Response of planktic foraminiferal size to late Quaternary climate change

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[1] Geographical size distribution within entire Holocene foraminiferal assemblages is related to global environmental gradients such as temperature, primary productivity, and environmental variability. This study demonstrates that these correlations are also recognizable in late Quaternary assemblages from three locations in the South Atlantic on temporal and latitudinal scales. The size response to temporal paleoenvironmental changes during glacial-interglacial cycles mimics the geographic Holocene size variability. The amplitude of size variability is directly related to the amplitude of the climatic fluctuations as shown by the stable size-temperature relationship over time. The documented changes in the assemblage size are caused by species replacement and intraspecific size variability. The relative importance of these processes depends on the environmental setting. Species have been shown to reach their maximum size and abundance under certain optimum conditions and decrease in size if environmental conditions differ from these optima. We confirm that late Quaternary species sizes were largest at paleotemperatures identical to Holocene ones.

INDEX TERMS: 3030 Marine Geology and Geophysics: Micropaleontology; 4267 Oceanography: General: Paleoceanography; 4815 Oceanography: Biological and Chemical: Ecosystems, structure and dynamics; 4855 Oceanography: Biological and Chemical: Plankton; 9325 Information Related to Geographic Region: Atlantic Ocean; KEYWORDS: planktic foraminifera, morphometry, paleoecology, climate change, Quaternary


1. Introduction

[2] Planktic foraminifers have, since their origin 140 million years ago, undergone three evolutionary radiations [Bollti et al., 1985] in both species richness and morphology [Cifelli, 1969; Norris, 1991]. Over this period, planktic foraminifers have grown from a negligible contribution to a major sink for pelagic carbonate. The excellent preservation, global occurrence and high abundance of planktic foraminifers within Cenozoic marine deep sea sediments are prime reasons for their extensive application in paleoceanographic and paleoclimatic studies. The analysis of species compositions [Imbrie and Kipp, 1971; Imbrie et al., 1973], stable isotopes [Shackleton and Odpyle, 1973; Hays et al., 1976], and other chemical tracers in the foraminiferan tests, e.g., Mg/Ca [Nürnberg et al., 1996; Elderfield and Ganssen, 2000], Cd/Ca ratios [Delaney and Boyle, 1987], and Boron isotopes [Sanyal et al., 1995] have proven to be valuable tools for paleoclimatic and paleoceanographic reconstructions.

[3] In addition, morphological variability within individual taxa, such as size, shape and coiling direction of the test were shown to be correlated to fluctuations in temperature [Ericson, 1959; Bé et al., 1973; Hecht et al., 1976; Malmgren and Kennett, 1978a, 1978b; Naidu and Malmgren, 1996] or fertility [Naidu and Malmgren, 1995]. Different adult sizes are mainly influenced by environmentally controlled growth rates [Caron et al., 1987a, 1987b; Bijma et al., 1990a] since the lifespan is determined and reproduction triggered by the synodic lunar cycles [Spindler et al., 1979; Bijma et al., 1990a; Schiebel et al., 1997].

[4] The response of size and morphology to paleoceanographic changes has been variable, depending on species and location. Distinct size fluctuations related to late Quaternary climatic cycles seem to have occurred in the vicinity of frontal systems or in upwelling-areas [Bé and Duplessy, 1976; Malmgren and Healy-Williams, 1978; Malmgren and Kennett, 1978b; Naidu and Malmgren, 1995]. In more stable environments observed stratigraphic size variability is seemingly uncorrelated to climatic cycles [Malmgren and Healy-Williams, 1978; Huber et al., 2000]. Despite successful application of size change for paleoceanographic reconstructions, these ambiguous correlations with environmental parameters have restricted the use of foraminifer size variability as a global paleoclimatic index.

[5] Most paleoceanographic and paleoclimatic reconstructions are based on the assumption that evolutionary adaptations of individual taxa do not change over the time periods considered, a hypothesis that has yet to be tested. Our size analyses of planktic foraminifera in globally distributed Holocene assemblages have allowed us to identify distinct size and abundance optima related to specific environmental conditions (D. N. Schmidt et al., Size distribution of Holocene planktic foraminifer assemblages:...

[6] We therefore can test the stability of these relationships through the late Quaternary climatic cycles in the selected cores. The maximum size of entire planktic foraminifera assemblages were found to generally increase from the poles to the tropics parallel to surface temperatures. Decreased sizes relative to this general trend were observed in assemblages from upwelling areas and frontal systems.

