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Planktonic foraminiferal depth habitat and $\delta^{18}O$ calibrations: Plankton tow results from the Atlantic sector of the Southern Ocean

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[1] Plankton tows conducted in the Atlantic sector of the Southern Ocean allow analysis of the influence of water column structure on planktonic foraminiferal abundance and $\delta^{18}O$ composition. Foraminiferal abundance varies by several orders of magnitude across a large gradient in sea surface temperature and other hydrographic features, demonstrating high sensitivity of foraminiferal populations to regional differences in water properties. The depth of maximum abundance for key species such as *Globigerina bulloides* and *Neogloboquadrina pachyderma* is not constant from station to station. The pattern suggests that their abundance and shell chemistry are tied to density horizons or other conditions (such as food availability) that become more sharply defined with depth in the northern subantarctic. The consistent observation of *Globorotalia inflata* and *Globoratalia truncatulinoides* as relatively deep-dwelling species confirms their utility as indicators of upper thermocline properties. In $\delta^{18}O$ all species are observed to be isotopically lighter than predicted from water properties, but the species-specific offset is fairly uniform at all stations. These observations define the utility of multispecies $\delta^{18}O$ for reconstructing temperature and density stratification from past surface oceans. *INDEX TERMS:* 4267 Oceanography: General: Paleoceanography; 4572 Oceanography: Physical: Upper ocean processes; 4870 Oceanography: Biological and Chemical: Stable isotopes; 3030 Marine Geology and Geophysics: Micropaleontology; *KEYWORDS:* stratification, $\delta^{18}O$

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1. Introduction

[2] A recurring problem in paleoceanography is to make inferences about the ocean in four dimensions from a one-dimensional sediment core record. Of course, this problem is greatly simplified if we assume that the chemistry of sedimentary populations of planktonic foraminifera is homogeneous and is acquired at one time and place in the water column. This is an implicit assumption in most studies, despite evidence that this does not hold for most species [*Lohmann*, 1995]. Vertically stratified plankton tows are among the more direct means of determining how these simplifying assumptions can be related to precise physical processes. The advantage of a plankton tow system, such as the multiple opening closing net and environmental sampling system (MOCNESS) [*Wiebe et al.*, 1976, 1985], is that it collects material on a depth-discrete basis at a fixed sampling time and location. This approach allows for real-time observation of the depth distribution of foraminiferal abundances and isotopic compositions for comparison to simultaneously collected data such as sea surface temperature (SST), salinity, and fluorescence (a proxy for chlorophyll a content) [*Schreiber et al.*, 1998].

[3] A variety of studies have documented the vertical distribution of planktonic foraminifera in the tropics [e.g., *Fairbanks et al.*, 1980, 1982; *Ravelo et al.*, 1990; *Ravelo and Fairbanks*, 1992; *Watkins et al.*, 1996, 1998], yet there is an equal need to calibrate the paleoceanographic proxies derived from planktonic foraminifera in higher-latitude regions. This is especially true given that foraminifera represent one of the few means for retrospective monitoring of the processes of deep-water formation and heat exchange between the high-latitude ocean and the atmosphere. Core-top calibration approaches reveal a few basic properties of modern high-latitude foraminiferal assemblages, but generally, they cannot discriminate the mechanisms through which sedimentary signatures are acquired. For example, *Globigerina bulloides*, one of the principal species studied at middle-to-high latitudes, follows the predicted $\delta^{18}O$ of calcite for North Atlantic surface waters only over a narrow range of about 1‰ (from 1 to 2‰); outside of this range, *G. bulloides* core-top $\delta^{18}O$ does not reflect mean surface conditions [*Bard et al.*, 1989]. The implication is that either seasonal growth or calcification at depth confounds the signal. By contrast, similar data from another planktonic species, *Neogloboquadrina pachyderma*, suggest a very different pattern in South Atlantic core tops: the $\delta^{18}O$ of this species follows the predicted $\delta^{18}O$ of calcite (and therefore SST variability) over a wide range of latitudes and hydrographic conditions [*Charles and Fairbanks*, 1990]. This pattern for *N. pachyderma* $\delta^{18}O$ is in marked contrast to that for the North Atlantic region [*Kohfeld et al.*, 1996; *Bauch et al.*, 1997]. Sorting

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out such differences between two widely used planktonic species at high latitudes, including the differences between Northern and Southern Hemisphere patterns, is an essential prerequisite for refining reconstructions of past surface ocean conditions.

[4] Here we present a description of modern middle-to-high—latitude planktonic foraminifera caught in MOCNESS tows taken in the South Atlantic sector of the Southern Ocean over a 1-month period during the austral summer of 1996. Specifically, we concentrate on the paleoceanographically important species that span a variety of depth habitats and latitudes. Previous work in the same study region made use of underlying core-top samples [*Niebler et al.*, 1999] to decipher water column stratification. Our work here complements this and other work with core tops in the Southern Ocean [*Labeyrie et al.*, 1996] because it allows a direct correlation between foraminiferal geochemistry and surface ocean properties. Our analysis does not consider all aspects of foraminiferal ecology, but we demonstrate that the unique intersection of depth habitat and South Atlantic water column structure might explain some of the main patterns of foraminiferal abundance and chemistry in the modern sediments (and by extension the paleoceanographic record).

2. Methods and Materials

[5] During January–March 1996 we collected MOCNESS plankton tow samples at or near piston coring stations that later became coring stations for Ocean Drilling Program (ODP) leg 177. The primary goals of this operation, on cruise TNO57 aboard the R/V *Thomas Thompson*, were twofold: (1) to document the vertical distribution of microfossil-producing plankton (foraminifera) and, by comparison with water column properties, to understand the ecological controls on their distribution and (2) to understand how and where in the water column the foraminifera acquire their chemical and isotopic signatures.

[6] Samples were collected from six stations spanning a latitudinal and longitudinal range between 41° and 53°S and 5° and 12°E, respectively (Figure 1). These subantarctic South Atlantic station locations were dictated by sediment coring interest, because they are areas with high sedimentation rates and important sedimentary sequences. However, these stations also happen to span surface waters that today exhibit, among other properties, an SST range of greater than 12°C in only 12° of latitude, making for one of the largest SST gradients in the global ocean [*Levitus and Boyer*, 1994]. The MOCNESS stations are therefore appropriately located in areas of interest for microfossil calibration.

[7] Of concern in any plankton tow study is the question of how representative such a ''snapshot'' view may be of seasonal or longer-term conditions. We assume that our results, collected between 4 February 1996 and 5 March 1996, are representative of the summer season of biologic production in the Southern Ocean. *Abelmann and Gersonde* [1991] summarized biosiliceous particle flux (radiolarians and diatoms) for time series sediment trap deployments in the Southern Ocean between 1983 and 1990. Their results demonstrated that the flux during the austral summers accounted for 70–95% of the total annual flux, suggesting that our snapshot is as representative of sedimentary conditions as is possible for a 1-month period. Because of ship time constraints, our sampling strategy could not explicitly resolve possible population migrations over diurnal or lunar-modulated [e.g., *Bijma et al.*, 1990] reproductive cycles.

[8] Vertically stratified plankton tow samples (150-μm mesh net within a 333-μm net used for structural support) were collected using a MOCNESS device described in detail by *Wiebe et al.* [1976, 1985]. The MOCNESS system was also equipped with sensors to measure in situ properties from the water column, including temperature, salinity (and σ_t), and fluorescence. The temperature and salinity data are presented in Figure 2, while the σ_t data are shown with fluorescence in Figure 3. The individual nets were sequentially opened and closed over discrete depth intervals between 0 and 800 m, and temperature, salinity, and fluorescence were measured in situ with attached conductivity-temperature-depth (CTD) and fluorometer probes. The nine sampled intervals and their vertical spacing varied from station to station and were chosen using hydrographic information obtained from a separate CTD/Rosette cast just prior to MOCNESS deployment. MOCNESS samples were stored in a 100% ethyl alcohol (ethanol) solution to prevent dissolution of foraminiferal shells and to minimize artifacts to isotopic measurements that can arise with other preservatives such as buffered formalin [*Ganssen*, 1981]. Splits of these samples were density-separated in a hypersaline solution according to a modification of a method described by *Bé* [1959].

