 852, where dissolution during Pleistocene interglacials distorts the record. It may be possible to decide what part is played by climatic constraints imposed by ecology and the dissolution history of the sediments by testing for a correlation between the fragmentation index of the samples (Coulbourn et al., 1980) and the relative abundance of these two species.

*Gs. sacculifer* prefers more productive waters than does *Gs. ruber* (Bé and Hutson, 1977), and it is more resistant to dissolution than is *Gs. ruber*. Thus, it is difficult to discern whether this species is more common at the convergence zone sites because the sites are deeper or because they are more productive. In the eastern holes, the influence of dissolution is greater and the percentage of *Gs. sacculifer* may well be simply preservationally enhanced. In the modern western equatorial Pacific, the mixed layer is thickest over the equator and thins slightly away to the north and the thermocline is drawn marginally closer to the surface (Levitus, 1982; Delcroix et al., 1987). *Gs. sac-*

*culifer* may reproduce in the thermocline, while *Gs. ruber* completes its ontogeny within the mixed layer (Bé, 1982; Hemleben et al., 1989). Consequently, *Gs. sacculifer* may have derived some advantage from the slight thinning of the mixed layer. *Gs. sacculifer* also includes a higher percentage of zooplankton in its diet than does *Gs. ruber* (Spindler et al., 1984). Zooplankton maxima exist at 2°N and 2°S on either side of the phytoplankton maximum that exists exactly over the equator (Mann and Lazier, 1991). Therefore, more *Gs. sacculifer* may be found at Site 807 through much of the last 6 Ma because of the greater zooplankton density north of the equator. If the modern situation has been present in some form over the last 3.8 to 3.5 m.y., then perhaps the immediate vicinity of the equator is optimal for *Gs. ruber* and the area 2° to 3° on either side is optimal for *Gs. sacculifer*.

### *Globigerinita glutinata*

Loubere (1981) found the geographic distribution of *Globigerinita glutinata* to be more closely correlated to salinity than to temperature. If that is the case, then little in the way of a pattern of salinity distribution emerges from the data collected for this study. Asymmetrical changes in abundance of *Globigerinita glutinata* across the Pacific may generally indicate how events affected salinity: salinity



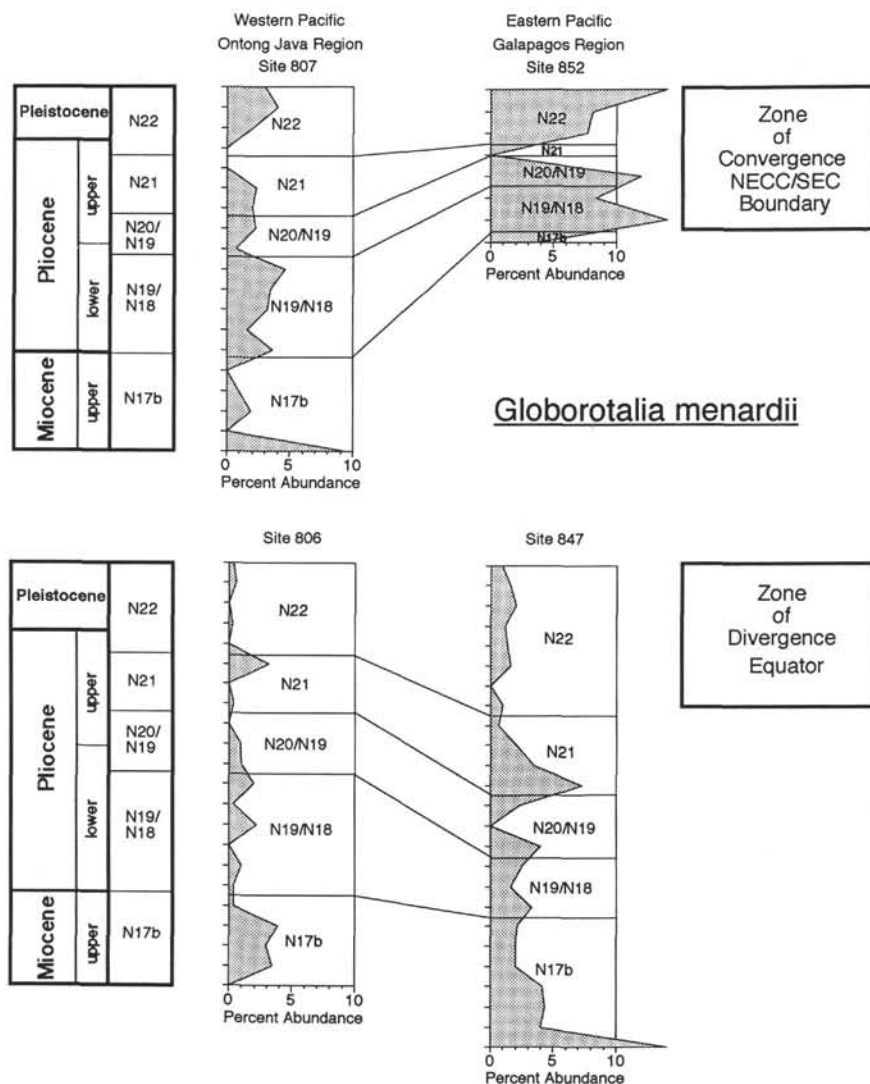


Figure 13. Relative abundance of *Globorotalia menardii* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3.

had opposite trends during the latest Miocene, similar trends during the mid-Pliocene seaway closing, and an indeterminate trend during the initiation of Northern Hemisphere glaciation.

### *Globorotalia tumida*

In the modern equatorial Pacific Ocean, *Globorotalia tumida* is most abundant in the central region. Because the position of the thermocline rises relative to the photic zone from west to east across the Pacific, the depth habitat of different thermocline-dwelling species successively intersects the bottom of the photic zone, where in the immediate presence of a plentiful food supply (Fairbanks and Wiebe, 1980; Fairbanks et al., 1980; 1982), it multiplies. *Pulleniatina obliquiloculata* is most common in the western equatorial Pacific, *Gr. tumida* in the central, and *Neogloboquadrina dutertrei* in the east (Kennett et al., 1985). During the late Miocene (8 Ma) time-slice of Kennett et al. (1985), this kind of provinciality did not exist. A strong return current (EUC) was established after the closing of the Indonesian seaway during middle to late Miocene time. The steepening of the equator-to-pole gradient strengthened the trade winds, increasing the strength of the NECC. Both of these currents carry warm water back across the Pacific Ocean and planktonic foraminifers with it, but

during the 8 m.y. since the Indonesian seaway closed, their influence has apparently been countered by the piling of warm surface water over the equator in the western equatorial Pacific Ocean.

The abundance peaks of *Globorotalia tumida* are too brief (one sample) at the equatorial sites (Fig. 12) to make an oceanographic interpretation in a study having such a coarse temporal resolution. The slightly more sustained peak (two samples) at Site 852 is in a very condensed interval and not interpretable (i.e., probably an artifact of dissolution). At Site 807, however, *Gr. tumida* represents >5% of the assemblage for five successive samples in the middle to upper Pliocene section (i.e., through the seaway-closing interval up to the intensification of Northern Hemisphere glaciation). This is an interval during which *Globigerinoides ruber* also became more abundant in this hole, making exaggeration of *Gr. tumida*'s representation by dissolution less likely. Apparently, hydrographic conditions were somewhat different at Sites 806 and 807 through the middle to upper Pliocene. Increased trade-wind strength (Hovan, this volume) may have been elevating the thermocline near the equator, but the build-up of the warm-water pool over the equator was having the opposite effect in the western equatorial region, depressing the thermocline most severely closest to the equator and pushing *Gr. tumida*'s habitat deeper than it may have been at 3°N.

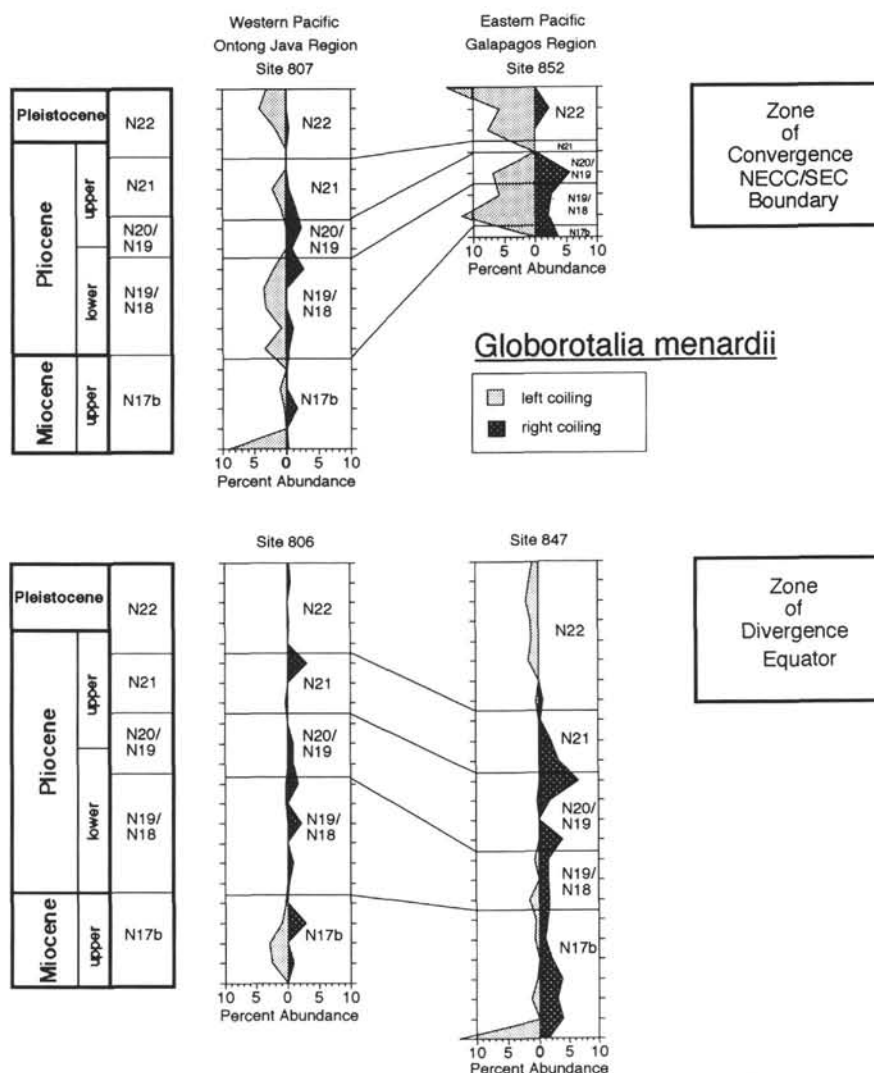


Figure 14. Relative abundance of *Globorotalia menardii* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3, but with a central axis dividing the abundances of left- and right-coiling specimens.

### Neogloboquadrinids

*Neogloboquadrina acostaensis* is the ecological equivalent of *Neogloboquadrina dutertrei* (Dowsett and Poore, 1990). In the eastern holes, a clear decline of the "Miocene" species and expansion of the modern one was seen. In the western holes, the transition from one morphology to the other was not as stratigraphically straightforward. The two morphologies coexist in smaller numbers in the west. The sum of their abundances in the west is approximately equal to the abundance of *N. acostaensis* alone in the east through the uppermost Miocene and lower Pliocene (Zones N17b and N18/N19). This is perhaps an indication that the western equatorial Pacific was already a suboptimal habitat for neogloboquadrinids by 5.8 Ma. The modern east-west zonation of thermocline dwellers (Kennett et al., 1985) was beginning to form.

### Pulleniatinids

As the smooth transition of one morphology to another took place in the optimal habitat for neogloboquadrinids, the initial coiling change and transition from the morphology of *Pulleniatina primalis* to *Pulleniatina obliquiloculata* took place more smoothly in the west-

ern equatorial Pacific, the modern optimal habitat of that genus (Kennett et al., 1985). The presence of Saito's (1976) short left-coiling intervals in the central equatorial region and the persistence of left-coiled specimens upsection in the eastern equatorial Pacific holes is further evidence of the connection between morphological consistency and the optimality of habitat (Hecht and Savin, 1972; Hecht, 1976).