[7] On the basis of these new insights, we attempt here to test the temporal stability of the observed correlation of size and environmental gradients. Specifically, the present study of assemblage size variability in the Quaternary will allow us to test the following hypotheses:

[8] 1. Foraminiferal size adaptation to specific environmental optima has been identified in the Holocene. Globally, Holocene planktic foraminiferal assemblage sizes depend on temperature, primary productivity, and environmental variability. By comparison with paleoproxy estimates in Pleistocene cores, the temporal stability of these species’ optima can be investigated. Quaternary climatic changes, e.g., glacial-interglacial cycles, should have led to temporal size fluctuations.

[9] 2. On the basis of the linear correlations of size and temperature in the Holocene, we expect that the size response was proportional to the extent of physical environmental change in any particular area.

[10] 3. Size changes of foraminiferal assemblages may be caused by changes in species composition and/or by intra-specific size variability. These two potential causes should be distinct and identifiable in specific biogeographic areas.

[11] To test these hypotheses, we focus our study on the last 300 kyr using cores from three different environmental settings in the South Atlantic (Figure 1): (1) the equatorial upwelling (core GeoB1105) with high-amplitude paleoproxy variability of temperature and productivity influencing a diverse assemblage, (2) the subtropical gyre (core GeoB1413) with minimal past variability, and (3) the subpolar frontal system (core PS2498) of intermediate variability and low species richness.

2. Environmental Settings and Faunal Composition

2.1. Modern Environmental Settings

[12] The modern South Atlantic is dominated by a large subtropical gyre, which is bordered by the equatorial current system in the north, the subtropical front in the south, the Benguela Current in the east and the Brazil current in the west (Figure 1). The three cores studied represent a transect along the southern Mid-Atlantic Ridge well above the lysocline (Table 1), with core GeoB1105 in the equatorial upwelling zone, core GeoB1413 at the edge of the subtropical gyre and core PS2498 near the subantarctic front (Figure 1). Age models, sedimentology and paleoceanography of these cores were described by Wefer et al. [1996] and Mackensen et al. [2001].

[13] The equatorial upwelling core (Table 2), GeoB1105, is from a location which today is characterized by strong seasonal upwelling leading to a seasonal sea-surface temperature variation from 23.1°C to 28.3°C [Levitus et al., 1994]. It is characterized by strong seasonal changes in the depth of thermocline [Wolff et al., 1999] and a high primary
Table 1. Core Location, Water Depth, Time Interval Investigated, Average Sedimentation Rate and Reference for the Age Models

<table>
<thead>
<tr>
<th>Core</th>
<th>Latitude, °</th>
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<th>Depth, m</th>
<th>Age, ka</th>
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<tbody>
<tr>
<td>GeoB1105</td>
<td>1°39.9 S</td>
<td>12°25.7 W</td>
<td>3225</td>
<td>300</td>
<td>4.80°</td>
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<tr>
<td>GeoB1413</td>
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Table 2. Environmental Characteristics for the Site Locations of Studied Cores

<table>
<thead>
<tr>
<th>Core</th>
<th>SST, °C</th>
<th>ΔTs, °C</th>
<th>ΔTgl, °C</th>
<th>Δof Th, m</th>
<th>PP, gCm⁻²a⁻¹</th>
<th>Fauna</th>
</tr>
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<tbody>
<tr>
<td>GeoB1105</td>
<td>25.9</td>
<td>4.5</td>
<td>4–5</td>
<td>20–30</td>
<td>100</td>
<td>G. ruber (w and p), G. sacculifer, G. menardii, G. siphonifera</td>
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<tr>
<td>PS2498</td>
<td>9.7</td>
<td>3.0</td>
<td>7–8</td>
<td>&lt;50 m</td>
<td>45–60</td>
<td>G. vulloides, G. glutinata, G. inflata, G. calida</td>
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Core SST, °C, ΔTs, °C, ΔTgl, °C, Δof Th, m, PP, gCm⁻²a⁻¹, Fauna

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individuals in the assemblage, additionally at a higher resolution but shorter time interval for *G. truncatulinoides* in samples representing the last 130 kyr. Foraminifers are well preserved in the two northernmost cores GeoB1105 and GeoB1413. In PS2498 a high proportion of siliceous microfossils was encountered, especially during the glacial intervals, and may reflect carbonate dissolution. However, the occurrence of *G. bulloides* indicates adequate fossil preservation since this species is solution susceptible [Berger, 1968]. The foraminifers were analyzed in the fraction >150 μm to allow comparison with the faunal composition data from Wefer et al. [1996] and Mix et al. [1999]. Additionally, this size fraction allows one to exclude juvenile forms and to focus on the adult stage within the ontogeny of the foraminifers.