[9] Depending on station-specific foraminiferal abundances, sample splits were counted with the aim of totaling ~300 specimens per sample. In some cases the total abundance was low enough that the total counts came from the whole sample at less than 300 specimens. The abundance of key species from these sites are presented (Figure 4) as number of shells per unit volume of seawater, a scale made possible because the volume of filtered seawater was measured with a flowmeter attached to the frame of the MOCNESS system. The flowmeter data should be considered only an approximate representation of the effective flow through the nets (especially if biomass concentrations are high enough to cause net clogging, lower flow estimation, and hence overestimation of foraminiferal standing stock). For most stations, however, the relationship between the flowmeter data and effective flow should be relatively uniform for all the nets on a given cast. Fluorescence (mg/m^3) is also presented with the absolute foraminiferal abundance data (Figure 4), after it was corrected by uniformly subtracting fluorescence contents below 500 m (which we assume to represent the background) for a given station. Planktonic foraminifera captured with the MOCNESS plankton tow system are not necessarily alive; however, their isotopic composition (discussed below) helps discern live from dead populations.

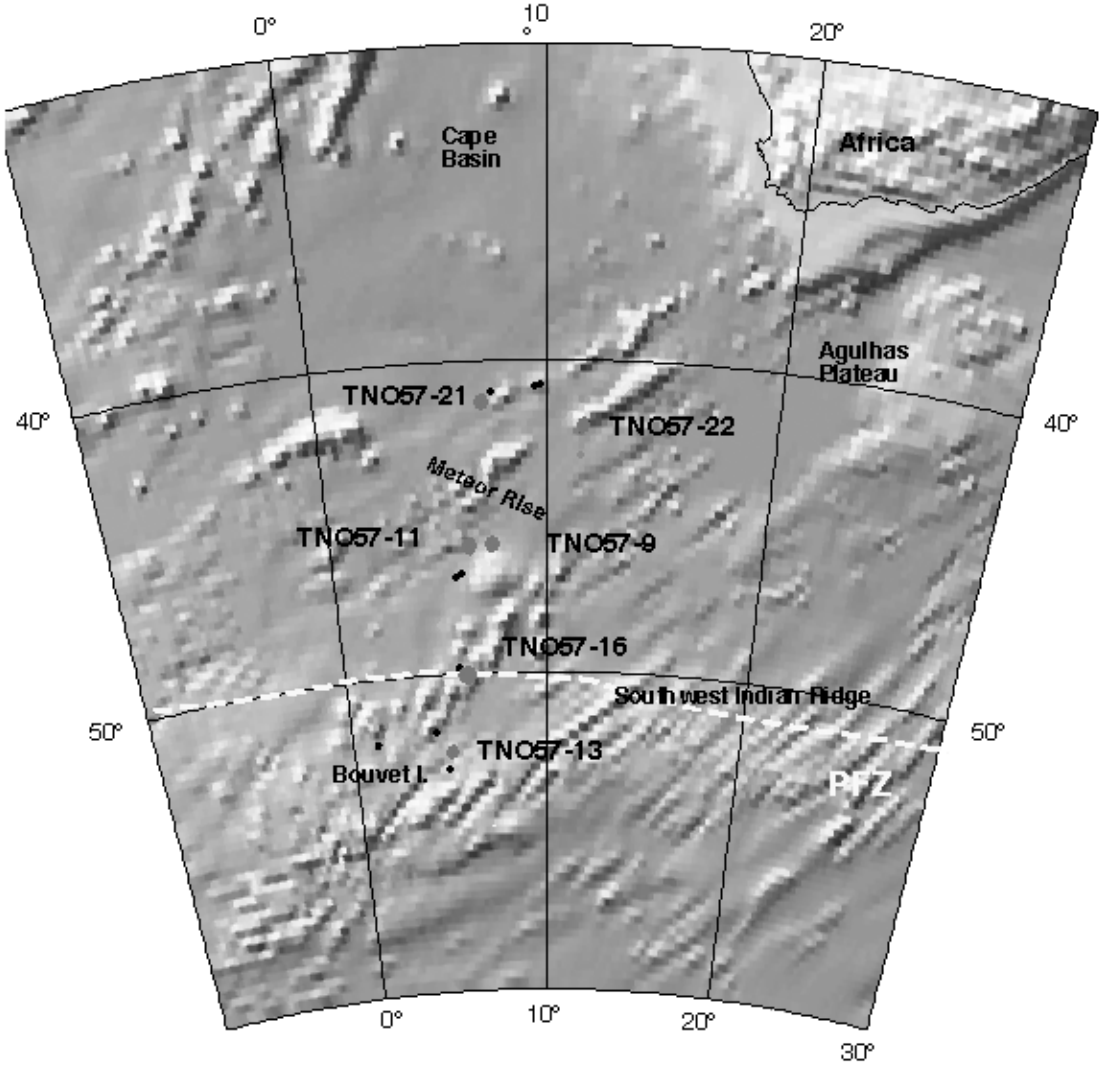


Figure 1. Map showing our plankton tow station locations between Africa and Antarctica. The dashed line corresponds to the mean position of the modern Polar Frontal Zone (PFZ), which is the northern terminus of the subsurface T_{min} layer bounded by the 2°C isotherm in the 100–300-m layer in the summer and the vertical 2°C isotherm in the winter [*Belkin and Gordon*, 1996].

[10] In order to minimize possible size-related differences, $\delta^{18}O$ analyses were carried out on the 150–250-μm fraction of *G. bulloides, N. pachyderma, Globorotalia truncatulinoides, Globorotalia inflata*, and *Orbulina universa*, where sufficient quantities were available. All samples were roasted under vacuum at 375°C for 1 hour prior to isotopic analysis. Measurements were made at the Scripps Institution of Oceanography (SIO) using a Carousel-48 automatic carbonate preparation device coupled to a Finnigan MAT 252 mass spectrometer. The $\delta^{18}O$ precision (1σ) of the NBS-19 standard was better than 0.09‰ for 190 standards run along with the samples over an 18-month period during which the samples were analyzed. We will not deal with the $\delta^{13}C$ for the foraminifera (though the data exist) because measurements of seawater $\delta^{13}C$ (total dissolved CO_2) were probably compromised by sample storage effects.