The initial change in coiling direction used as a datum at 3.8 Ma (Zones N18/N19–N19/20; Chaisson and Leckie, 1993) in all of the ODP holes examined also is evident in Saito's (1976) central Pacific cores. In two of Saito's (1976) central equatorial Pacific piston cores that include the coiling-change interval and in the western equatorial Pacific ODP cores (Holes 806B and 807B), the change above 3.8 Ma is complete from left to right and continues to be complete until ~2.4 Ma. However, in the eastern Pacific, left-coiling specimens of *P. primalis* persist into the Pleistocene (Zone N22). A series of short left-coiling intervals in the central Pacific begins at 2.4 Ma and persists up to approximately 0.9 Ma (Saito, 1976). The beginning of this interval corresponds with the intensification of Northern Hemisphere glaciation and its end with the switch from higher-frequency, lower-amplitude glacial/interglacial cycles to larger 100K amplitude cycles in the mid-Pleistocene (Thunell and Williams, 1983; Joyce et

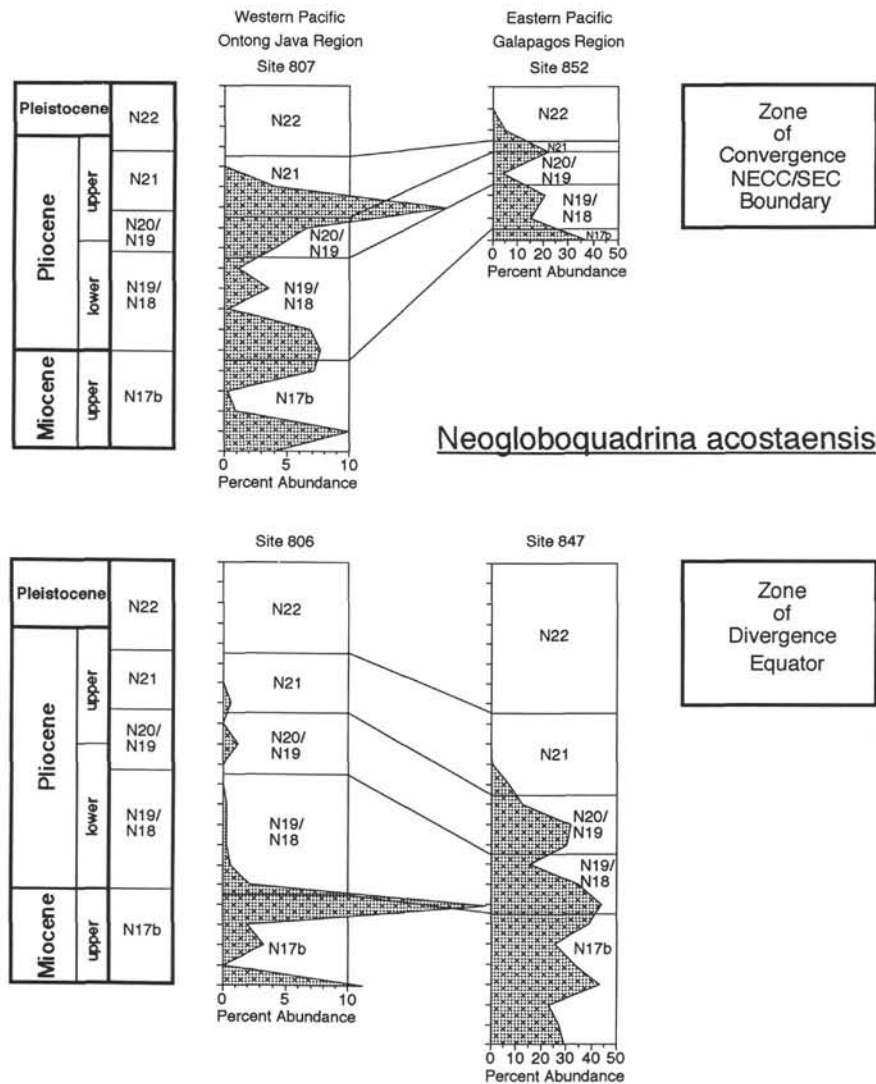


Figure 15. Relative abundance of *Neogloboquadrina acostaensis* in cores from Sites 806, 807, 847, and 852 arranged as in Figure 3. Abundance axes have been expanded to 50% at the eastern sites.

al., 1990). No sign of these left-coiling intervals can be seen in the western equatorial Pacific ODP holes.

### Depth Habitat

Separation of the planktonic foraminiferal species into groups defined by their depth habitat and inspection of their changing abundances in time-series provide the clearest indication of the hydrographic asymmetry that developed in stages through the late Neogene and that exists in the modern equatorial Pacific.

The asymmetry initially developed after the closing of the Indonesian seaway (Kennett et al., 1985; Chaisson and Leckie, 1993) and continued with the closing of the Central American seaway. This was accompanied by climatic cooling at the higher latitudes and further intensified gyral circulation. The thermocline was lifted to new, more shallow depths in the photic zone of the eastern equatorial Pacific, and the thermocline was submerged ever deeper beneath a thickening mixed layer in the western equatorial Pacific.

The decline of the thermocline dwellers in the west is a steady trend over the entire 5.8-m.y. period examined in the Leg 130 cores. The expansion of the thermocline dwellers in Hole 847B (-4H-4) in the mid-Pleistocene was abrupt and uneven and may correspond with

a switch to 100-k.y. glacial/interglacial cycles (Thunell and Williams, 1983; Joyce et al., 1990).

### Spinosity and Trophic Level

Interpretation of the changes in the proportion of each trophic group through time-series is not as clear as that for depth habitat. The clear relative increase of herbivorous species at Sites 806 and 807 through the seaway-closing interval suggests an increase in upwelling and, consequently, productivity, but the herbivorous species show no similar excursion at the eastern sites and, indeed, show no significant excursions at all.

The diatom flux data of Iwai (this volume) for Hole 852B show a precipitous decline from ~5.8 Ma to the seaway-closing interval, which strongly suggests a sharp reduction in productivity at this site through this interval (middle Pliocene). The abundance of the probable diatom consumer *Neogloboquadrina acostaensis* matches the diatom flux curve well through this interval, but the representation of herbivorous species as a group does not decline because the opportunistic *Globigerinita glutinata* (Coulbourn et al., 1980) replaced the more specialized neogloboquadrinid. These sorts of *quid pro quos* obscure the correlation of trophic level group proportions with oceanographic

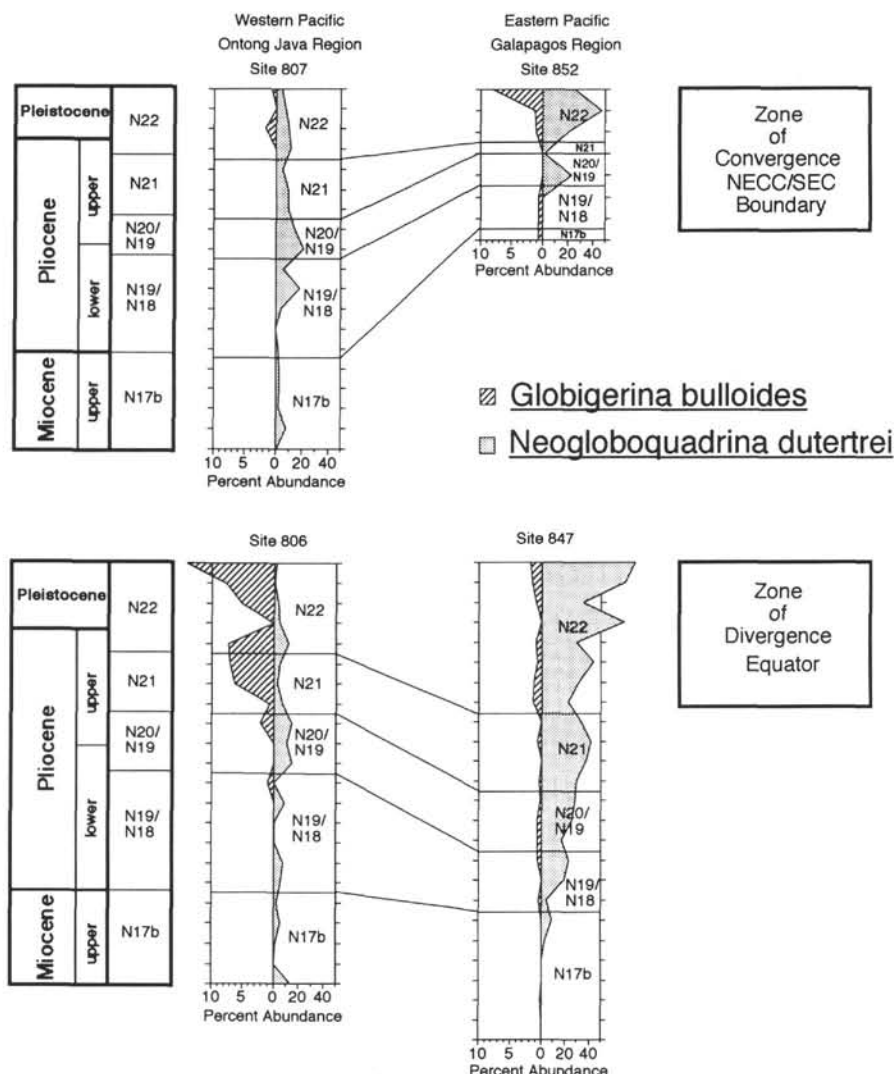


Figure 16. Relative abundance of "upwelling indicators" (Duplessy et al., 1981), *Neogloboquadrina dutertrei* and *Globigerina bulloides* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3. Abundance axes have been expanded to 50% at Sites 807, 847 and 852 for *Neogloboquadrina dutertrei*.

change. More detailed knowledge of the diets of planktonic foraminifers must be gathered and applied for this ecological parameter to be correlated usefully with changes in the physical environment.

While the abundance of trophic level groups does not seem to correlate with temporal changes in productivity at a given location, the obvious difference in the proportion of omnivorous vs. herbivorous species in the western vs. the eastern equatorial records for the last 5.8 m.y. is a clear indication of the long-maintained difference in nutrient levels and consequent productivity on opposite ends of the equatorial Pacific circulation system. In addition, the trophic level of important species such as *Globigerina woodi* and *G. apertura* remains uncertain.

### Diversity

The peak of species richness and diversity in the upper Pliocene section of the western sites results from the overlapping in the ranges of disappearing "Miocene" species and emerging modern species. Through this interval, *Globigerinoides obliquus* was replaced by *G. ruber*; *Globigerina woodi* and *G. apertura* by *G. rubescens*; *Globoquadrina venezuelana* by *Gq. pseudofoliata/conglomerata*; *Neogloboquadrina acostaensis* by *N. humerosa/dutertrei*, and *Pulleniatina*

*primalis* by *P. obliquiloculata*. Therefore, the values for species richness and diversity are more an evolutionary response to oceanographic change than an ecological or biogeographic one.

The diversity curves calculated from the entire assemblage follow the trend of the richness curves, because as most new species are added they remain rare and do not contribute much to the index. The difference in the character of the response of mixed-layer- and thermocline-dwelling species groups to expansion of their representation in the sediment assemblage is curious. Mixed-layer dwellers apparently become more diverse as their proportion of the assemblage is enlarged, in spite of the fact that their habitat is a homogeneous environment in many respects because it is wind-mixed. The maintenance of a steady level of diversity means that the species that are present are there in equitable numbers (i.e., several species are of approximately equal abundance). How they partition the mixed layer is not known. By contrast, the overall diversity of the assemblage in the east declines as the thermocline-dwelling group became more common during the Pleistocene. The thermocline-dwelling group was dominated by *Neogloboquadrina dutertrei*, a species adapted to exploit the seasonally variable, nutrient-rich shallow thermocline of the eastern equatorial Pacific.