3.2. Size Analysis

[18] In the present study, three different estimators for size changes are considered: (1) a variable of the size distribution within the entire assemblage, (2) the maximum test size attained for single species and (3) the average size of the species *Globorotalia truncatulinoides*.

3.2.1. Assemblage Size

[19] To characterize the size distribution within an entire assemblage, a complete split of each sample was analyzed, containing on average 2012 individuals (minimum 779, maximum 4414). The entire data set consists of 462961 measurements. Using an automated image analysis system [Bollmann et al., 2003], the maximum diameter of each randomly oriented foraminifer was measured since this size parameter is least affected by orientation. We have calculated the accuracy of diameter determination at the applied magnification of 160× to be 3.31 μm. In order to test the accuracy and the reproducibility of measurements, standard glass microbeads have been analyzed (mean diameter with standard deviation of 168 μm ± 7.4 μm, 331 μm ± 14.1 μm, and 655 μm ± 29.0 μm, Duke Scientific cooperation). Repeated preparations and measurements of these microbeads showed a good reproducibility and an accuracy (172 μm ± 5.1 μm; 330 μm ± 3.51 μm; 636 μm ± 24.2 μm) of mean diameter for all microbeads. The reproducibility of 10-times repeated measurements of a natural foraminiferal sample of the mean size of the distribution is ±4.1μm, that of the median is ±3.9 μm and that of the 95-percentile is ±9.71 μm, which represents an error of 1.5 to 2.2%. Confidence intervals for the mean range from 1.5 μm (minimum value in PS2498) to 6.8 μm (maximum value in GeoB1413). The use of the 95th percentile prevents the use of the confidence interval for statistical precision.

[20] Because the minimum diameter is given by the sieve size (＞150 μm), it represents an artificial cut-off of the natural size distribution and therefore has no biological significance. Since the distributions are highly skewed toward larger sizes, the most suitable descriptor is the measured size value separating the largest five percent of the assemblage from the smaller 95% (*size*assemblages). Details of the measuring technique and the choice of descriptors to characterize the assemblages are by Schmidt et al. (submitted manuscript, 2003).

3.2.2. Maximum Size of Single Species

[21] The results of the Holocene survey indicate that the maximum test size measured for individual foraminiferal species is characteristic of its ecological optimum. To trace these optima back in time, we identified the largest size for all species represented among the 40 largest individuals encountered. This was done in three representative glacial and interglacial samples from each core. The environmental conditions leading to maximum size were determined by comparison of measured size and environmental proxies.

3.2.3. Average Size of *Globorotalia Truncatulinoides*

[22] To test the impact of environmental change at the scale of a species, the size variability of *G. truncatulinoides* was analyzed. This taxon was selected because it is present in all cores throughout the investigated time span. Its abundance in the total foraminiferal assemblages ranged from 0.1 to 6%. Because of these low abundances, *G. truncatulinoides* measurements may provide independent evidence from that of the entire assemblage. A representative split of the fraction >150 μm was picked and oriented, including on average 40 specimens (minimum 8, maximum 76). The maximum diameter measured for the spiral side was chosen as the size estimator (*size*trunc), because it is most comparable to the diameters determined in unoriented tests of the other size measurements in this study (assemblage size and maximum size per species).

3.3. Paleoenvironmental Proxies

[23] Quantification of paleoenvironmental change is largely based on the use of “proxy” evidence. Proxies are measurable characteristics of sediments and fossil biota, which, via transfer functions, can be used to reconstruct the paleoenvironment. To calibrate our observed foraminiferal assemblage size changes in the past, we compiled data from several published paleo-proxy analyses (Table 3). These include oxygen and carbon isotopes studies of various planktic and benthic foraminifers, temperature

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<td>carbon/oxygen isotopes of <em>F. wuellerstorfi</em></td>
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<td>Schneider et al. [1996]</td>
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<td>alkenone temperature</td>
<td>Wefer et al. [1996]; P. Müller (unpublished data, 1999)</td>
</tr>
<tr>
<td>GeoB1413</td>
<td>carbon/oxygen isotopes for <em>G. ruber, G. crassaformis</em></td>
<td>Wefer et al. [1996]</td>
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*Paleotemperature estimates are based on changes in the composition of radiolarian or foraminiferal faunas [Wefer et al., 1996; Brathauer and Abelmann, 1999; Mix et al., 1999] or on alkenone measurements [Schneider et al., 1996]. The mass accumulation of total organic carbon in the sediments (Corg), density, and porosity have been used to calculate paleoproductivity.*

Table 3. Overview of Paleoenvironmental Proxies Considered in the Present Study

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and primary productivity reconstructions, and estimators of species richness.