[11] In order to compare equilibrium calcite $\delta^{18}O$ ($\delta^{18}Oec$) values against measured foraminiferal values we estimated the $\delta^{18}O$ of calcite precipitated in isotopic equilibrium with seawater. We first predicted the $\delta^{18}O$ composition of the seawater using our own salinity measurements obtained from the MOCNESS downcasts and a South Atlantic salinity-$\delta^{18}O$ (water) relationship from *Geochemical Ocean Sections Study* (*GEOSECS*) [1987] data shown by *Charles and Fairbanks* [1990]. The applicability of this relationship is assessed by representative $\delta^{18}O$ (water) (D. Hodell, personal communication, 1996) and salinity analyses from our own downcasts of the CTD (Figure 5). We then used the predicted $\delta^{18}O$ (water) and the MOCNESS temperature data to estimate the $\delta^{18}Oec$, according to a standard mean ocean water (SMOW) to Peedee belemnite (PDB) unit conversion [*Hut*, 1987] and a carbonate-water isotopic temperature scale from *O'Neil et al.* [1969]. These predicted $\delta^{18}Oec$

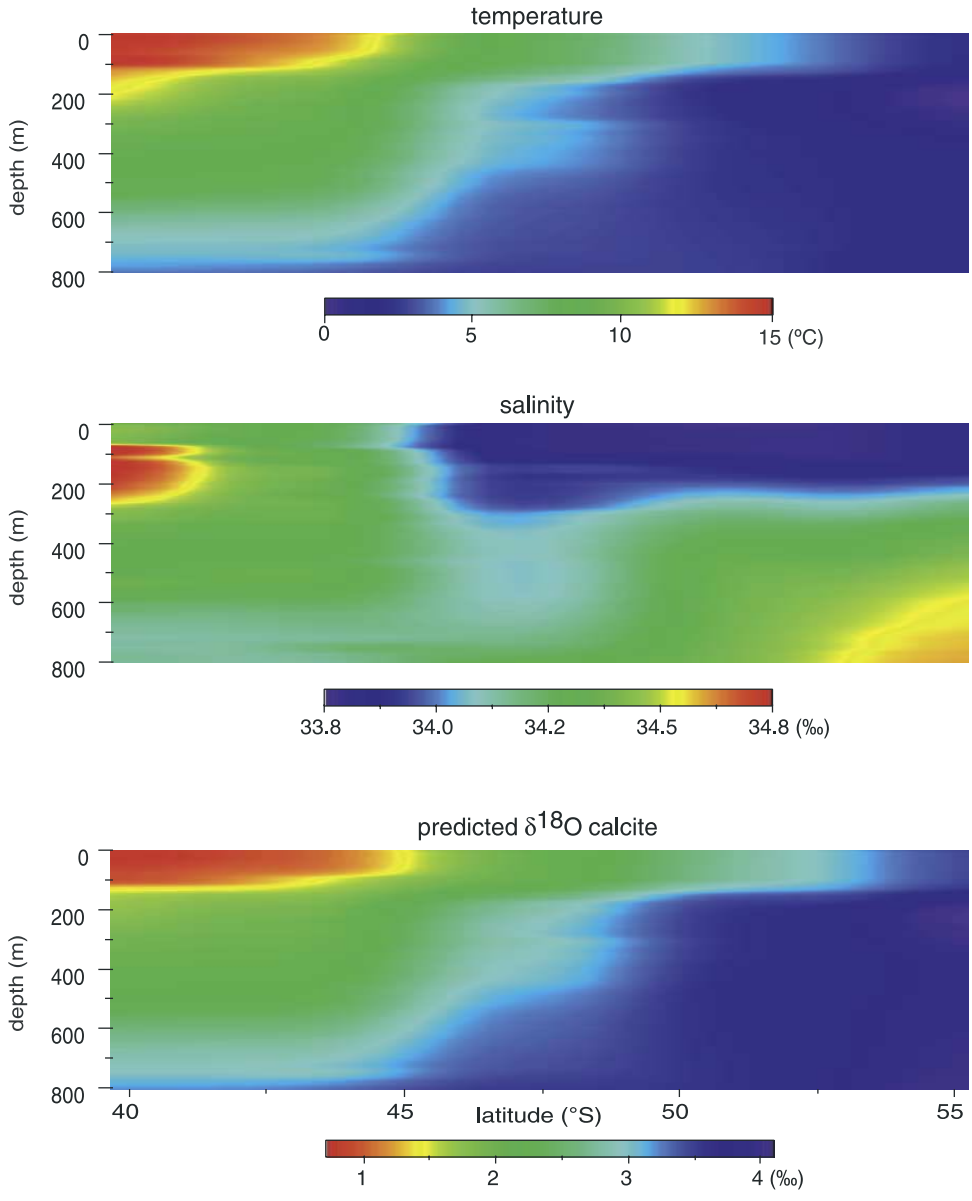


Figure 2. Latitudinal sections of temperature, salinity, and the predicted $\delta^{18}O$ of equilibrium calcite. The temperature and salinity data are downcast measurements collected with the CTD system, while the predicted $\delta^{18}O$ (calcite) data are calculated using $\delta^{18}O$ (standard mean ocean water (SMOW)) = 0.5(salinity) - 17‰ [*Charles and Fairbanks*, 1990], the *Hut* [1987] SMOW to Peedee belemnite (PDB) correction factor of −0.27‰, and the *O'Neil et al.* [1969] paleotemperature equation (see Figure 6 caption for further details).

data are then compared against $\delta^{18}O$ measurements from foraminifera collected in the water column in Figure 6, while also shown in latitudinal section form in Figure 2.

[12] Among the various $\delta^{18}O$ paleotemperature equations proposed in the literature [e.g., *Bemis et al.*, 1998, and references therein] we chose the inorganic calcite equation of *O'Neil et al.* [1969] as our reference point because it was the only one calibrated to temperatures as low as 0°C. However, we recognize that this definition of equilibrium calcite is arbitrary and perhaps not even directly applicable to living planktonic foraminifera. Over the temperature range of interest here (0–15°C) the absolute offset between measured foraminiferal $\delta^{18}O$ and "predicted equilibrium" varies significantly if other equations are extrapolated to the low temperature range [e.g., *Kim and O'Neil*, 1997; *Erez and Luz*, 1982]. Because there is as yet no agreement on how best to define equilibrium for biologically precipitated calcite, we cannot interpret the average apparent disequilibrium. On the other hand, the choice of paleotemperature equation does not affect the relative interspecies and intraspecies offsets from equilibrium, an important point that we discuss below.