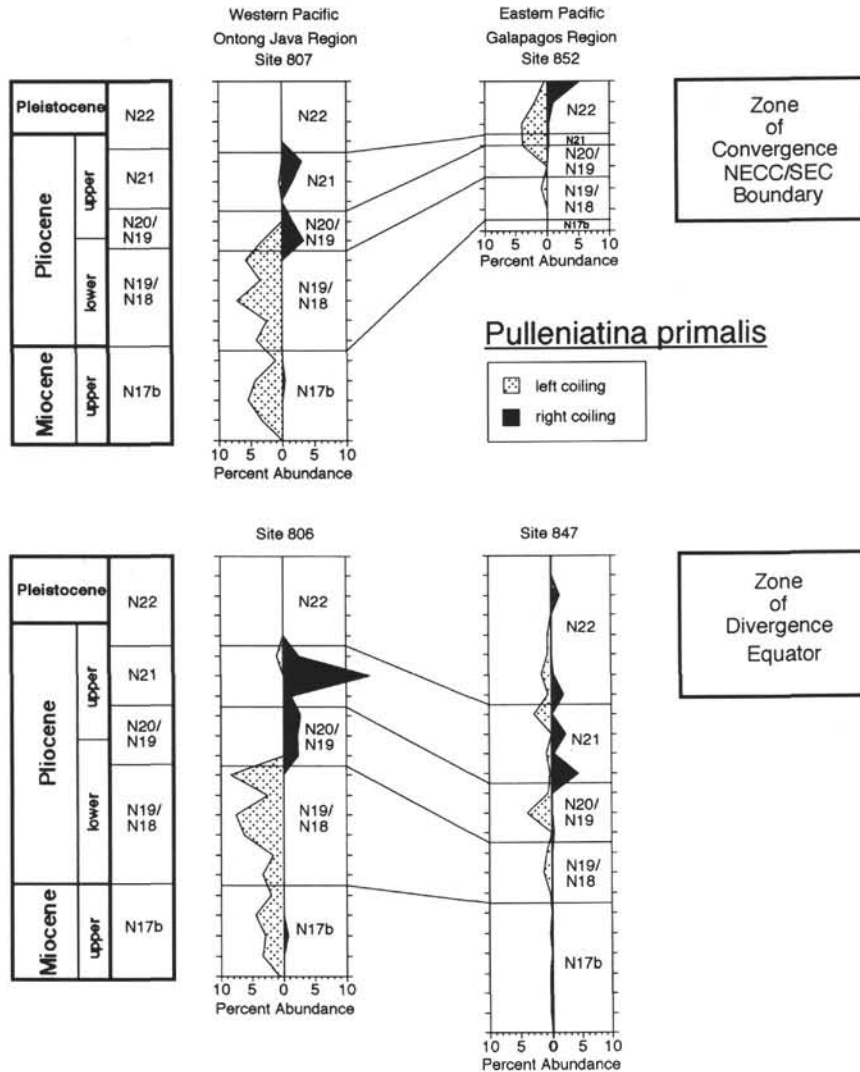


Figure 17. Relative abundance of *Pulleniatina primalis* in cores from Sites 806, 807, 847, and 852, arranged as in Figure 13.

## CONCLUSIONS

The temporal resolution of this time-series is too coarse to monitor more than general oceanographic change. The closing of the Central American seaway and the intensification of Northern Hemisphere glaciation are detectable by inspection of the relative abundances of certain species with known ecologies, and these events are obvious in the records of the western equatorial Pacific sites when species are grouped by depth habitat. The pile up of warm surface water in the western equatorial Pacific proceeded throughout the last 5.8 m.y. with accelerated steps coincident with the closing of the Central American seaway and the intensification of Northern Hemisphere glaciation.

Both the closing of the Central American seaway during the middle Pliocene and the intensification of the Northern Hemisphere glaciation during late Pliocene time are marked by increases in average eolian grain size in the sediments of the eastern equatorial Pacific (Hovan, this volume). This proxy indicator suggests that increases in tradewind strength occurred during both of these geologic events. The oceanographic response to increased strength in trade winds in the tropical Pacific is a piling of warm surface water on the western side and an increase in upwelling caused by the Coriolis sign change at the equator.

In the western tropics, these two effects work to cross purposes; the piling of the warm water thickens the mixed layer, even as divergence

at the equator lofts the thermocline higher in the water column. In the eastern tropics, both effects work in concert. The mixed layer is swept away and the thermocline rises in the water column. The planktonic foraminiferal populations register these oceanographic developments most clearly when species are grouped together by depth habitat. In the upper Miocene and lower Pliocene sections, both sides of the Pacific show similar proportions of thermocline- and mixed-layer-dwelling foraminifers. The groups include different species on either side of the Pacific; however, evidently in the west, the thermocline was not too deeply buried by piling, and divergence was strong enough to sustain deeper-dwelling, possibly omnivorous, globigerinids in large numbers; and in the east, the shallower thermocline sustained large numbers of probably phytoplanktivorous neoglobobulids.

The closing of the Central American seaway may have disrupted this ecological symmetry. In a model experiment, Maier-Reimer et al. (1990) removed the Central American isthmus while fixing atmospheric conditions. Removal of the isthmus caused the surface of western Pacific surface to lower slightly with corresponding rises in the Atlantic. The raising of the Central American isthmus, then, may have caused a redistribution of hydrostatic head even with fixed atmospheric conditions. The increase in mixed-layer dwellers at both western sites suggests that increased trade winds thickened the warm-

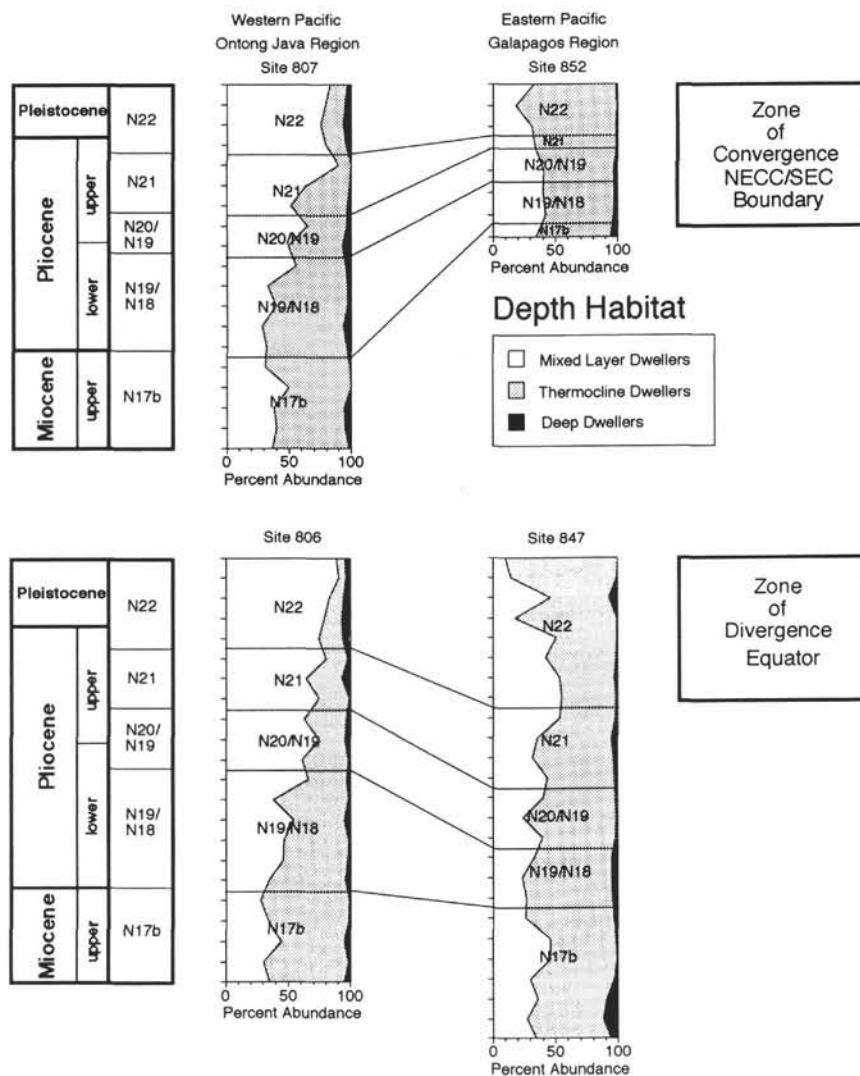


Figure 18. The relative abundance of depth habitat groups in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3.

water layer (Fig. 18). However, divergence still reached the photic zone, as is suggested by the increase in tropical neogloboquadrinids at the western sites (Fig. 22) in the middle Pliocene. At Site 847 in the eastern tropical Pacific, the proportion of the thermocline dwellers in the samples does not change appreciably until the Pleistocene, perhaps indicating little change in mixed-layer thickness until that period. The proportion of tropical neogloboquadrinids, however, increases at Site 847 from the upper Miocene to the lower Pliocene; they constitute ~50% of the sediment assemblage through the middle Pliocene. *Neogloboquadrina dutertrei* is considered an indicator of fertility in the modern ocean (Duplessy et al., 1981), and *Neogloboquadrina acostaensis* is considered to be its ecological equivalent (Dowsett and Poore, 1990). Therefore, an increase in the neogloboquadrinid portion of the total thermocline-dwelling group at Site 847 through the lower Pliocene to middle Pliocene indicates an increase in productivity, rather than a significant change in mixed-layer depth.

The second step of the development of oceanographic asymmetry in the tropical Pacific occurs after the intensification of Northern Hemisphere glaciation in the upper Pliocene. Subsequent to the seaway-closing, the western sites were approximately 60% mixed layer/40% thermocline dwellers in the west and the reverse in the east. In the upper Pliocene section, this asymmetry became even more

pronounced, approximately 80% to 20%. *Neogloboquadrina dutertrei* accounts for nearly all of the thermocline dwellers at Site 847 and, in the dissolved assemblages of Site 852, even outnumbers the more solution-resistant *Globorotalia tumida* (Parker and Berger, 1971) in the upper Pleistocene. *Neogloboquadrina dutertrei* declines to very low levels in the western sites, especially at the equatorial Site 806, where the warm-water pile is the thickest (Levitus, 1982) and the EUC disrupts the thermocline (Delcroix et al., 1987). This indicates that in the western tropical Pacific, the piling of warm water ended significant introduction of nutrients to the upper column by upwelling with the intensification of Northern Hemisphere glaciation at 2.5 Ma, rather than directly after the closing of the Central American seaway (3.2 Ma).