[24] In equatorial core GeoB1105, paleoenvironmental reconstructions include isotopic analysis of benthic and planktic foraminifera, paleotemperatures based on foraminalferal transfer functions, modern analogue technique, and alkenones. Paleoproductivity estimates are based on organic carbon contents. Additionally, changes in functional groups of foraminifers, such as upwelling indicators, tropical species, symbiont-bearing and nonsymbiont bearing ones (Table 3), have been calculated on the basis of faunal counts of Wefer et al. [1996].

[25] In subtropical gyre core GeoB1413 only the isotopic composition of planktic foraminiferal shells are available. This is used for correlation with nearby core V22-174 (Figure 1), from which paleotemperature estimates are available on the basis of faunal transfer functions [Imbrie et al., 1984, 1989; Mix et al., 1999].

[26] In subpolar core PS2498, paleoproductivity estimates based on organic carbon accumulation rate are taken from Mackensen et al. [2001]. Paleotemperature estimates were taken from core PS2082 (Figure 1) and are based on transfer functions compiled from radiolarian assemblages [Brathauer and Abelmann, 1999]. Since both cores are at similar latitudes within the circumpolar current and today's environmental settings are very similar, we assume that this relationship prevailed back in time.

3.4. Statistical Analysis

[27] The relationship of size\textsubscript{assemblage}5 and size\textsubscript{trunc} with environmental proxies was tested using a simple linear regression. The size difference between glacial and interglacial measurements was examined with a Student's t-test with the null hypothesis that mean glacial sizes are different from interglacial ones. The hypothesis was rejected based on the t-value and the probability ($p$).

4. Results and Interpretation

4.1. Assemblage Size Changes and Paleotemperature Variability

[28] The smallest size\textsubscript{assemblage}5 values (300–492 $\mu$m) are found in the subpolar core PS2498, the largest sizes (472–568 $\mu$m) in the subtropical gyre core GeoB1413, and intermediate sizes (378–527 $\mu$m) in the equatorial core GeoB1105 (Figure 2). Linear correlation (Table 4) indicates a positive correlation of size and temperature on a global scale (Figure 3), when all three cores are considered together ($r = 0.909$, $p < 0.001$). A similar relationship (Figure 3) prevails on a local scale in the subpolar ($r = 0.798$, $p < 0.001$) and the equatorial upwelling samples ($r = 0.629$, $p < 0.001$). The largest range in size is observed in subpolar core PS2498, associated with a corresponding paleotemperature range from 14.1°C to 5.8°C. Equatorial core GeoB1105 is also characterized by large size fluctuations in accord with a paleotemperature variability from 24.6°C to 13°C. Little size change is found in subtropical gyre core GeoB1413 with associated paleotemperature changes of 5°C derived from the nearby core V22-174. Since size and temperature changes are minimal, no significant correlation between size and paleotemperature is found in core GeoB1413 in the subtropics. Despite this lack
of correlation, the results of GeoB1413 clearly fit into the regional pattern (Figure 3). Therefore both the geographical and temporal size variability in the Quaternary are consistent with today’s biogeographic size changes (Schmidt et al., submitted manuscript, 2003). This is consistent with the results of the Holocene study (Schmidt et al., submitted manuscript, 2003), where productivity leads to only minor departures from the global size-temperature trend. However, the effect of productivity on size seems to differ according to the local setting, as represented by the discrepancy in the slopes of the size-productivity regressions at the sites PS2498 and GeoB1105 (Figure 4).

### 4.3. Assemblage Size Changes and Species Composition

[31] Changes in temperature, productivity and frontal dynamics, characterized by high turbulence, frequently appearing eddies [Beckmann et al., 1987], and storm events [Schiebel et al., 1995], can affect assemblage size by altering the faunal composition. We tested the effect of species replacement in the equatorial upwelling core GeoB1105, where changes of faunal composition related to a strengthening of the upwelling during glacial have previously been documented [Wefer et al., 1996]. Species replacement occurs within this core according to the intensity of the upwelling situation. An upwelling assemblage is characterized by increased abundances of Neogloboquadrina dutertrei, G. bulloides and N. pachyderma.