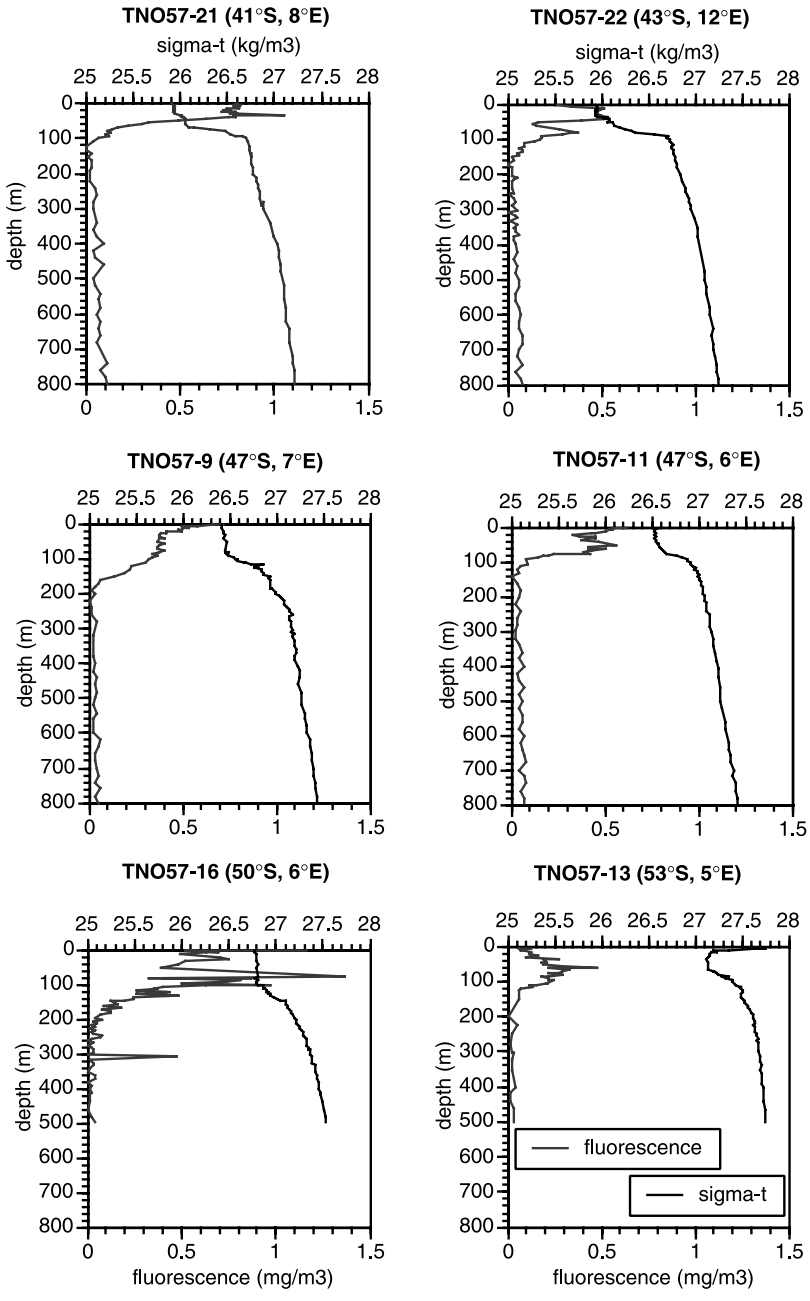
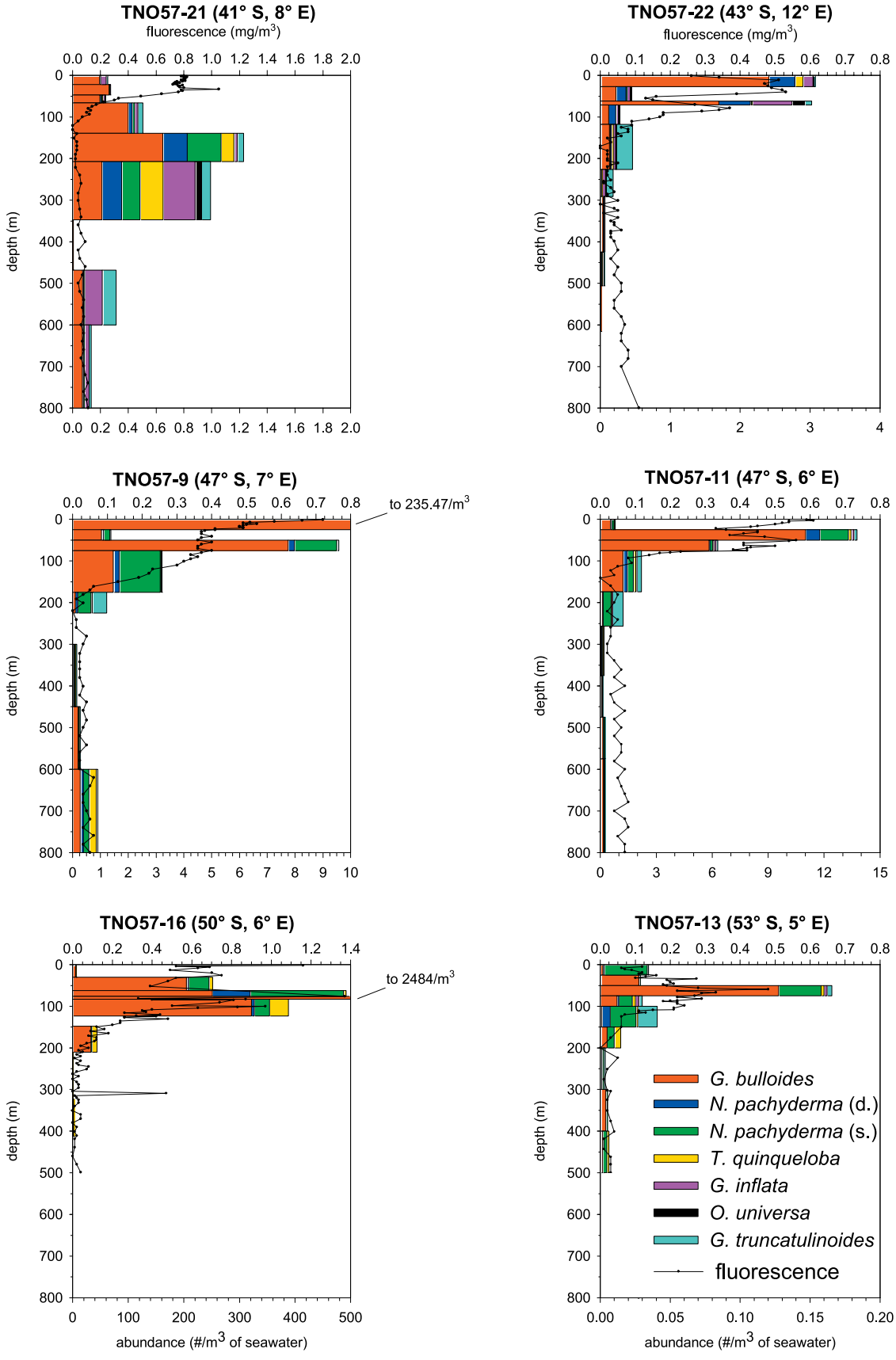


Figure 3. In situ fluorescence and σ_t profiles based on downcast data collected with the MOCNESS system. Panels representing data from individual stations are arranged from north to south. Fluorescence profiles are shown along the left side of each panel, while σ_t profiles are shown along the right side of each panel. Fluorescence is reported in concentration units as it is a proxy for chlorophyll *a* content [*Schreiber et al.*, 1998]. Note that the data are limited to 500-m depth at the southernmost stations, TNO57-16 and TNO57-13.

[13] In order to compare the foraminiferal $\delta^{18}O$ from the water column to that from material at the modern sediment-water interface, we also measured "core-top" samples beneath three of the six stations where material permitted. Core-top material is not presented from TNO57-22, TNO57-9, and TNO57-11 since we have reason to doubt the presence of modern or even late Holocene sediments at these locations. The representative data from the other stations are shown along the lines beneath individual panels of Figure 6. These samples were provided by either multicore or trigger core from each individual station for the depth interval of either 0–1 cm or 0–2 cm into the sediment. Table 1 presents a summary of the core samples used for the core-top data. Species-specific foraminiferal samples were generally picked from the 150–250-μm size fraction, although in one case (TNO57-21) it was necessary to


TNO57-21 (41° S, 8° E)
fluorescence (mg/m3)
TNO57-22 (43° S, 12° E)
fluorescence (mg/m3)
TNO57-9 (47° S, 7° E)
to 235.47/m3
TNO57-11 (47° S, 6° E)
TNO57-16 (50° S, 6° E)
to 2484/m3
TNO57-13 (53° S, 5° E)
depth (m)
abundance (#/m3 of seawater)
G. bulloides
N. pachyderma (d.)
N. pachyderma (s.)
T. quinqueloba
G. inflata
O. universa
G. truncatulinoides
fluorescence

supplement this with material from the >250-μm size fraction.

3. Results

3.1. Oceanographic Setting

[14] Figure 2 shows that the surface temperature ranges from about 1 to 13°C across the 12° latitudinal span of our study area. The density structure becomes much better defined to the north, with a relatively shallow thermocline and a clear surface mixed layer. The salinity section (Figure 2) shows generally more salty surface waters in the north, while also illustrating southern middepth anomalies that are likely the result of interleaving layers of water with different origin. Thus the local structure affecting the foraminiferal population is certainly partly a product of eddy mixing, which must be a perennial process associated with the Antarctic Circumpolar Current [*Savchenko et al.*, 1978; *Gille et al.*, 2000].