The development of the thermocline species zonation across the Pacific (Kennett et al., 1985) seems also to have occurred subsequent to the intensification of Northern Hemisphere glaciation, not directly after the closing of the Central American seaway. Berger et al. (1993) suggested that increases in the abundances of *Globorotalia tumida* (-*Gr. menardii*) and *Neogloboquadrina dutertrei* in the Ontong Java region are indicators of western expansion of higher productivity. In the Pleistocene sections, a pronounced decrease in the abundances of these two species is seen at the western sites. *Pulleniatina obliquilo-*

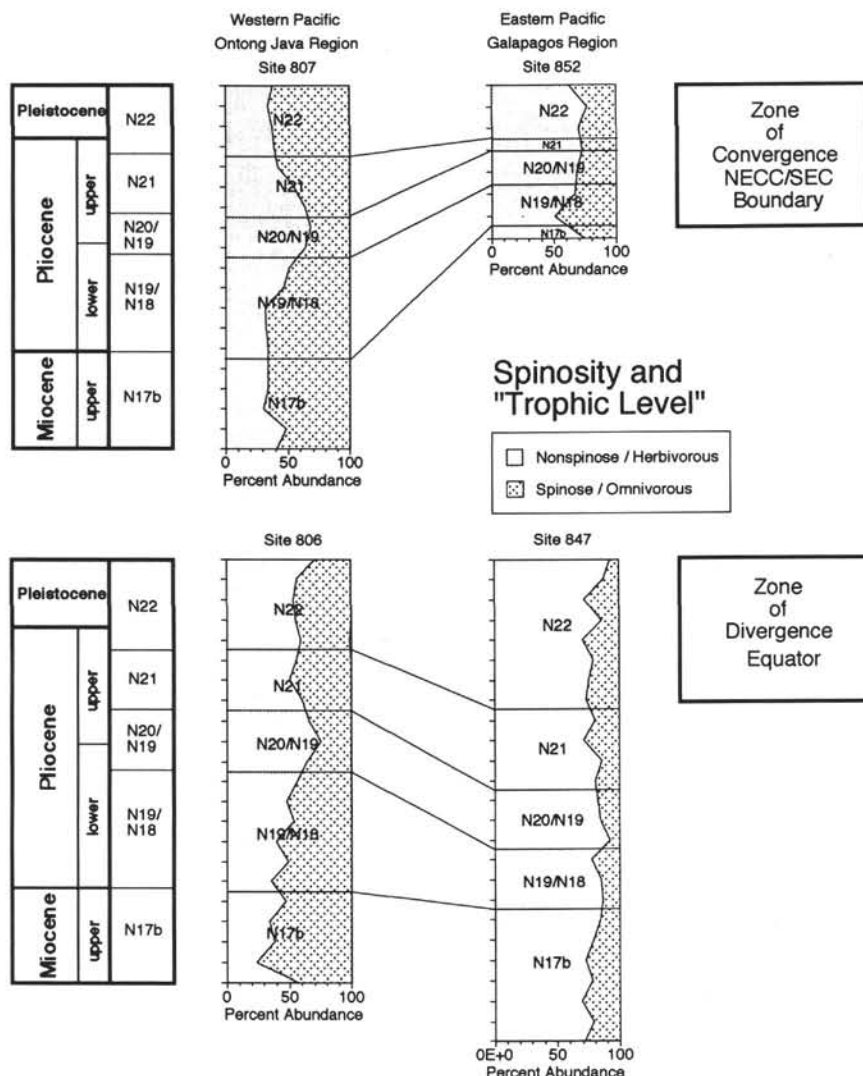


Figure 19. Relative abundance of "trophic level" groups in cores from Sites 806, 807, 847, and 852 arranged as in Figure 3.

*culata* increases significantly in abundance (Fig. 23) in the Pleistocene section only at Site 807; however, at Site 806, it is more common than either *N. dutertrei* or *Gr. tumida* (or *Gr. menardii*).

A corollary to the development of the longitudinal zonation of thermocline-dwelling species across the Pacific above the upper Pliocene is the biostratigraphic difficulties that presaged the development of this zonation. *Pulleniatina obliquiloculata* and *Neogloboquadrina dutertrei* are the modern representatives of their genera and generally are accepted as having appeared during the late Pliocene (e.g., Kennett and Srinivasan, 1983). But in the upper Miocene, *N. dutertrei*-type specimens appeared in the western holes and *P. obliquiloculata*-type specimens appeared in the eastern holes. *Pulleniatina primalis* and *Neogloboquadrina acostaensis* morphotypes, the Neogene representatives of these genera, persisted farther upsection in the east and west, respectively, than is generally acknowledged. Increased morphologic variation is apparently an indicator of environmental stress (e.g., Hecht and Savin, 1972).

The Pliocene segregation of left- and right-coiling *Globorotalia menardii* by current is startling. Left-coiling specimens dominate in the lower salinity NECC (Wyrki, 1981), while right-coiling specimens dominate the equatorial sites in the SEC. The complete absence of left-coiled *Gr. menardii* in the Pleistocene of Site 806 also is noteworthy.

The designation of species trophic level as either omnivorous or herbivorous was not as informative as was hoped. The categories of herbivore and omnivore, never accurate, are too general to extract much information from the sediment record of planktonic foraminifers. The diets of individual species must be known and defined in more detail before this approach will be useful.

The effect of differential dissolution on the relative abundance of planktonic foraminiferal species was not considered quantitatively in this study, and so how much of the east-west asymmetry of planktonic foraminiferal assemblages is the result of preservational differences is not known. Both of the western sites are well above the position of the modern lysocline, while both eastern sites lie below it (Parker and Berger, 1971).

Fluctuations in the abundance of individual species of planktonic foraminifer with known ecologies did not contradict information gathered from other proxy records, such as the stable isotope records, the eolian particle flux record (Hovan, this volume) and the diatom flux record (Iwai, this volume). The patterns of species having known ecologies and their responses to known oceanographic events can be compared with the patterns of extinct species to make assumptions about their paleoecologies. An example is the record of *Globigerina aperture*. The pattern of abundance demonstrated by this species sug-

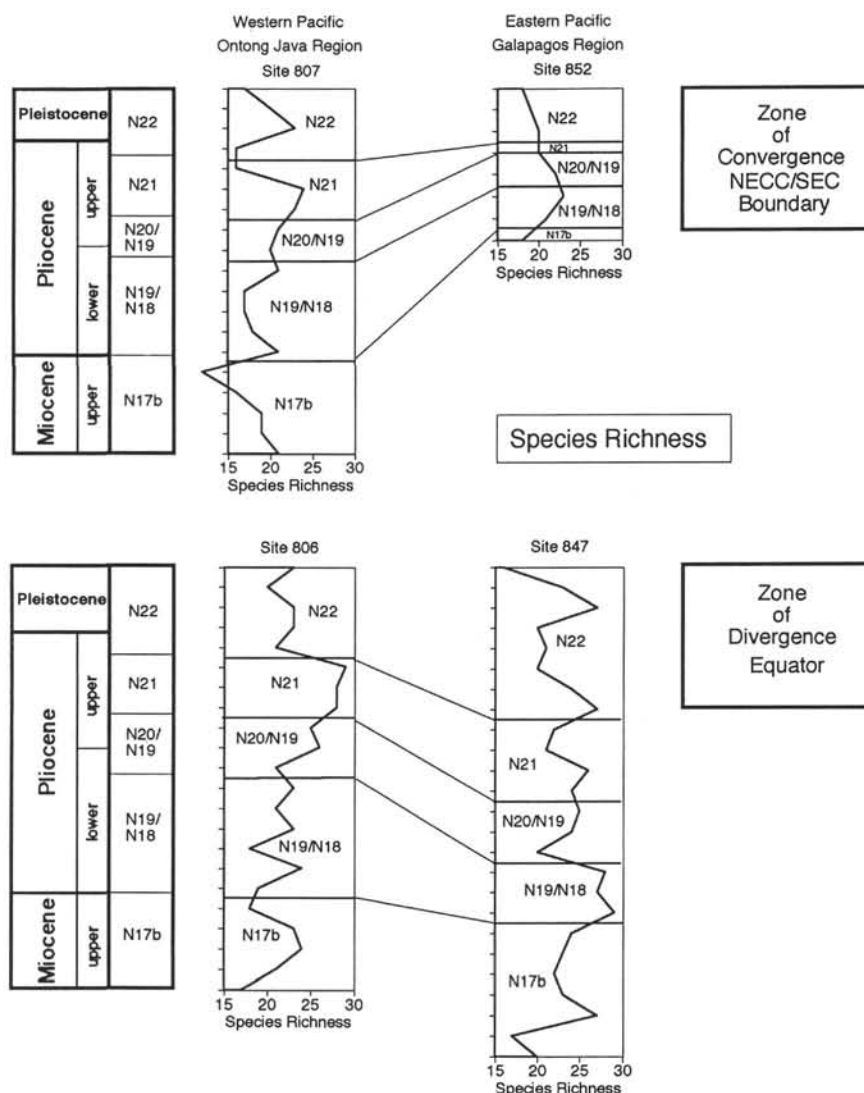


Figure 20. Species richness in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3.

gested it may have been a dweller low in the surface layer. This may now be checked isotopically.

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\* Abbreviations for names of organizations and publication titles in ODP reference lists follow the style given in *Chemical Abstracts Service Source Index* (published by American Chemical Society).



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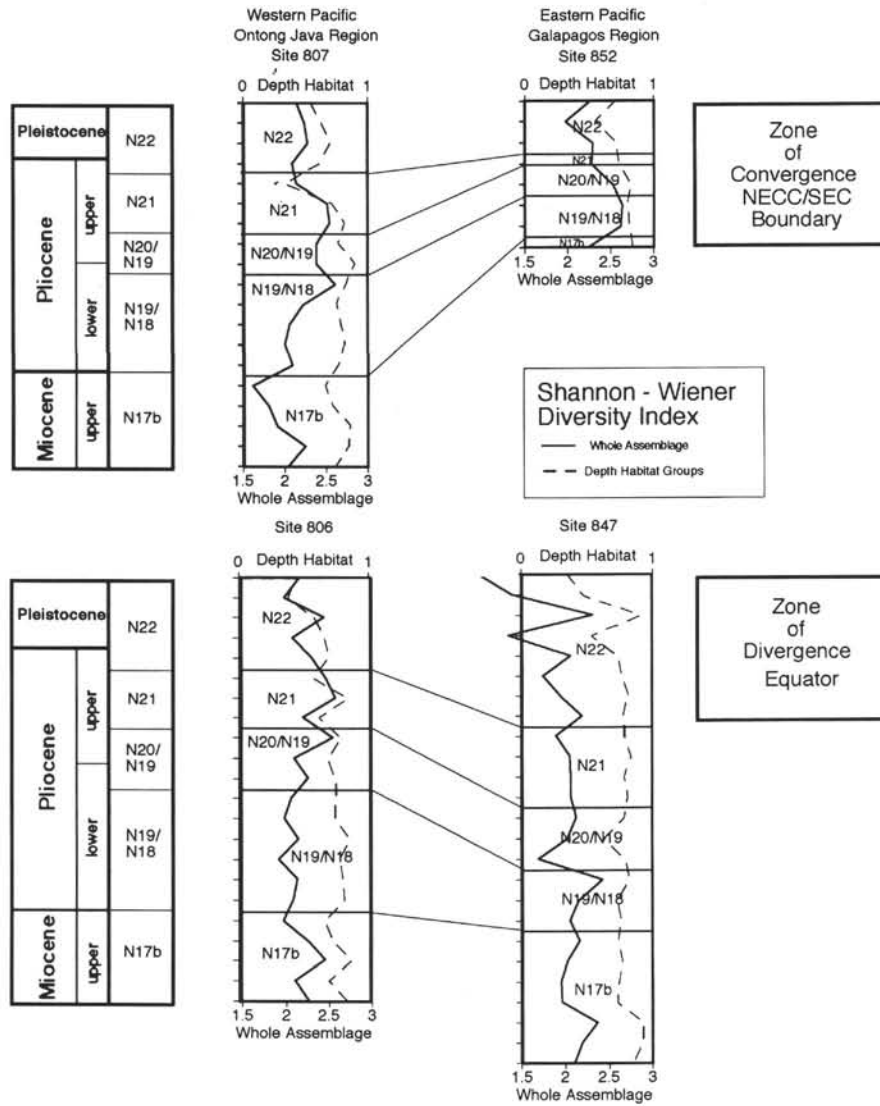


Figure 21. Species diversity of the whole assemblage (solid line) and diversity of the depth-habitat groups (dashed line). Scale for whole assemblage is at the bottom of the graph, and scale for depth-habitat groups is at the top.