### Table 4. Linear Correlation of Environmental Factors With Size\textsubscript{assemblage} for All Cores

<table>
<thead>
<tr>
<th>Proxy</th>
<th>All Cores</th>
<th>GeoB1105</th>
<th>GeoB1413</th>
<th>PS2498</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oceanography</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\delta^{18}O) F. wuellerstorfi</td>
<td>-0.577</td>
<td>-0.741</td>
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<td></td>
</tr>
<tr>
<td>(\delta^{13}C) F. wuellerstorfi</td>
<td></td>
<td>0.55</td>
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<td></td>
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<tr>
<td>(\delta^{18}O) G. ruber</td>
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<td>-0.205</td>
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<tr>
<td>(\delta^{13}C) G. ruber</td>
<td>0.359</td>
<td>0.114</td>
<td></td>
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<tr>
<td>(\delta^{18}O) G. inflata</td>
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<tr>
<td>(\delta^{13}C) G. inflata</td>
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<tr>
<td>(\delta^{18}O) G. crassaformis</td>
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<tr>
<td>(\delta^{13}C) G. crassaformis</td>
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<tr>
<td>Temperature</td>
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<tr>
<td>SST warm MAT</td>
<td>0.716</td>
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<td></td>
<td></td>
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<tr>
<td>SST cold MAT</td>
<td>0.798</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST warm TF</td>
<td>0.446</td>
<td>-0.163</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST cold TF</td>
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<td>0.017</td>
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<tr>
<td>SST warm</td>
<td>0.909</td>
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<td></td>
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</tr>
<tr>
<td>SST cold</td>
<td>0.802</td>
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<td></td>
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<tr>
<td>SST radiolaria</td>
<td>0.622</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>SST alkenone</td>
<td>0.629</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| Productivity   |           |          |          |        |
| TOC accumulation | -0.049   | -0.641  | -0.582  |        |

| Diversity      |           |          |          |        |
| S              | 0.608     | 0.092    |          |        |

*Values indicated are correlation coefficients (r). Bold values indicate significant correlation (p < 0.05); values in italic in “all” are based on only two cores (SST cold for GeoB1105 and GeoB1413, primary productivity for GeoB1105 and PS2498). For references, see Table 3. Abbreviations are as follows: MAT, Modern analogue technique; TF, transfer functions refer to paleotemperature estimates based on faunal composition (see Wefer et al. [1996] for explanation); TOC, total organic carbon; S, species richness.

4.2. Assemblage Size Changes and Paleoproductivity Variability

[30] In Holocene assemblages, negative deviations from the general size-temperature relationship could be related to high primary productivity (Schmidt et al., submitted manuscript, 2003). In the late Quaternary, significant negative correlations between paleoproductivity and size\textsubscript{assemblage} are observed in subpolar core PS2498 and in the equatorial upwelling core GeoB1105 (Figure 2), although no universal size-paleoproductivity correlation could be found within our data set (Table 4).
compared to a tropical assemblage, which is dominated by
G. menardii, G. ruber, G. sacculifer, Globigerinella
siphonifera, G. calida, Globigerina digitata, and Pull-
eniatina obliquiloculata [Hemleben et al., 1989]. On the
basis of these differences, we used the ratio of tropical
versus upwelling species as an indicator for species
replacement. Accordingly, we also calculated the ratio of
symbiont bearing (G. menardii, G. ruber, G. sacculifer,
G. siphonifera, Orbulina universa, G. calida, Globigerina
falconensis) versus the nonsymbiont bearing species
(G. truncatulinoides, N. dutertrei, Globorotalia scitula,
Globigerinoidesestenellus, P. obliquiloculata, G. inflata,
Globorotalialeshexagonus). We have not grouped any of
the species with an unclear assignment to one of the groups
[Hemleben et al., 1989; R. Schiebel, ETH, Zurich, personal
communication, 2002]. The ratio of tropical versus upwel-
ing species covaries (r = 0.761, p < 0.001) with assemblage
sizes in core GeoB1105 (Figure 5), as does the ratio of
symbiont bearing to nonsymbiont bearing ones (r = 0.815,
p < 0.001). During times of intense upwelling, the relative
abundance of tropical species or symbiont bearing ones is
reduced by increasing numbers of upwelling indicators and
nonsymbiont bearing species. The sizeassemblage5 is smaller
during times with high abundances of upwelling species
and nonsymbiont bearing ones. The observed size ranges in
GeoB1105 (378–527 μm) fluctuate between values char-
teristic for Holocene upwelling assemblages (451 μm)
and those characteristic for subtropical/tropical assem-
blages (509/625 μm) (Schmidt et al., submitted manuscript,
2003).