[15] Phytoplankton abundance, as in many other areas of the world's oceans, is sensitive to the hydrographic properties associated with the pycnocline. Figure 3 shows that fluorescence maxima all occur within the mixed layer, but usually at relatively deep depths near the top of the pycnocline. The origin of the so-called ''deep chlorophyll maximum'' in other regions has been a source of long standing debate, and the possible mechanisms for its occurrence include the intersection of high nutrients and high light, the effect of density gradients on settling, or preferential grazing patterns. It is also possible that fluorescence peaks are partly the result of phytoplankton photoadaptation, involving changes in the carbon to chlorophyll or carbon to fluorescence ratios. Without ancillary evidence our data cannot test these various possibilities. Accordingly, we only note the relationship between fluorescence and foraminifera on a descriptive (nonmechanistic) level.

3.2. Planktonic Foraminiferal Abundance

[16] Several important observations can be drawn from the abundance data presented in Figure 4. One is that the overall abundances vary considerably from site to site, by as much as 4–5 orders of magnitude between TNO57-16 and TNO57-13. The TNO57-9 site shows the highest surface foraminiferal abundance, about 235/m^3 of seawater, in apparent response to a phytoplankton bloom suggested by the coincident peak in fluorescence (>0.7 mg/m^3). The TNO57-16 site shows the highest middepth (75–100 m water depth) abundance, about 2484/m^3 of seawater, also in association with a fluorescence peak of about 1.4 mg/m^3. The highest deep (>100 m water depth) abundances are shown at TNO57-16, TNO57-9, and TNO57-11.

[17] The association of total foraminiferal abundance peaks with fluorescence maxima is not always straightforward. For instance, surface peaks in fluorescence at sites TNO57-21 and TNO57-11 are not coincident with abundance peaks at those stations. Also, fluorescence peak depths vary from site to site. For example, the peaks occur well below the surface at the TNO57-16 and TNO57-13 sites, while they generally occur closer to the surface at the other stations. Despite these differences, however, there is reasonable correspondence between foraminiferal abundance and fluorescence maxima. In fact, TNO57-22 shows a double fluorescence peak in the upper 100 m, with high foraminiferal abundances closely associated with each.

[18] It is possible to separate the abundance patterns by species. Despite the fact that *G. bulloides* is encountered over a wide depth range the maximum of this species is consistently associated with a fluorescence peak (the only exception being TNO57-21), suggesting that *G. bulloides* closely tracks phytoplankton blooms. The next most abundant species is *N. pachyderma* (left-coiling), which shows a wide range of occurrence for abundance maxima (anywhere from the surface at TNO57-13 to the 75–175 m depth at TNO57-9. *N. pachyderma* (right-coiling) is observed mostly at middepths, with one exception (TNO57-22). *Turborotalita quinqueloba* also generally shows its highest abundances below 100 m, although the surface maximum at TNO57-22 is also an exception. *G. inflata* is consistently most abundant at subsurface depths (between 50 and 300 m), while the maximum abundances of *G. truncatulinoides* are always deeper than 100 m. The maxima of this species are even deeper at TNO57-21 and TNO57-9, roughly 500 and 200 m, respectively. *O. universa* is the least abundant planktonic species in these tows, showing measurable middle-to-deep quantities at only TNO57-21 and TNO57-22.

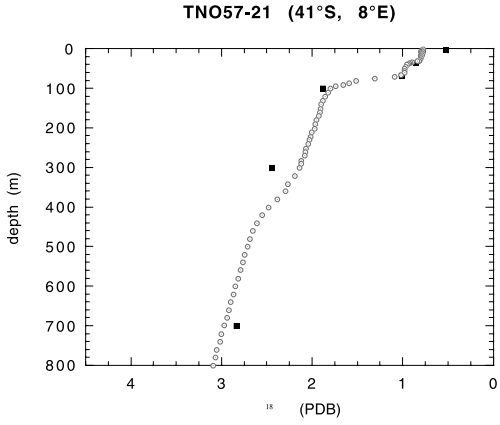
[19] In addition to this close association with a probable food source in phytoplankton (suggested by the fluorescence peaks), maximum foraminiferal abundances generally occur within the mixed layer and just above the pycnocline (the only exception being TNO57-21). In all cases, *G. bulloides* maxima coincide with overall foraminiferal maxima because it is everywhere the most dominant species.

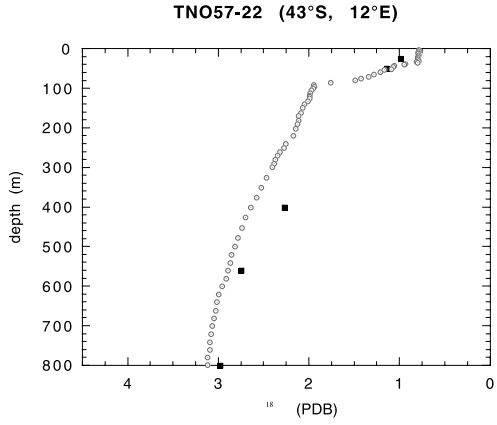
3.3. Oxygen Isotopic Signatures and Water Column $\delta^{18}O$ Gradients

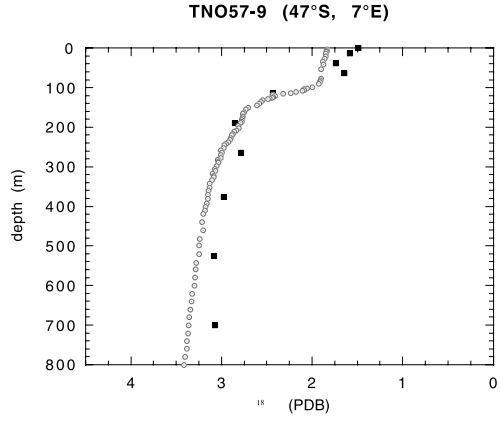
[20] Oxygen isotopic data ($\delta^{18}O$ in ‰PDB) from the water column and core-top samples are presented in Figure 6. In the water column at all stations, predicted $\delta^{18}O$ curves are more positive in $\delta^{18}O$ relative to foraminiferal measurements, implying that all species are well outside our

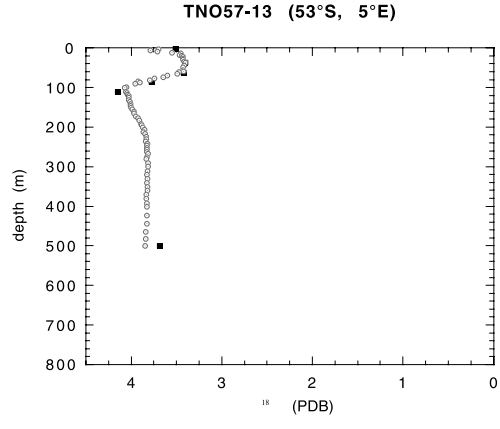
Figure 4. (opposite) Water column abundances of various species of planktonic foraminifera presented from each of our six stations, arranged as in Figure 3, along with in situ fluorescence data from the MOCNESS system. In each stacked histogram figure the varying column thickness corresponds to the towed depth interval in the water column, while the foraminiferal species absolute and relative abundances are shown along the bottom *x* axis according to the legend color scheme. The fluorescence data are shown in each panel along the upper *x* axis in concentration units of mg/m^3 (as in Figure 3).

calculations of isotopic equilibrium (using the *O'Neil et al.* [1969] equation) in this region. However, at the depth of maximum abundance for any given species, the species-specific offset from expected equilibrium is fairly constant. We specifically calculated this $\delta^{18}O$ departure for *G. bulloides, N. pachyderma, G. inflata*, and *G. truncatulinoides*, using all six stations and all appropriate depths (where peak abundances coincided with measurable $\delta^{18}O$). This collective analysis yielded an average $\delta^{18}O$ departure from equilibrium of 1.0 ± 0.4‰, with a high degree of similarity for each species (*G. bulloides* = 0.95, *N. pachyderma* = 1.00, *G. inflata* = 0.94, and *G. truncatulinoides* = 1.10).