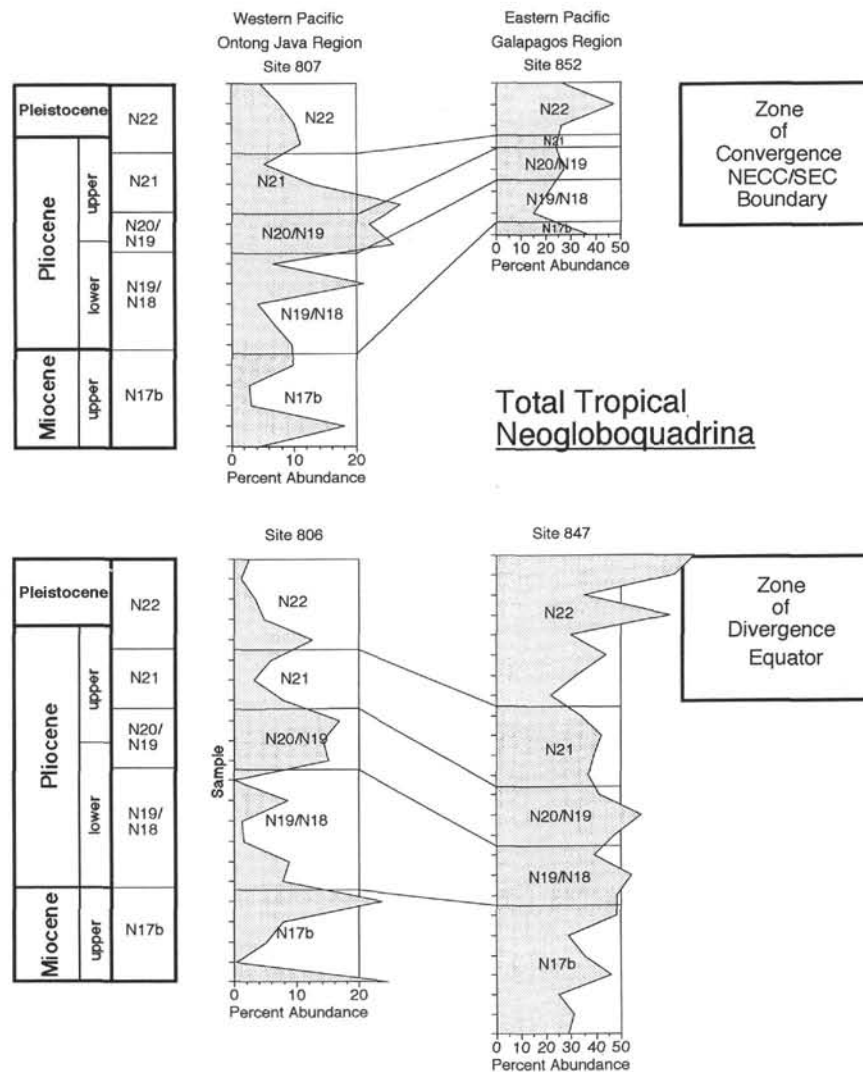


Figure 22. Relative abundance of tropical species of *Neogloboquadrina* (*N. acostaensis*, *N. dutertrei*–*N. humerosa*) in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3.



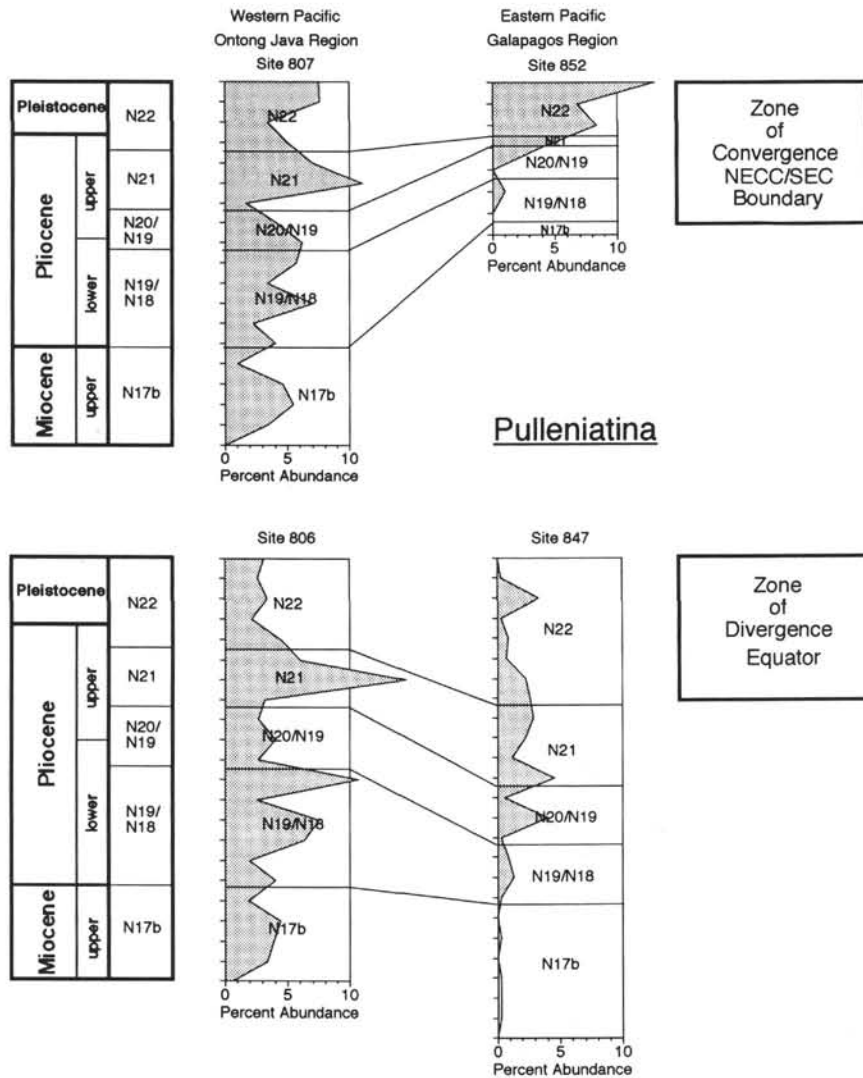


Figure 23. Relative abundance of the genus *Pulleniatina* (*P. primalis*, *P. spectabilis*, *P. obliquiloculata*) in cores from Sites 806, 807, 847, and 852, arranged as in Figure 3.

## APPENDIX A

Site 806	N22					N21			N20/N19			N19/N18						N17b											
	Core catchers					1H	2H	3H	4H	5H	6H	7H	8H	9H	10H	11H	12H	13H	14H	15H	16H	17H	18H	19H	20H	21H	22H		
<i>Streptochilus</i>		0	1	7	0	6		0	12	0		0	0	0		0	0	1	0	0	0	0	0	0	1	0	0	3	
<i>Globigerina quinqueloba</i>	21																												
<i>Globigerina bulloides</i>	45	27	15	0	23	22	19	2	7	0	0	3																	
<i>Globigerina woodi</i>				11	1	4	8	18	4	7	11	32	35	32	68	43	84	82	92	69	122	57							
<i>Globigerina apertura</i>			1	2	6	9	45	23	13	1	35	43	106	61	78	72	83	51	45	48	46	28							
<i>Globigerina nepenthes</i>												2	0	0	4	1	0	14	24	0	23	22							
<i>Globigerina rubescens</i>	52	59	58	51	33	42	4	30	11	5	12																		
<i>Globigerinoides obliquus</i>							4	0	12	16	10	2	5	4	6	2	5	3	5	4	3	0							
<i>Globigerinoides extremus</i>							2	2	4	0	0	1	0	4	1	0	0	0	1	0	2	6							
<i>Globigerinoides conglobatus</i>	0	1	1	0	0	0	1	2	1	0	0	0	0	1	0	0	1	0	0	2	0	0							
<i>Globigerinoides sacculifer</i>	11	9	1	7	16	3	7	2	9	3	7	2		2	5	8	12	6	6	22	14	13							
<i>Gs. sacculifer (no sac)</i>	2	7	16	8	15	3	6	18	21	15	14	10		10	9	14		3	5	19	10	0							
<i>Globigerinoides fistulosus</i>					4	0	5																						
<i>Globigerinoides ruber</i>	11	53	32	51	29	38	18	12	19	11																			
<i>Globigerinoides tenellus</i>	4	4	5	2	3	1	1			1			1																
<i>Orbulina universa</i>	0	0	0	1	2	0	0	1	0	0	0	0	0	0	0	1	0	0	0	2	0	0							
<i>Globorotalia menardii (r)</i>	1	2	0	1	0	10	0	0	0	3	3	5	0	7	0	3	1	0	9	0	3	0							
<i>Globorotalia menardii (l)</i>				0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	3	9	8	0							
<i>Globorotalia limbata</i>						3	0	0	0	0	0	1	1						1		1								
<i>Globorotalia scitula</i>	1	1		2	1	2	1	1	1	0	0	0	0	1															
<i>Globorotalia juanai</i>																				1	3								
<i>Globorotalia cibaoensis</i>																		1	0	3									
<i>Globorotalia margaritae</i>									3	3	2																		
<i>Globorotalia crassaformis</i>	4	0	0	0	0	0	1																						
<i>Globorotalia tosaensis</i>					2	1	0	1																					
<i>Globorotalia truncatulinoides</i>	0	8	9	18	4																								
<i>Globorotalia merotumida</i>																													
<i>Globorotalia plesiotumida</i>						1	0	0	0	3	2	3	8	5	1	1	0	0	0	0	0	1							
<i>Globorotalia tumida</i>	7	7	7	5	13	1	16	1	28	2	2	2	6	13	2	5	2												
<i>Globorotalia unguolata</i>	3	6	5	4	0	0	1	2	4																				
<i>Globorotalia anfracta</i>	1	0	5	1	0	2																							
<i>Turborotalita humilis</i>		17					21	2	1	2			1						5					2	2	1	1		
<i>Globoquadrina venezuelana</i>							8			0	4	9	3	8	3	12	5	7	2	3	2	13	2	10					
<i>Globoquadrina dehiscens</i>																				1	1	1	0						
<i>Globoquadrina baroemoensis</i>																						1	1						
<i>Globoquadrina conglomerata</i>	3	1	1	0	1	1	0	0	6	4	1	0	1	1	1					2			1						

APPENDIX A (continued).

Site 806 Core catchers	N22					N21			N20/N19			N19/N18						N17b				
	1H	2H	3H	4H	5H	6H	7H	8H	9H	10H	11H	12H	13H	14H	15H	16H	17H	18H	19H	20H	21H	22H
<i>Dentoglobigerina altispira</i>								19	9	12	14	23	24	7	11	10	8	0	14	18	10	28
<i>Neogloboquadrina acostaensis</i>								2	0	4	0	0	1	1	1	2	7	67	6	10	0	34
<i>Neogloboquadrina humerosa</i>						2	0	0	7	8												
<i>Neogloboquadrina dutertrei</i>	8	4	10	16	39	17	10	23	49	34	45	0	26	3	4	24	18	8	19	6	1	41
<i>Pulleniatina primalis (l)</i>						3	0	0	0	0	0	26	8	24	20	5	11	6	14	9	11	2
<i>Pulleniatina primalis (r)</i>						8	42	4	9	7	7									2		
<i>Pulleniatina spectabilis</i>												1										
<i>Pulleniatina obliquiloculata</i>	10	9	10	7	14	8	2	6	0	6	1	6	0	0	0	1	2	0	0	1		
<i>Sphaeroidinellopsis seminulina</i>								2	0	2	5	5	1	4	4	1	1	2	1	3		
<i>Sphaeroidinellopsis kochi</i>																1						
<i>Ss. paenadehiscens</i>						1	0	0	0	0	2	0	0	3	0	1	2	0	0	6		
<i>Sphaeroidinella dehiscens</i>	2	1	2	2	0	5	3	1	2													
<i>Beella praedigitata</i>				1	0	0	0	0	0	3	1						10	2				
<i>Tenuitellids</i>	4	0	0	0	0	0	3	1														
<i>Globorotaloides hexagona</i>	6	2	1	4	2	2	0	2	2	1	1	1	0	2	0	0	13	1	0	0	1	1
<i>Globigerinita glutinata</i>	122	138	75	128	98	98	76	134	97	161	112	127	77	119	95	89	61	65	58	54	48	56
<i>Globigerinita uvula</i>	3	0	3																			
<i>Candeina nitida</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1			
<i>Globigerinella aequilateralis</i>	2	8	9	2	0	6	3	2	8	2	3	2	2	1	0	1	1	1	2	2	0	0
<i>Globigerinella obesa</i>	0	0	0	1	0	0	0	0	1	1	2	0	3	2	0	0	0	0	0	0	2	0
<i>Globigerinella calida</i>	2	0	2	3	1	2	3	3	0	0	3	1	0	0	0	1						
Totals	325	348	292	328	313	317	304	316	331	324	300	307	312	319	316	299	324	318	314	307	323	305