4.4. Size Increases Within Species: Indicator of
Optimum Ecological Conditions

Previous studies demonstrated that test sizes within
individual species vary systematically with changing envi-
ronmental conditions [Hecht, 1976; Schmidt et al., submit-
ted manuscript, 2003]. Maximum test size measured for
individual foraminiferal species is characteristic for its
ecological optimum. To trace these optima back in time, we
identified the largest size for all species represented among
the 40 largest individual encountered in representative
glacial (three out of LGM, stages 4, 6 and 8, interstadial 5.2)
and interglacial (three out of stage 3, 5.1, 5.5, 7.3) samples
from each core.

[33] The maximum size of the cosmopolitan species
Globorotalia truncatulinoides, G. inflata, and G. crassa-
formis increased with increasing paleotemperature from 7°C
to 26°C paleotemperature. This trend is parallel to the size
increase in Holocene sediments (Figure 6a) and confirms
the general temperature/size relationship found in Holocene
sediments. In contrast, maximum sizes of Globigerinoides
sacculifer, Globorotalia menardii and G. tumida, were
found to be consistently smaller than in the Holocene
(Figure 6b). This reduced maximum size might be caused
by consistently lower Pleistocene than Holocene tempera-
ture estimates for the analyzed cores. Consequently largest
Pleistocene test sizes are smaller than their optimum size
(Figure 6b). Nevertheless the general species-specific

Figure 4. Plot of paleoproductivity (gCm-2a-1) versus
sizeassemblage5 (μm) for core GeoB1105 (gray squares) and
core PS2498 (black circles). Primary productivity estimates
for PS2498 from Mackensen et al. [2001] and for
GeoB1105 based on data from P. Müller (unpublished data,
1999) and Wefer et al. [1996]. For correlation coefficients,
see Table 4.

Figure 5. Plot of sizeassemblage5 (μm) (black circles) versus
ratio of tropical to upwelling species (dark gray triangles)
and symbiont bearing to nonsymbiont bearing species (gray
rectangles) in core GeoB1105. Ratios based on data from
Wefer et al. [1996].
relationship of maximum test size and water temperature is constant over the analyzed time period (stages 2 to 8) and the data show a good general agreement (Figure 6c), indicating a stable relationship.

To increase our understanding of the influence of the intraspecific variability on size assemblage, we studied in detail the reaction of *G. truncatulinoides* to the environmental change in the last 130 kyr. Since determinations of maximum size are affected by a random bias, we have picked on average 40 specimens and calculated the average size of the species per sample. Additionally, we increased the resolution in comparison to the maximum size data set of three glacial interglacial samples up to 32 samples a core.

However, the intraspecific size variability of *G. truncatulinoides* does not show clear glacial-interglacial size variability over the past 130 kyr in cores PS2498 and GeoB1413 (Student’s t-test: null hypothesis sizes are different for glacial and interglacial: $p = 0.576$, $p = 0.422$ respectively). None of the cores (Figure 7) record a significant correlation between size$_{trunc}$ and size$_{assemblage5}$ (linear correlation GeoB1105: $r = 0.610$, $p = 0.061$; GeoB1413: $r = 0.184$, $p = 0.359$; PS2498: $r = 0.062$, $p = 0.807$). Either the correlations of size and paleotemperature may only prevail at large scales, or alternatively the biology and ecology of *G. truncatulinoides* are more complicated than those of other taxa.

5. Discussion

5.1. Stability of Abiotic Size Controls During the Late Quaternary

Our data strongly suggest that the Holocene relationship between planktic foraminiferal assemblage size and temperature, productivity and frontal dynamics (Schmidt et al., submitted manuscript, 2003) persisted over the past 300 kyr. As in the Holocene, the main trend emerging at both regional and local temporal scales is the positive correlation of size and temperature. Size-temperature relationships have been documented for various planktic foraminiferal species in the Holocene in laboratory cultures [Caron et al., 1987a, 1987b; Bijma et al., 1990b; Spero et al., 1991], plankton tows [Ortiz et al., 1995] and sediments [Kennett, 1968; Bé et al., 1973; Hecht, 1976; Malmgren and Kennett, 1976]. This makes sense from a physiological standpoint since metabolic rates are
known to increase with temperature [Caron et al., 1987a, 1987b; Bijma et al., 1990b; Spero et al., 1991]. Additionally, higher species richness at warm temperatures [Rutherford et al., 1999] would increase the likelihood of the presence of larger taxa in the assemblages (see Schmidt et al., submitted manuscript, 2003).