[21] Figure 6 illustrates shallow-to-deep $\delta^{18}O$ gradients in different foraminiferal species that mimic the profiles of the predicted $\delta^{18}O$-calcite data. Considering *G. bulloides* and *N. pachyderma* as shallow dwellers (at northern and southern sites, respectively) and *G. inflata* and *G. truncatulinoides* as deep dwellers (at all sites), some relevant gradient observations could be made. The shallower species show a near-constant offset from the predicted curve of about 1‰ above 100 m, while the deeper species show a similar offset below that depth. Data from TNO57-22, TNO57-9, and TNO57-11 are sufficient to illustrate this pattern, while those from the other stations are not available. At stations where *G. bulloides* $\delta^{18}O$ is invariant with depth we assume the deeper signal simply reflects the descending populations that calcified at shallower depths. If we connect the shallow *G. bulloides* data or the shallow *N. pachyderma* data to the *G. inflata* or *G. truncatulinoides* data below 100 m at TNO57-22 and TNO57-9, a reasonable similarity to the predicted equilibrium curve is observed. Thus, by combining species the foraminiferal $\delta^{18}O$ tracks the basic structure of the thermocline with a relatively uniform 1‰ $\delta^{18}O$ offset. Similarly, at TNO57-11, analogous observations can be made with the gradient between shallow *G. bulloides* $\delta^{18}O$ data and deeper *G. truncatulinoides* $\delta^{18}O$ data.

[22] The core-top foraminiferal $\delta^{18}O$ data are shown along the bottom lines for each representative panel in Figure 6. The paucity of enough individual shells of a given species often prevented analysis, but where sufficient material was available, some comparisons could be made. In all cases the core-top foraminiferal $\delta^{18}O$ was more positive relative to that from the water column, by as much as 1.2–1.4‰ for *G. inflata* at TNO57-21, 1.25‰ for *G. bulloides* at TNO57-16, and 0.75‰ for *N. pachyderma* at TNO57-16.

4. Discussion

[23] The following discussion is organized around the questions of (1) whether unique inferences of depth habitat can be established for the four principal species found in the high latitude sediments and (2) what influence these ecological tendencies have on the $\delta^{18}O$ compositions of foraminifera and therefore the sedimentary record of high-latitude climate change. A number of analogous studies from different regions of the global ocean offer useful comparisons [e.g., *Ortiz et al.*, 1995; *Kohfeld et al.*, 1996], and general similarities in the ecological relationships of major species do exist among the various high-latitude regions of the ocean. However, we emphasize that the intersection of these ecological tendencies with the unique hydrographic conditions in the South Atlantic sector of the Southern Ocean creates unique impacts on the sedimentary record. Thus results from other regions, for example, the high-latitude North Atlantic, cannot necessarily be extrapolated to the Southern Ocean.

[24] One major question is whether there exists a truly surface-dwelling planktonic foraminiferal species in the South Atlantic. Our abundance data show high foraminiferal occurrence to be associated with peaks in fluorescence concentration at relatively deep portions of the surface mixed layer (Figure 4). This suggests that the foraminifera captured in our plankton tows are closely associated with a phytoplankton food source that is controlled by the density structure of the water column, which is not surprising since the top of the pycnocline likely sees high diffusion of underlying nutrients [*Anderson et al.*, 1972]. Thus there is no reason to suspect that any of the most common subpolar species are restricted to the surface mixed layer.

[25] From the sediment trap work of *Thunell and Reynolds* [1984], *Reynolds and Thunell* [1985], and *Sautter and Thunell* [1989] it is evident that *G. bulloides* is abundant in a wide range of thermal environments (at least 5–20°C) and increases in abundance during periods of high phytoplankton productivity due to upwelling or bloom conditions [*Sautter and Thunell*, 1991]. Other MOCNESS studies in upwelling environments have found peak *G. bulloides* abundances to be associated with a chlorophyll maximum and relatively high biomass contents [*Fairbanks et al.*, 1982; *Ortiz et al.*, 1995]. Our results, although with much higher abundance counts than encountered in these previous MOCNESS studies, show a similarly strong correspondence of *G. bulloides* to fluorescence maxima. This observation is consistent with the idea that this species is tightly coupled with phytoplankton blooms but is inconsistent with the idea that this species is strictly surface dwelling. These considerations also raise the possibility that the shallower populations of *G. bulloides* caught in our surface net tows may simply have been mixed upward from deeper portions of the mixed layer.

[26] *N. pachyderma* typically dominates the foraminiferal assemblage in other high-latitude regions of the ocean, and

Figure 5. (opposite) Comparison of the predicted equilibrium $\delta^{18}O$ (in ‰PDB) of calcite estimated with the same method but with two different starting points. The first involves the prediction of the $\delta^{18}O$ of seawater based on salinity (light circles), while the second involves actual measurements of the $\delta^{18}O$ of seawater (dark squares, D. Hodell, unpublished data, 1996) where data are available from four of the six stations. The results of this comparison justify the use of a South Atlantic salinity versus $\delta^{18}O$ (water) relationship derived from *GEOSECS* [1987] data (see text for details). With either starting point the $\delta^{18}O$ (water) information is necessary to take the prediction to the next step. The $\delta^{18}O$ (water) prediction is converted to PDB units [*Hut*, 1987] and then used to estimate the $\delta^{18}O$ of equilibrium calcite according to the paleotemperature equation of *O'Neil et al.* [1969]. Panel arrangement is consistent with previous figures, and locations for which this comparison was not possible (TNO57-11 and TNO57-16) are not shown.

there have been various attempts to determine the controls on the modern depth habitat of this species (e.g., *Ortiz et al.* [1995] for the North Pacific and *Kohfeld et al.* [1996] for the North Atlantic). Our South Atlantic results suggest this species is most abundant at pycnocline depths (strongly dictated by thermocline depths) and chlorophyll maxima in the sub-Antarctic (Figures 3 and 4), an observation that is generally consistent with the other previous