## W. CHAISSON

Site 807	N22				N21			N20/N19		N19/N18					N17b				
Core catchers	1H	2H	3H	4H	5H	6H	7H	8H	9H	10H	11H	12H	13H	14H	15H	16H	17H	18H	19H
<i>Streptochilus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Globigerina quinqueloba</i>	6	0	0	0	12														
<i>Globigerina bulloides</i>	2	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Globigerina woodi</i>					9	4	18	3	23	32	73	115	128	121	142	122	144	99	123
<i>Globigerina apertura</i>					2	17	10	2	1	23	25	36	23	23	24	14	14	14	11
<i>Globigerina nepenthes</i>											2	2	13	1	6	4	0	3	6
<i>Globigerina rubescens</i>	60	59	51	30	19	22	18	4											
<i>Globigerinoides obliquus</i>		1				6	10	12	19	21	5	1	0	6	6	0	8	7	3
<i>Globigerinoides extremus</i>		2	0	0	0	0	1	5	1	2	0	0	0	0	0	0	1	1	
<i>Globigerinoides conglobatus</i>	5	2	1	0	0	0	2	1	0	1	0	0	0	1	1	0	0	2	0
<i>Globigerinoides sacculifer</i>	9	9	11	14	11	3	10	16	7	5	5	10	6	11	4	15	10	5	2
<i>Gs. sacculifer (no sac)</i>	15	12	28	28	23	8	10	23	23	19	11	15	24	8	10	36	18	22	15
<i>Globigerinoides fistulosus</i>						6													
<i>Globigerinoides ruber (w)</i>	39	63	73	81	63	11	16	1	0	2	1	0	0	0	0	0	0	0	0
<i>Globigerinoides tenellus</i>	0	1	0	0	2	1													
<i>Orbulina universa</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	2	0	2	1
<i>Globorotalia menardii (l)</i>	8	11	5	0	0	5	2	0	0	5	9	10	2	10	0	3	1	0	30
<i>Globorotalia menardii (r)</i>	0	0	1	0	0	1	4	6	2	8	0	0	3	1	0	0	5	0	1
<i>Globorotalia scitula</i>	1	0	1	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Globorotalia cibaoensis</i>													1	2	0	0	2	0	0
<i>Globorotalia crassaformis</i>	2	1																	
<i>Globorotalia margaritae</i>												1	0	0	0	0	0	3	0
<i>Globorotalia tosaensis</i>			8	0	0	0	1												
<i>Globorotalia truncatulinoides</i>	0	2	4	0															
<i>Globorotalia merotumida</i>																			8
<i>Globorotalia plesiotumida</i>										11	0	4	1	2	0	8	0	0	5
<i>Globorotalia tumida</i>	5	5	6	7	0	22	16	12	16	13	3	0	2	0					
<i>Globorotalia unguolata</i>	0	2	2	1	0	1	1	2											
<i>Globorotalia anfracta</i>	0	0	2																
<i>Turborotalita humilis</i>					3				4	3				1					



APPENDIX A (continued).

Site 807	N22				N21			N20/N19		N19/N18					N17b				
Core catchers	1H	2H	3H	4H	5H	6H	7H	8H	9H	10H	11H	12H	13H	14H	15H	16H	17H	18H	19H
<i>Globoquadrina dehiscens</i>																		1	0
<i>Globoquadrina venezuelana</i>						2	3	8	14	10	5	9	18	10	0	1	15	14	3
<i>Globoquadrina baroemoensis</i>															0		2	2	3
<i>Globoquadrina conglomerata</i>	5	7	4	5	0	0	5	0	3										
<i>Dentoglobigerina altispira</i>							16	21	2	32	14	14	0	0	0	0	5	50	48
<i>Neogloboquadrina acostaensis</i>						10	52	18	11	3	9	1	21	23	21	1	3	33	13
<i>Neogloboquadrina humerosa</i>																			1
<i>Neogloboquadrina dutertrei</i>	12	21	30	32	15	24	27	40	59	16	47	12	0	6	8	8	7	26	1
<i>Pulleniatina primalis (l)</i>						1	0	0	8	16	9	22	7	12	3	14	17	11	0
<i>Pulleniatina primalis (r)</i>					9	4	0	4	9	0	0	0	0	0	0	1	0	0	0
<i>Pulleniatina obliquiloculata</i>	20	21	10	14	11	23	5	7											
<i>Sphaeroidinellopsis seminulina</i>												1	3	2	0	1	0	0	1
<i>Ss. paenedehiscens</i>													4	3	0	0	0	0	1
<i>Sphaeroidinella dehiscens</i>	0	2	0	3	1	5	1	0	5	0	2								
<i>Beella praedigitata</i>			1	2															
<i>Tenuitellids</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Globorotaloides hexagona</i>	0	3	0	4	1	1	0	0	1	2	2	0	2	1	0	0	0	0	0
<i>Globigerinita glutinata</i>	67	49	47	52	90	74	66	81	61	55	40	57	47	54	68	92	59	32	50
<i>Globigerinita uvula</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Candeina nitida</i>	0	0	1	0	0	0	0	1	0	0	0	0	0	0	2	0	2	0	0
<i>Globigerinella aequilateralis</i>	4	2	4	1	13	2	0	1	0	1	0	4	1	2	0	3	1	2	1
<i>Globigerinella obesa</i>	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Globigerinella calida</i>	6	0	2																
Totals	265	276	297	281	286	256	294	269	273	282	263	315	308	303	296	325	317	327	328

## W. CHAISSON

[illegible]

APPENDIX A (continued).

Site 847	N22								N21				N20/N19			N19/N18			N17b													
	Samples ( xH-4)								1H	2H	3H	4H	5H	6H	7H	8H	9H	10H	11H	12H	13H	14H	15H	16X	17X	18X	19X	20X	21X	22X	23X	24X
<i>Globorotalia tosaensis</i>				1	0	2	8	0	0	4																						
<i>Globorotalia truncatulinoides</i>	0	0	1	1																												
<i>Globorotalia merotumida</i>																													1	0	4	
<i>Globorotalia plesiotumida</i>											1	1	1	2	0	7	1	2	2	1	1	1	3	0	9							
<i>Globorotalia margaritae</i>																													1			
<i>Globorotalia tumida</i>	2		4	1	30	0	3	14	8	6	2	2	13	8	3	12	2	1														
<i>Globorotalia unguata</i>	2	1	3	2	3	0	2	0	1	3																						
<i>Turborotalita humilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Globoquadrina dehiscens</i>																															1	
<i>Globoquadrina baroemoensis</i>								1	0	0	0	3	1	0	2	2	1	2	2	0	0	0	1	0	0							
<i>Globoquadrina conglomerata</i>	0	0	0	0	1	0	0	0	0	7																						
<i>Globoquadrina venezuelana</i>			4								7	2	5	2	6	12	8	10	5	4	2	3	20	32	8							
<i>Dentoglobigerina altispira</i>											6	2	2	1	1	4	0	1	1	0	0	0	0	0	0							
<i>Neogloboquadrina pachyderma (l)</i>	0	1	1	2	0	0	0	1	0	0	0	0	0	4	3	3	3	20	19	20	3	0	0	0	0							
<i>Neogloboquadrina pachyderma (r)</i>	11	19	1	12	3	0	0	0	1	0	0	0	0	0	0	0	0	4	12	0	0	2	1	23	0							
<i>Neogloboquadrina acostaensis</i>											2	22	38	95	91	50	107	147	129	77	100	137	75	88	89							
<i>Neogloboquadrina humerosa</i>																1	0		0	0	5	8	7	11								
<i>Neogloboquadrina dutertrei</i>	261	235	105	226	94	134	97	67	106	126	122	91	87	78	51	74	59	13	31	10												
<i>Pulleniatina obliquiloculata</i>	0	1	6	1	1	0	1																									
<i>Pulleniatina primalis (l)</i>					2	2	5	2	9	0	3	1	2	12	0	3	4	1	0	1	0	1	1	1	0							
<i>Pulleniatina primalis (r)</i>			4					1	0	7	1	13	0	0	1																	
<i>Sphaeroidinellopsis seminulina</i>											2	5	8	1	4	0	15	5	4	8	4	5	3	1	2							
<i>Ss. paenedehiscens</i>													3	2	1	1	3	2	2	4	3	1			2							
<i>Sphaeroidinella dehiscens</i>	0	0	0	0	0	1	3	1	3	0	1	0	0	0	0	1	1															
<i>Beella praedigitata</i>		2						1	0	0	0	0	0	0	0	0	1	1														
<i>Globorotaloides hexagona</i>	1	2	16	2	1	3	2	3	7	5	6	4	2	2	0	3	6	2	6	1	0	6	10	8	9							
<i>Tenuitellids</i>	3	5	2	1	1	2	1	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0							
<i>Globigerinita glutinata</i>	18	11	63	19	84	89	106	112	116	60	67	99	93	50	113	72	51	72	61	113	96	73	93	79	88							
<i>Globigerinita uvula</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	1	1	0	0	0							
<i>Candeina nitida</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0							

APPENDIX A (continued).

Site 847	N22								N21				N20/N19			N19/N18			N17b														
	Samples ( xH-4)								1H	2H	3H	4H	5H	6H	7H	8H	9H	10H	11H	12H	13H	14H	15H	16X	17X	18X	19X	20X	21X	22X	23X	24X	25X
<i>Globigerinella aequilateralis</i>	<i>Globigerinella calida</i>	<i>Globigerinella obesa</i>	2	5	6	0	0	1	1	0	2	1	2	2	1	0	0	5	3	1	6	5	2	2	5	0	3						
			0	0	3	0	0	3	0	1	0	1																					
			10	7	3	4	10	13	4	3	0	0	2	4	4	2	1	2	3	2	2	5	1	2	5	3	0						
Totals			331	333	303	326	316	306	307	302	314	303	322	302	308	300	301	319	307	335	330	304	303	316	329	324	306						

APPENDIX A (continued).