[37] In the Holocene and the late Quaternary, secondary effects influencing size are productivity and variability of the environment, especially in upwelling areas and frontal systems. An excellent example of the local dominance of primary productivity changes on foraminiferal species’ sizes was presented by Naidu and Malmgren [1995] in the Arabian Sea. They recorded positive correlation between upwelling strength, indicated by the accumulation of G. bulloides, and size for several distinct species. However, within the paleoproductivity range of this study (30–160 gCm$^{-2}$a$^{-1}$), size and productivity display a negative correlation. Our own Holocene analyses have demonstrated that upwelling areas and frontal systems, apparently because of their high seasonal variability, prevent single species from attaining their size and abundance optima (Schmidt et al., submitted manuscript, 2003), that they are able to reach in more stable areas. The dynamics of the frontal systems lead to expatriation [Berger, 1970; Weyl, 1978] and vertical displacement of biota. Fronts appear to function as environmental barriers [Schiebel et al., 2002] between stable ecosystems, each harboring groups of well-adapted species able to grow to large sizes. Based on this, the negative size-productivity relationships in equatorial upwelling core GeoB1105 and the subpolar front data set (PS2498) are most likely the result of increased environmental variability. On the basis of our Holocene data, we infer that increasing seasonality of temperatures during glacial times lead to a size reduction despite higher paleoproductivities and consequently resulting in the observed negative correlation between paleoproductivity and size in two or our cores (Figure 4).

5.2. Biotic Processes: Species Replacement and Intraspecific Size Variability

[38] In general, assemblage size differences are a combined result of modifications in faunal composition coupled
with size changes within single species as a response to environmental variability. In addition, different species have specific size spectra [Hecht, 1976] and specific environmental optima. The size response to a change in a particular environmental parameter will show a positive correlation below and a negative correlation above the optimum conditions. For instance, *Globigerina bulloides* is known to have replaced subtropical and tropical species in the equatorial upwelling areas during glacial times. Since *G. bulloides* is generally smaller then the species it replaces, e.g., *G. menardii*, *G. sacculifer*, *G. ruber*, the total assemblage size decreases.

In addition to species replacement, there is evidence for size reduction of single species in upwelling areas [Ortiz et al., 1995; Schmidt et al., submitted manuscript, 2003]. Growth of foraminifera under nonoptimum conditions may be limited by spatial heterogeneity of, e.g., temperature, nutrients, or turbidity. Increasing turbidity was found to favor asymbiotic species [Ortiz et al., 1995] which are smaller than symbiont-bearing ones [Hecht, 1976]. In addition, symbiotic species grow to smaller sizes under light limited conditions [Bé et al., 1982]. Both processes may be influential in our size record of equatorial core GeoB1105 (Figure 5). During intensive glacial upwelling the proportion of symbiont-bearing species decreases to 20% relative to 60% in interglacial periods, causing a decrease in size assemblage5. In contrast, in the subtropical gyre, the same species dominate cold and warm intervals in the record. Assemblage size changes in these cores are therefore not the result of species replacement and may be representative of intraspecific size variability.

We have attempted to characterize intraspecific size changes in *G. truncatulinoides*. The size of *G. truncatulinoides* increases among the cores in parallel with their general paleotemperature estimates (Figure 7). Despite these biogeographic patterns, the fine-scale stratigraphic size variability is not very closely correlated to paleotemperature estimates [Renaud and Schmidt, 2003]. The absence of the expected correlation underlines the ecological and taxonomic complexity of this species. First, *G. truncatulinoides* lives in deep waters down to ~2000 m [Hemleben et al., 1985, 1989]. Paleotemperature estimates of surface waters may not be relevant to the past habitat changes experienced by this species [Lohmann and Schweitzer, 1990]. Second, genetic analyses by de Vargas et al. [2001] indicate that *G. truncatulinoides* consists of four different genetic species, three of which have been found segregated along a temperature gradient. Species replacement is therefore likely to occur. Hence the down core size measurements may be a combined result of intraspecific size variability and replacement by species of differing sizes [Renaud and Schmidt, 2003].