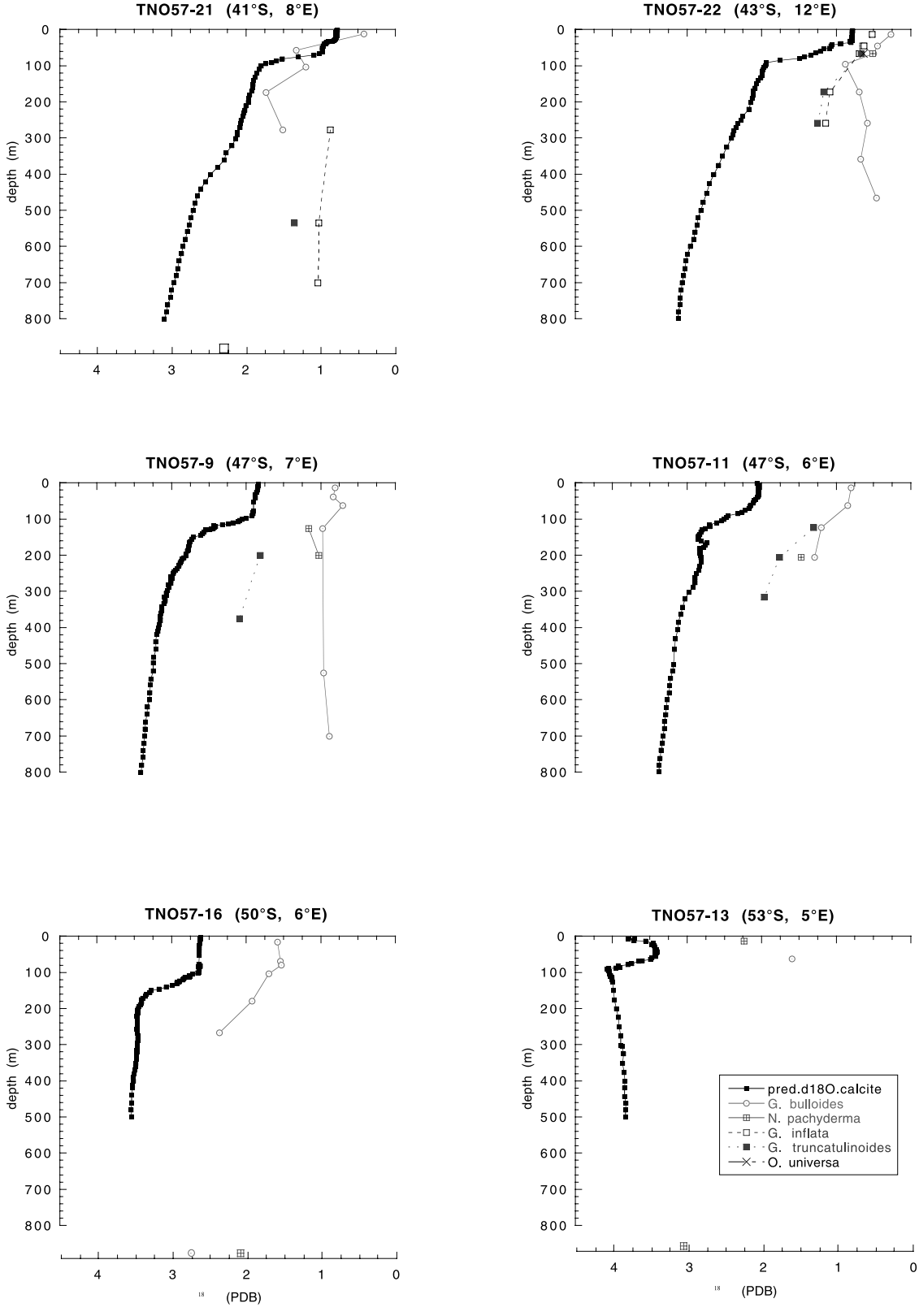


Table 1. Summary of Core-Top Sample Material Used in This Study

Site	Core-Type	Water Depth, m	Available Planktonic Species	Size Fraction, μm	Sample Interval, cm
TNO57-21	multicore	4978.5	*G. inflata*	>250	0–1
TNO57-16	trigger core	3665	*G. bulloides, N. pachyderma*	150–250	0–2
TNO57-13	multicore	2851	*N. pachyderma*	150–250	0–1

studies. In our study area the *N. pachyderma* abundance peak south of the modern polar front constitutes a case where the maximum does not coincide with a fluorescence peak below the pycnocline (Figures 3 and 4). This observation suggests that at higher latitudes, *N. pachyderma* may indeed be more surface-restricted. Other northern high-latitude MOCNESS studies [*Carstens et al.*, 1997; *Bauch et al.*, 1997] found the modern distribution of *N. pachyderma* tobe dictated more by water mass differences in the surface ocean. On the basis of either our results or those of *Ortiz et al.* [1995] and *Kohfeld et al.* [1996] the possibility exists that other nonbiological influences (i.e., eddy mixing or advection) potentially influence *N. pachyderma* abundances in the water column. In our case here the slope of the isopyncal surfaces might facilitate communication between surface dwelling populations south of the Antarctic Polar Front and thermocline dwelling populations to the north [*Mortyn et al.*, 2002].

[27] Despite the fact that there was not one truly surface-dwelling species that spanned our South Atlantic study region there were species of planktonic foraminifera that were at least restricted to deeper depths. Our results from higher latitudes in the South Atlantic corroborate earlier findings [*Fairbanks et al.*, 1980; *Hemleben et al.*, 1989] and support the idea that *G. inflata* is a relatively deep dweller. In our tows, *G. inflata* is consistently most abundant at depths between 50 and 300 m. Similarly, our South Atlantic observations corroborate previous findings [*Fairbanks et al.*, 1980; *Hembleben et al.*, 1985, 1989] that *G. truncatulinoides* is adeep dweller, consistently shown beneath 100 m and well below both the fluorescence maxima and pycnocline depths at each of our stations. Our South Atlantic abundances are much lower than in other studies, on the order of 1 shell/m^3. This difference might result from the fact that we sampled during the austral summer at a time of year when this species does not typically reproduce [*Lohmann and Schweitzer*, 1990]. In any case it is clear that at least in the summer months, two of the dominant species of foraminifera are not observed in the surface mixed layer of the high-latitude South Atlantic, regardless of thermal structure. This observation suggests that the shell chemistry of these species should reflect thermocline, or perhaps even subthermocline, conditions.

[28] If various planktonic foraminiferal species are stratified with depth, then it is appropriate to consider whether their respective (or combined) $\delta^{18}O$ composition reflects this depth distribution. Synthesizing a large body of previous work [e.g., *Emiliani*, 1955, 1966; *Bé and van Donk*, 1971; *Hecht and Savin*, 1972; *Shackleton et al.*, 1973; *Vergnaud-Grazzini*, 1976; *Williams et al.*, 1977; *Shackleton and Vincent*, 1978; *Kahn*, 1977, 1979; *Fairbanks et al.*, 1980; *Curry and Matthews*, 1981; *Kahn and Williams*, 1981], one might conclude that there is no systematic picture of how the $\delta^{18}O$ of any particular species deviates from equilibrium and therefore that the exercise of resolving vertical water column structure from foraminiferal $\delta^{18}O$ might be inherently problematic. However, many of the apparent previous interpretations of disequilibrium may have been the result of an evolving range of calibrations and equations used for estimating equilibrium calcite $\delta^{18}O$ values [e.g., *Bemis et al.*, 1998, and references therein]. We observe offsets from arbitrarily defined equilibrium calcite values that are consistent across a range of stations. Our field-based data also tend to support extrapolation of culture-based $\delta^{18}O$ calibration of *Bemis et al.* [1998], though our data are not sufficient to conclude that subantarctic foraminifera precipitate their skeletons in equilibrium with seawater according to a universal linear trend. In any event the observation of constant offsets from calculated equilibrium would at least seem to minimize the strictly biogeochemical complications of foraminiferal $\delta^{18}O$.