Site 852 Samples	N22			N20/N19		N19/N18		N17b
	1H-4	2H-4	3H-4	4H-4	5H-4	6H-4	7H-4	8H-4
<i>Globigerina bulloides</i>	23	4	3	0	0	2	1	2
<i>Globigerina nepenthes</i>					2	5	13	5
<i>Globigerina woodi</i>	4	0	1	12	12	20	11	17
<i>Globigerina apertura</i>				0	4	20	0	5
<i>Globigerinoides obliquus</i>	3			7	4	0	8	9
<i>Globigerinoides conglobatus</i>	0	5	1	0	0	0	1	0
<i>Globigerinoides sacculifer</i>	12	0	11	8	2	5	5	10
<i>Gs. sacculifer (no sac)</i>	11	6	14	20	7	14	9	15
<i>Globigerinoides fistulosus</i>				1				
<i>Globigerinoides ruber</i>	0	3	9	10				
<i>Orbulina universa</i>	1	9	3	8	1	0	3	4
<i>Globorotalia menardii (l)</i>	41	18	23	0	12	18	17	0
<i>Globorotalia menardii (r)</i>	0	7	0	0	10	8	3	11
<i>Globorotalia scitula</i>	2	0	1	0	1	0	1	5
<i>Globorotalia crassula</i>				1				
<i>Globorotalia tosaensis</i>		2	0					
<i>Globorotalia plesiotumida</i>						9	10	10
<i>Globorotalia tumida</i>	39	42	90	98	7	14	0	
<i>Globorotalia unguata</i>	0	0	0	0	1			
<i>Turborotalita humilis</i>	0	0	0	0	0	2	0	0

Site 852 Samples	N22			N20/N19		N19/N18		N17b
	1H-4	2H-4	3H-4	4H-4	5H-4	6H-4	7H-4	8H-4
<i>Globoquadrina dehiscens</i>								2
<i>Gq. baroemoensis</i>	1	0	0	0	0	0	0	0
<i>Gq. venezuelana</i>		2		1	5	8	3	10
<i>Dentoglobigerina altispira</i>					3	7	0	0
<i>Neogloboquadrina dutertrei</i>	76	145	64	5	41	0	0	0
<i>N. pachyderma (l)</i>	0	0	0	2	1	5	1	3
<i>N. pachyderma (r)</i>	11	26	6	14	0	10	0	15
<i>N. acostaensis</i>			14	69	7	64	22	112
<i>Pulleniatina obliquiloculata</i>	21	12	13					
<i>Pulleniatina primalis (l)</i>	1	6	12	12	0	3	0	0
<i>Pulleniatina primalis (r)</i>	15	3	0	0	0	0	0	0
<i>Sphaeroidinellopsis kochi</i>						2	2	0
<i>Ss. paenedehiscens</i>				2	5	3	3	0
<i>Ss. seminulina</i>			1		23	33	11	22
<i>Sphaeroidinella dehiscens</i>	0	11	20	11	0	0	0	0
<i>Beella praedigitata</i>	0	2	0	1	0	0	0	0
<i>Globorotaloides hexagona</i>	1	0	5	4	1	2	1	0
<i>Globigerinita glutinata</i>	27	4	5	18	26	48	19	45
<i>Globigerinella aequilateralis</i>	1	2	4	7	2	7	1	0
Totals	290	309	300	311	177	309	145	302

## APPENDIX B

Site 806 Core catchers	N22					N21			N20/N19			N19/N18						N17b				
	1H	2H	3H	4H	5H	6H	7H	8H	9H	10H	11H	12H	13H	14H	15H	16H	17H	18H	19H	20H	21H	22H
<i>Streptochilus</i>	0.0	0.3	2.4	0.0	1.9	0.0	3.9	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	1.0
<i>Globigerina quinqueloba</i>	6.5																					
<i>Globigerina bulloides</i>	13.8	7.8	5.1	0.0	7.3	6.9	6.3	0.6	2.1	0.0	0.0	1.0										
<i>Globigerina woodi</i>				3.4	0.3	1.3	2.6	5.7	1.2	2.2	3.7	10.4	11.2	10.0	21.5	14.4	25.9	25.8	29.3	22.5	37.8	18.7
<i>Globigerina apertura</i>			0.3	0.6	1.9	2.8	14.8	7.3	3.9	0.3	11.7	14.0	34.0	19.1	24.7	24.1	25.6	16.0	14.3	15.6	14.2	9.2
<i>Globigerina nepenthes</i>												0.7	0.0	0.0	1.3	0.3	0.0	4.4	7.6	0.0	7.1	7.2
<i>Globigerina rubescens</i>	16.0	17.0	19.9	15.5	10.5	13.2	1.3	9.5	3.3	1.5	4.0											
<i>Globigerinoides obliquus</i>							1.3	0.0	3.6	4.9	3.3	0.7	1.6	1.3	1.9	0.7	1.5	0.9	1.6	1.3	0.9	0.0
<i>Globigerinoides extremus</i>							0.7	0.6	1.2	0.0	0.0	0.3	0.0	1.3	0.3	0.0	0.0	0.0	0.3	0.0	0.6	2.0
<i>Globigerinoides conglobatus</i>	0.0	0.3	0.3	0.0	0.0	0.0	0.3	0.6	0.3	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.3	0.0	0.0	0.7	0.0	0.0
<i>Globigerinoides sacculifer</i>	3.4	2.6	0.3	2.1	5.1	0.9	2.3	0.6	2.7	0.9	2.3	0.7	0.0	0.6	1.6	2.7	3.7	1.9	1.9	7.2	4.3	4.3
<i>Gs. sacculifer (no sac)</i>	0.6	2.0	5.5	2.4	4.8	0.9	2.0	5.7	6.3	4.6	4.7	3.3	0.0	3.1	2.8	4.7	0.0	0.9	1.6	6.2	3.1	0.0
<i>Globigerinoides fistulosus</i>					1.3	0.0	1.6															
<i>Globigerinoides ruber</i>	3.4	15.2	11.0	15.5	9.3	12.0	5.9	3.8	5.7	3.4												
<i>Globigerinoides tenellus</i>	1.2	1.1	1.7	0.6	1.0	0.3	0.3	0.0	0.0	0.3	0.0	0.0	0.3									
<i>Orbulina universa</i>	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.7	0.0	0.0
<i>Globorotalia menardii (r)</i>	0.3	0.6	0.0	0.3	0.0	3.2	0.0	0.0	0.0	0.9	1.0	1.6	0.0	2.2	0.0	1.0	0.3	0.0	2.9	0.0	0.9	0.0
<i>Globorotalia menardii (l)</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.3	1.0	2.9	2.5	0.0
<i>Globorotalia limbata</i>						0.9	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.3	0.0
<i>Globorotalia scitula</i>	0.3	0.3	0.0	0.6	0.3	0.6	0.3	0.3	0.3	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Globorotalia juanai</i>																				0.3	0.9	0.0
<i>Globorotalia cibaoensis</i>																		0.3	0.0	1.0	0.0	0.0
<i>Globorotalia margaritae</i>									0.9	0.9	0.7											
<i>Globorotalia crassaformis</i>	1.2	0.0	0.0	0.0	0.0	0.0	0.3															
<i>Globorotalia tosaensis</i>					0.6	0.3	0.0	0.3														
<i>Globorotalia truncatulinoides</i>	0.0	2.3	3.1	5.5	1.3																	
<i>Globorotalia merotumida</i>												0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
<i>Globorotalia plesiotumida</i>						0.3	0.0	0.0	0.0	0.9	0.7	1.0	2.6	1.6	0.3	0.3	0.0	0.0	0.6	0.0	3.4	0.0
<i>Globorotalia tumida</i>	2.2	2.0	2.4	1.5	4.2	0.3	5.3	0.3	8.5	0.6	0.7	0.7	1.9	4.1	0.6	1.7	0.6					
<i>Globorotalia unguata</i>	0.9	1.7	1.7	1.2	0.0	0.0	0.3	0.6	1.2													
<i>Globorotalia anfracta</i>	0.3	0.0	1.7	0.3	0.0	0.6																
<i>Turborotalita humilis</i>	0.0	0.0	5.8	0.0	0.0	6.6	0.7	0.3	0.0	0.0	0.7	0.0	0.3	0.0	0.0	1.7	0.0	0.6	0.6	0.3	0.0	0.3
<i>Globoquadrina venezuelana</i>							2.6	0.0	1.2	2.8	1.0	2.6	1.0	3.8	1.6	2.3	0.6	0.9	0.6	4.2	0.6	3.3
<i>Globoquadrina dehiscentis</i>																			0.3	0.3	0.3	0.0
<i>Globoquadrina baroemouensis</i>																					0.3	0.3
<i>Globoquadrina conglomerata</i>	0.9	0.3	0.3	0.0	0.3	0.3	0.0	0.0	1.8	1.2	0.3	0.0	0.3	0.3	0.3	0.0	0.0	0.0	0.0	0.7	0.0	0.3



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## APPENDIX B (continued).

Site 807 Core catchers	N22				N21			N20/N19		N19/N18					N17b				
	1H	2H	3H	4H	5H	6H	7H	8H	9H	10H	11H	12H	13H	14H	15H	16H	17H	18H	19H
<i>Streptochilus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Globigerina quinqueloba</i>	6	0	0	0	12														
<i>Globigerina bulloides</i>	2	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Globigerina woodi</i>					9	4	18	3	23	32	73	115	128	121	142	122	144	99	123
<i>Globigerina apertura</i>					2	17	10	2	1	23	25	36	23	23	24	14	14	14	11
<i>Globigerina nepenthes</i>											2	2	13	1	6	4	0	3	6
<i>Globigerina rubescens</i>	60	59	51	30	19	22	18	4											
<i>Globigerinoides obliquus</i>		1				6	10	12	19	21	5	1	0	6	6	0	8	7	3
<i>Globigerinoides extremus</i>		2	0	0	0	0	1	5	1	2	0	0	0	0	0	0	1	1	
<i>Globigerinoides conglobatus</i>	5	2	1	0	0	0	2	1	0	1	0	0	0	1	1	0	0	2	0
<i>Globigerinoides sacculifer</i>	9	9	11	14	11	3	10	16	7	5	5	10	6	11	4	15	10	5	2
<i>Gs. sacculifer (no sac)</i>	15	12	28	28	23	8	10	23	23	19	11	15	24	8	10	36	18	22	15
<i>Globigerinoides fistulosus</i>						6													
<i>Globigerinoides ruber (w)</i>	39	63	73	81	63	11	16	1	0	2	1	0	0	0	0	0	0	0	0
<i>Globigerinoides tenellus</i>	0	1	0	0	2	1													
<i>Orbulina universa</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	2	0	2	1
<i>Globorotalia menardii (l)</i>	8	11	5	0	0	5	2	0	0	5	9	10	2	10	0	3	1	0	30
<i>Globorotalia menardii (r)</i>	0	0	1	0	0	1	4	6	2	8	0	0	3	1	0	0	5	0	1
<i>Globorotalia scitula</i>	1	0	1	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Globorotalia cibaoensis</i>													1	2	0	0	2	0	0
<i>Globorotalia crassaformis</i>	2	1																	
<i>Globorotalia margaritae</i>												1	0	0	0	0	0	3	0
<i>Globorotalia tosaensis</i>			8	0	0	0	1												
<i>Globorotalia truncatulinoides</i>	0	2	4	0															
<i>Globorotalia merotumida</i>																			8
<i>Globorotalia plesiotumida</i>										11	0	4	1	2	0	8	0	0	5
<i>Globorotalia tumida</i>	5	5	6	7	0	22	16	12	16	13	3	0	2	0					
<i>Globorotalia unguolata</i>	0	2	2	1	0	1	1	2											
<i>Globorotalia anfracta</i>	0	0	2																
<i>Turborotalita humilis</i>					3			4		3				1					

## APPENDIX B (continued).

[illegible]

APPENDIX B (continued).