**5.3. Differential Response to Environmental Change of Various Amplitudes**

Our results show that the relative importance of species replacement and intraspecific size changes depends on the environmental setting. Warm water species have narrow ecological tolerances, resulting in temperature optima which are very close to each other (Figure 6c). Relatively minor temperature changes will therefore lead to species replacement. In contrast, few species are adapted to cold waters, limiting the role of species replacement in polar and subpolar areas. Observed size changes are thus much more likely to be due to intraspecific size variability. Our cores are suitable for testing these hypotheses.

**5.3.1. GeoB1105: Species Replacement in Equatorial Upwelling Systems**

Temperatures were lower and primary productivity was higher during the glacial and stadial phases [Wefer et al., 1996] than today. The glacial/interglacial summer-temperature variability ranged from 18 to 27°C. Several tropical and subtropical species have their optimum in this temperature range. Most of these species show a strong decrease in size outside their temperature optima, which eliminates their influence on the size of the largest 5% of the assemblage. Possible intraspecific size variability is attenuated by the dramatic turnover in species composition as expressed by order of magnitude changes in the ratio of tropical versus upwelling species (Figure 5). Upwelling species (*N. dutertrei*, *G. bulloides*, and *N. pachyderma*) dominate the glacial assemblages while tropical species (e.g., *G. sacculifer*, *G. ruber*, *G. menardii*) prevail during interglacial periods (Figure 5). In cold intervals, with vigorous upwelling and decreased temperatures, large tropical symbiont bearing species disappear. A conflation of these three processes (decrease in the number of (large) symbiont-bearing species and of (large) tropical species, coupled with observed size decrease of the persisting symbiont-bearing species) contributes to smaller size during cold intervals.

**5.3.2. GeoB1413: Environmental and Size Stability in the Central Gyre**

The position of this core in the northern part of the subtropical gyre suggests relatively stable Quaternary environmental conditions as indicated by the limited range in sea surface temperatures [Imbrie et al., 1989] and relatively constant assemblage characteristics [Mix et al., 1999]. This signal may have been additionally dampened by the low sedimentation rates of GeoB1413 (1 cm/kyr) since bioturbation reduces the glacial-interglacial amplitudes. The restricted size variability cannot solely be attributed to the low sedimentation rates because even in long ranging glacials such as stage 6 no size reduction in comparison to the interglacials can be measured. Accordingly, the small variability of size assemblage5 through time is related to more stable environmental conditions in the subtropical gyre than in the two other environmental settings.

**5.3.3. PS2498: Subpolar Frontal Dynamics and Intraspecific Size Variability**

The polar front today is about 6° to the south of core PS2498 [Peterson and Whitworth, 1989] and shifted relative to the core location during glacials [Mackensen et al., 1994; Brathauer and Abelmann, 1999], when temperatures were lower, primary productivity was higher and frontal dynamics increased. Size assemblage5 closely matched these changes. The largest species encountered are *G. bulloides*, *G. truncatulinoides* and *N. pachyderma*, which all grow to similar sizes under low-temperature conditions.
Thus intraspecific size variability seems to be more important than the size effects of species replacement.

6. Conclusions

[45] We tested hypotheses about the processes controlling foraminiferal assemblage size variability in the late Quaternary with the following results:

[46] 1. The size response to temporal environmental changes during glacial-interglacial cycles mimics the spatial Holocene size variability. In the late Quaternary, as in the Holocene, planktic foraminiferal assemblage size variability is primarily affected by paleotemperature. Paleoproductivity and frontal dynamics also seem to have affected assemblage sizes.

[47] 2. The amplitude of size change matches the extent of the inferred paleoclimatic fluctuations.

[48] 3. Changes in abiotic parameters also affect biotic responses such as species replacement and intraspecific size variability. The relative importance of these depends on the environmental setting of the core. In the subtropics and tropics, represented by GeoB1413 and GeoB1105 respectively, the species have narrow ecological niches and species replacement is most likely to occur. In the subpolar environment, species have wider environmental preferences and grow to similar sizes, but they still display intraspecific size decrease if moved away from their ecological optimum. Therefore intraspecific size change without species replacement is more likely to occur in this environment.

[49] The similarity of the results observed in both the Holocene and late Quaternary records provide evidence that the ecological preferences of the investigated species did not change much during the last 300 kyr. Therefore the assumption of an analogous situation for paleoceanographic reconstructions based on planktic foraminiferal temperature optima is supported by our results. Expanding our approach to a longer time record might permit the recognition of incipient nonanalogue situations, where the influence of evolutionary change would conceivably become the dominant factor.

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