[29] The core-top foraminiferal $\delta^{18}O$ values, however, are consistently higher than those from the water column, in some cases by amounts that exceed the 0.2–0.3‰ that might be attributable to the warming of the 20th century alone. This generalization includes the deeper-dwelling *G. inflata* as well as *G. bulloides*. Since there were no reasons to question the integrity of the representative core-top data that we report here, such as physical evidence for bioturbation or a systematic trend with carbonate saturation state (core tops were distributed both above and below the present carbonate lysocline [*Hodell et al.*, 2001]), other processes must be involved. For example, significant calcification in colder seasons than we sampled by the plankton tows (peak of the summer) is one obvious possibility. Another plausible explanation for these observa-

Figure 6. (opposite) Oxygen isotopic data ($\delta^{18}O$ in ‰PDB) for each site, similar to the arrangement in previous figures. Each *y* axis corresponds to depth in the water column to 800 m, and each *x* axis corresponds to $\delta^{18}O$ from 0 to 4.5‰. In each panel the line with the most data points and the heaviest isotopic values corresponds to that of predicted $\delta^{18}O$ of calcite (using predicted $\delta^{18}O$ (water) rather than measured $\delta^{18}O$ (water), see Figure 5), while the other lines correspond to species-specific $\delta^{18}O$ (calcite) measurements according to the legend in the lower right panel. Isotopic analyses were made on any sample that yielded enough foraminiferal specimens for measurement. Core-top $\delta^{18}O$ data are shown along the bottom line of the panels where representative data were available, at TNO57-21, TNO57-16, and TNO57-13 (see text for details).

tions is that all species acquire a calcite crust at a depth below that of our plankton tows, i.e., somewhere below 800 m in the water column while enroute to the sediment-water interface (at lower temperatures and therefore with higher $\delta^{18}O$). This process has at least been documented for *G. truncatulinoides* and seems plausible for *G. inflata* but is less well established for species such as *G. bulloides* [*Hemleben et al.*, 1989]. If only the deeper-dwelling species acquire secondary calcite preferentially, the sedimentary $\delta^{18}O$ differences between them and the shallower species should be accentuated. Our data do not show evidence for such differential secondary calcification between shallow and deep-dwelling species (Figure 6). We therefore have a stronger basis for interpreting their $\delta^{18}O$ differences from the sedimentary record as a reflection of changes in the upper surface ocean or foraminiferal habitat.

[30] Does the water column depth habitat at least explain the geographic pattern, if not the absolute value, of $\delta^{18}O$ observed in sediment core-top samples? Prior compilations of Southern Ocean (Indian and Atlantic sectors) core-top *G. bulloides* and *N. pachyderma* $\delta^{18}O$ data canbe used to address this problem (Figure 7). From these data it is evident that core-top *G. bulloides* $\delta^{18}O$ values deviate from the trend of predicted $\delta^{18}O$ values at higher temperatures (northern sub-antarctic). In contrast, the core-top *N. pachyderma* $\delta^{18}O$ pattern follows the slope of predicted $\delta^{18}O$ over the full range of the data set (compare solid squares against open triangles in Figure 7).

[31] The tow and hydrographic data suggest a possible interpretation for this difference. The northern hydrographic conditions enhance the temperature contrast between water at the base of the mixed layer and water just below the mixed layer, such that any diapycnal mixing and entrainment across this boundary would stir up relatively cold water and allow proliferation of *G. bulloides* populations with a relatively positive $\delta^{18}O$ signature. In the warmer regions of the sub-antarctic, and therefore where predicted $\delta^{18}O$ is relatively low, the *G. bulloides* $\delta^{18}O$ signal is more effectively ''smeared'' up from below the mixed layer, and measured $\delta^{18}O$ values are consequently heavier than predicted for the surface mixed layer. This process is best illustrated by our results that show shallow *G. bulloides* $\delta^{18}O$ values much closer to predicted values in our more northern stations (Figure 6).

[32] Despite this potential bias it appears that *G. bulloides* $\delta^{18}O$ does track the predicted $\delta^{18}O$ of calcite throughout the upper 100 m at several stations, while *G. inflata* and *G. truncatulinoides* $\delta^{18}O$ reliably trace the profile of predicted $\delta^{18}O$ of calcite below this depth (Figure 6, stations TNO57-22, TNO57-9, and TNO57-11 especially). Thus, if these deeper *G. inflata* or *G. truncatulinoides* data are combined with the shallow (</ = 100 m) *N. pachyderma* or *G. bulloides* data, the structure of the predicted equilibrium $\delta^{18}O$ of calcite profile is reproduced well in the depth-discrete tow samples. Because $\delta^{18}O$ is a strong reflection of the ocean's thermal and density structure (Figure 2), this shallow-deep $\delta^{18}O$ differencing signature can, in effect, be used as a recorder of water column structure conditions in regions where the abundance profiles of the different species are sharply resolved peaks. Sediment cores from the central part of the subantarctic zone might be ideal for this purpose, especially since paleostratification in this region bears on biological productivity, nutrient cycling, and carbon export [*Sigman and Boyle*, 2000], as well as deep water formation in climatically sensitive areas [*Keeling and Stephens*, 2001a, 2001b].

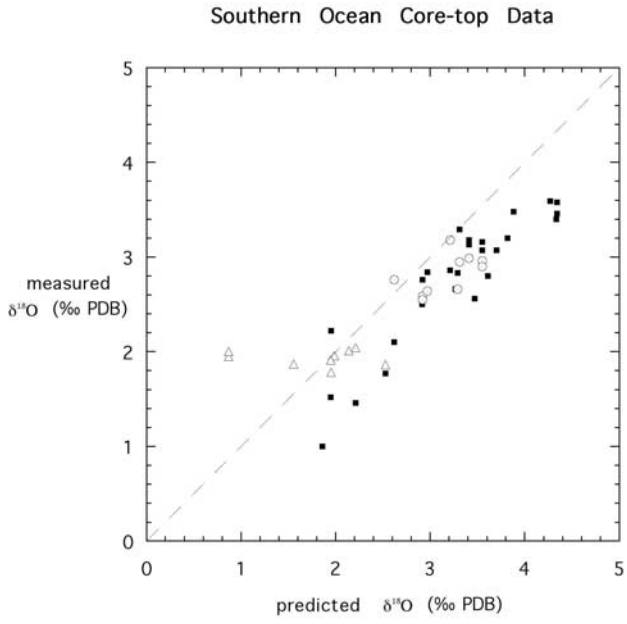


Figure 7. Plot of measured $\delta^{18}O$ (‰PDB) versus predicted $\delta^{18}O$ (‰PDB) for Southern Ocean core-top data compiled from both *Labeyrie et al.* [1996] and this study. Predicted values are all derived from austral summer temperature and salinity data in order to minimize seasonality effects (see *Labeyrie et al.* [1996] and text of this study for details). Foraminiferal species shown from both the south Indian and South Atlantic sectors are *G. bulloides* and *N. pachyderma* (left-coiling). The dashed line corresponds to a 1:1 slope where measured values follow those that are predicted. *N. pachyderma* data are represented by solid squares; *G. bulloides* (where predicted values are >2.6‰) data are represented by open circles; and *G. bulloides* (predicted values <2.6‰) data are represented by open triangles. Note that the *N. pachyderma* and the *G. bulloides* (predicted >2.6‰) data follow the 1:1 slope, while the *G. bulloides* (predicted <2.6‰) data do not, indicating that *G. bulloides* $\delta^{18}O$ from warmer regions farther north are typically heavier than predicted, a pattern that does not occur farther south (see text for details). One of the *G. bulloides* data points (predicted value of 0.87‰) comes from a core location close to TNO57-21 and is not presented elsewhere in this study.

5. Conclusion

[33] The combined ecological and geochemical approach of the MOCNESS plankton tow sampling suggests that the $\delta^{18}O$ of both deep- and shallow-dwelling species reflects the

three-dimensional thermal structure of the upper ocean throughout much of the subantarctic region. Though the results clearly imply that any one planktonic foraminferal record from the sediment may be affected by the complexities of upper ocean structure, the conclusion is relevant for paleoceanographic work in a number of specific ways. For example, it provides an explanation for why the amplitude of planktonic foraminiferal $\delta^{18}O$ signals in the northern sub-Antarctic may differ from their counterparts in other regions. Second, it suggests that changes in the difference between shallow- and deep-dwelling species is a legitimate strategy for monitoring surface water stratification, provided that the most appropriate shallow indicator species is chosen (*G. bulloides* in the central sub-Antarctic and *N. pachyderma* to the south). Third, it provides constraints on the possible interpretations of high-latitude carbon cycling from various existing foraminiferal records of the Southern Ocean [e.g., *Rickaby and Elderfield*, 1999]. Thus the hydrographic and ecological complexities may offer opportunities as well as challenges.

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