Site 847	N22								N21				N20/N19			N19/N18			N17b													
	Samples ( xH-4)								1H	2H	3H	4H	5H	6H	7H	8H	9H	10H	11H	12H	13H	14H	15H	16X	17X	18X	19X	20X	21X	22X	23X	24X
<i>Globigerina quinqueloba</i>	0	0.3	0.3	0	0	0	0	0	1																							
<i>Globigerina falconensis</i> (?)																	0.3			4.3												
<i>Globigerina bulloides</i>	1.8	1.5	1	0	0.9	0.7	1.3	1.3	0	0.7	0	0.3		0.3	0.7	0.7	0.6	0	0.6	0	0	0	0	0.3	0	0						
<i>Globigerina nepenthes</i>														0.3	0.3	0	1.9	2	0	1.2	0.7	0.3	2.5	5.5	5.6	4.2						
<i>Globigerina woodi</i>			0.7	0.3	0.9	1	2.6	4.6	2.9	6.6	1.2	0.3		3.6	6	0.7	5	3.3	3.9	3.6	7.9	8.9	6.3	10	5.9	2.9						
<i>Globigerina apertura</i>						0.7	2.3	2.6	1.9	4.3	0.3	0		0.6	1.7	1.3	3.8	1	1.2	0.3	0.7	2.3	2.5	1.2	1.9	1						
<i>Globigerina rubescens</i>	1.2	2.7	3.6	5.2	3.8	0	2	2.6	1																							
<i>Globigerinoides obliquus</i>								0.3	1.9	1.3	1.2	1.7		4.2	1	0.3	3.8	1.6	2.1	1.2	1.6	3.3	3.2	2.4	0.9	2						
<i>Globigerinoides extremus</i>										1	0	0		0.3	0	0	0	0.3	0	0	0	0	0.6	0.9	0.6	0						
<i>Globigerinoides sacculifer</i>	0.3	0.6	1.3	0.6	0.6	0	0.7	1	0	0.3	0.6	0.7		1.9	0.3	0	0.3	1	0	0.3	0	0.3	0	0.6	0	0.3						
<i>Gs. sacculifer</i> (no sac)	0	0.9	4.6	0.9	4.4	0.3	1.3	2.3	3.2	3.6	1.2	2.3		1.6	1.3	0.3	2.2	0.7	0.3	2.1	0.3	3.3	0.6	1.5	0.9	1.3						
<i>Globigerinoides fistulosus</i>						2.3	0.3																									
<i>Globigerinoides ruber</i> (p)		0.3																														
<i>Globigerinoides ruber</i> (w)	1.2	2.1	6.6	4	12	6.5	11	6.3	3.5	5.9	3.7	0		0.3																		
<i>Globigerinoides tenellus</i>	0	0	0.7	0	0.3	0	0.3																									
<i>Orbulina universa</i>	0.3	0.3	1.7	0.6	1.9	2.6	0.7	1.7	1.3	1	0.3	0.7		0	0.3	0	0.3	0	0.9	2.1	0.3	5.9	0.6	0.6	0.6	1.3						
<i>Globorotalia miocenica</i>														1																		
<i>Globorotalia menardii</i> (l)	0.9	1.5	2	1.2	1.3	1.6	0	0.3	0	0	0	0		0.3	0	0	0.6	0	1.5	0.6	0.7	0	0.3	1.2	0	13						
<i>Globorotalia menardii</i> (r)	0	0	0	0	0	0	0	0.7	0.3	2	3.4	6.6		1.9	0	4	1.6	1.6	1.8	1.5	1	2	3.8	3	4	1.6						
<i>Globorotalia limbata</i> (r)									0.3	0	0	0.7		0	0	0	0.3	0	0	0	0.3											
<i>Globorotalia limbata</i> (l)									0	0	0	0		0	0	0	0	0	0	0	0											
<i>Globorotalia anfracta</i>	0	0	0	0	0	0	0	0	0	0	1.6	2.3																				
<i>Globorotalia theyeri</i>	0	2.4	4	3.7	0	0	0	0.3	0.3																							
<i>Globorotalia scitula</i>	0.6	0.3	0.3	0	0.9	2.3	1.3	4.3	0.6	0.7	0.6	1.3		0	0.7	0.3	0.6	0.7	0.9	1.5	0.3	1	2.5	3.6	3.7	2.3						
<i>Globorotalia juanai</i>																																
<i>Globorotalia cibaoensis</i>																	0.3	0	0.3	0	0	0.3	0	0	0	0						
<i>Globorotalia puncticulata</i>						0.3	0	0	0	0	16																					
<i>Globorotalia inflata</i>	0	0	0	0	0	0	0	0	0	0	0.6																					
<i>Globorotalia crassula</i>								0.3																								
<i>Globorotalia crassaformis</i>	0.3																															

APPENDIX B (continued).

Site 847	Samples ( xH-4)	N22							N21				N20/N19			N19/N18			N17b							
		1H	2H	3H	4H	5H	6H	7H	8H	9H	10H	11H	12H	13H	14H	15H	16X	17X	18X	19X	20X	21X	22X	23X	24X	25X
<i>Globorotalia tosaensis</i>				0	0.3	0	0.7	2.6	0	0	1.3															
<i>Globorotalia truncatulinoides</i>		0	0	0.3	0.3				0																	
<i>Globorotalia merotumida</i>																								0.3	0	1.3
<i>Globorotalia plesiotumida</i>											0.3	0.3		0.3	0.7	0	2.2	0.3	0.6	0.6	0.3	0.3	0.3	0.9	0	2.9
<i>Globorotalia margaritae</i>																								0.3	0	0
<i>Globorotalia tumida</i>		0.6	0	1.3	0.3	9.5	0	1	4.6	2.5	2	0.6	0.7	4.2	2.7	1	3.8	0.7	0.3							
<i>Globorotalia unguata</i>		0.6	0.3	1	0.6	0.9	0	0.7	0	0.3	1															
<i>Turborotalita humilis</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0.3	0	0	0	0	0	0	0
<i>Globoquadrina dehiscens</i>																					0.3	0	0	0	0	0.3
<i>Globoquadrina baroemoensis</i>									0.3	0	0	0	1	0.3	0	0.7	0.6	0.3	0.6	0.6	0	0	0	0.3	0	0
<i>Globoquadrina conglomerata</i>		0	0	0	0	0.3	0	0	0	0	2.3															
<i>Globoquadrina venezuelana</i>				1.3	0	0	0	0	0	0	0	2.2	0.7	1.6	0.7	2	3.8	2.6	3	1.5	1.3	0.7	0.9	6.1	9.9	2.6
<i>Dentoglobigerina altispira</i>												1.9	0.7	0.6	0.3	0.3	1.3	0	0.3	0.3	0	0	0	0	0	0
<i>Neogloboquadrina pachyderma (l)</i>		0	0.3	0.3	0.6	0	0	0	0.3	0	0	0	0	0	1.3	1	0.9	1	6	5.8	6.6	1	0	0	0	0
<i>Neogloboquadrina pachyderma (r)</i>		3.3	5.7	0.3	3.7	0.9	0	0	0	0.3	0	0	0	0	0	0	0	0	1.2	3.6	0	0	0.6	0.3	7.1	0
<i>Neogloboquadrina acostaensis</i>												0.6	7.3	12	32	30	16	35	44	39	25	33	43	23	27	29
<i>Neogloboquadrina humerosa</i>																		0.3	0	0	0	1.7	2.5	2.1	3.4	0
<i>Neogloboquadrina dutertrei</i>		79	71	35	69	30	44	32	22	34	42	38	30	28	26	17	23	19	3.9	9.4	3.3					
<i>Pulleniatina obliquiloculata</i>		0	0.3	2	0.3	0.3	0	0.3																		
<i>Pulleniatina primalis (l)</i>						0.6	0.7	1.6	0.7	2.9	0	0.9	0.3	0.6	4	0	0.9	1.3	0.3	0	0.3	0	0.3	0.3	0.3	0
<i>Pulleniatina primalis (r)</i>				1.3	0	0	0	0.3	2	0	2.3	0.3	4.3	0	0	0.3										
<i>Sphaeroidinellopsis seminulina</i>												0.6	1.7	2.6	0.3	1.3	0	4.9	1.5	1.2	2.6	1.3	1.6	0.9	0.3	0.7
<i>Ss. paenedehiscens</i>														1	0.7	0.3	0.3	1	0.6	0.6	1.3	1	0.3	0	0	0.7
<i>Sphaeroidinella dehiscens</i>		0	0	0	0	0	0.3	1	0.3	1	0	0.3	0	0	0	0	0.3	0.3								
<i>Beella praedigitata</i>		0	0.6	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0	0.3	0.3							
<i>Globorotaloides hexagona</i>		0.3	0.6	5.3	0.6	0.3	1	0.7	1	2.2	1.7	1.9	1.3	0.6	0.7	0	0.9	2	0.6	1.8	0.3	0	1.9	3	2.5	2.9
<i>Tenuitellids</i>		0.9	1.5	0.7	0.3	0.3	0.7	0.3	0.7	1.3																
<i>Globigerinita glutinata</i>		5.4	3.3	21	5.8	27	29	35	37	37	20	21	33	30	17	38	23	17	21	18	37	32	23	28	24	29
<i>Globigerinita uvula</i>														0.3	0		0	0	0.6	0	0	0.3	0.3	0	0	0
<i>Candeina nitida</i>																			0.3							



APPENDIX B (continued).

Site 847	N22								N21				N20/N19			N19/N18			N17b													
	Samples ( xH-4)								1H	2H	3H	4H	5H	6H	7H	8H	9H	10H	11H	12H	13H	14H	15H	16X	17X	18X	19X	20X	21X	22X	23X	24X
Globigerinella aequilateralis		0.6	1.5	2	0	0	0.3	0.3	0	0.6	0.3	0.6	0.7	0.3	0	0	1.6	1	0.3	1.8	1.6	0.7	0.6	1.5	0	1						
Globigerinella calida		0	0	1	0	0	1	0	0.3	0	0.3																					
Globigerinella obesa		3	2.1	1	1.2	3.2	4.2	1.3	1	0	0	0.6	1.3	1.3	0.7	0.3	0.6	1	0.6	0.6	1.6	0.3	0.6	1.5	0.9	0						
Totals		100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	

APPENDIX B (continued).

Site 852	Samples	N22			N20/N19		N19/N18		N17b
		1H-4	2H-4	3H-4	4H-4	5H-4	6H-4	7H-4	8H-4
	<i>Globigerina bulloides</i>	23	4	3	0	0	2	1	2
	<i>Globigerina nepenthes</i>					2	5	13	5
	<i>Globigerina woodi</i>	4	0	1	12	12	20	11	17
	<i>Globigerina apertura</i>				0	4	20	0	5
	<i>Globigerinoides obliquus</i>	3			7	4	0	8	9
	<i>Globigerinoides conglobatus</i>	0	5	1	0	0	0	1	0
	<i>Globigerinoides sacculifer</i>	12	0	11	8	2	5	5	10
	<i>Gs. sacculifer (no sac)</i>	11	6	14	20	7	14	9	15
	<i>Globigerinoides fistulosus</i>				1				
	<i>Globigerinoides ruber</i>	0	3	9	10				
	<i>Orbulina universa</i>	1	9	3	8	1	0	3	4
	<i>Globorotalia menardii (l)</i>	41	18	23	0	12	18	17	0
	<i>Globorotalia menardii (r)</i>	0	7	0	0	10	8	3	11
	<i>Globorotalia scitula</i>	2	0	1	0	1	0	1	5
	<i>Globorotalia crassula</i>				1				
	<i>Globorotalia tosaensis</i>		2	0					
	<i>Globorotalia plesiotumida</i>						9	10	10
	<i>Globorotalia tumida</i>	39	42	90	98	7	14	0	
	<i>Globorotalia unguolata</i>	0	0	0	0	1			
	<i>Turborotalita humilis</i>	0	0	0	0	0	2	0	0

Site 852	Samples	N22			N20/N19		N19/N18		N17b
		1H-4	2H-4	3H-4	4H-4	5H-4	6H-4	7H-4	8H-4
	<i>Globoquadrina dehiscens</i>								2
	<i>Gq. baroemoensis</i>	1	0	0	0	0	0	0	0
	<i>Gq. venezuelana</i>		2		1	5	8	3	10
	<i>Dentoglobigerina altispira</i>					3	7	0	0
	<i>Neogloboquadrina dutertrei</i>	76	145	64	5	41	0	0	0
	<i>N. pachyderma (l)</i>	0	0	0	2	1	5	1	3
	<i>N. pachyderma (r)</i>	11	26	6	14	0	10	0	15
	<i>N. acostaensis</i>			14	69	7	64	22	112
	<i>Pulleniatina obliquiloculata</i>	21	12	13					
	<i>Pulleniatina primalis (l)</i>	1	6	12	12	0	3	0	0
	<i>Pulleniatina primalis (r)</i>	15	3	0	0	0	0	0	0
	<i>Sphaeroidinellopsis kochi</i>						2	2	0
	<i>Ss. paenedehiscens</i>				2	5	3	3	0
	<i>Ss. seminulina</i>			1		23	33	11	22
	<i>Sphaeroidinella dehiscens</i>	0	11	20	11	0	0	0	0
	<i>Beella praedigitata</i>	0	2	0	1	0	0	0	0
	<i>Globorotaloides hexagona</i>	1	0	5	4	1	2	1	0
	<i>Globigerinita glutinata</i>	27	4	5	18	26	48	19	45
	<i>Globigerinella aequilateralis</i>	1	2	4	7	2	7	1	0
	Totals	290	309	300	311	177	309	145	302