Sensitivity of planktonic foraminifera to Mid-Pleistocene climate change in the SE Atlantic

Based on:
Sensitivity of planktonic foraminifera to Mid-Pleistocene climate change in the SE Atlantic. E. Ufkes and D. Kroon, accepted in Palaeontology
Abstract

In this paper we describe a record of planktonic foraminiferal relative abundance changes in Core T89-40 retrieved from the Walvis Ridge, SE Atlantic. The planktonic foraminiferal relative abundance changes reflect past (sub)surface water hydrography during the Mid-Pleistocene Transition. Statistical analysis shows that most variability in the planktonic foraminiferal relative abundance record was caused by cycles in eutrophic (nutrient-rich) versus oligotrophic (nutrient-poor) (sub)surface water conditions, driven by shifts in subtropical SE-Atlantic gyre and/or tropical northern Angolan waters versus Benguelan upwelling waters over the site. Oligotrophic waters occurred during peaks of boreal insolation within, or just preceding, the interglacials, and eutrophic conditions prevailed during glacials. Large oligotrophic-eutrophic cycles began around 600 ky at the end of the Mid-Pleistocene Transition, in line with the late Pleistocene amplification of the large amplitudinal glacial-interglacial cycles. The abundance patterns of left- and right-coiled *Globorotalia truncatulinoides* and left-coiled *Neogloboquadrina pachyderma* are of special interest. The left-coiled *G. truncatulinoides* exited from the record at around 960 ky at the onset of the Mid-Pleistocene Transition, when (sub)surface waters cooled as evidenced in stable oxygen isotopes, and this species remained absent during the course of the Mid-Pleistocene Transition until about 600 ky. The left-coiled *N. pachyderma* shows anomalously high abundances during Marine Isotopic Stage (MIS) 9, 11 and 31, reflecting strong upwelling during these interglacials, whilst the presence of the tropical species *Globorotalia menardii* during the same MIS 9, 11 and 31 reflects on flow of Indian Ocean waters into the S. Atlantic at the same time.

Introduction

The last one million years are important in terms of climate development during the so-called Mid-Pleistocene Transition (MPT) when amplification of the glacial-interglacial cycles occurred (e.g. Clark et al., 2006). The start of the MPT has been described to have emerged at about 1250 ky (Clark et al., 2006), although others have mentioned initiation to have occurred at about 900 ky (Berger and Jansen 1994; Mudelsee and Schulz 1997; Raymo et al., 1997). The MPT ended at about 700 ky (Clark et al., 2006) to 600 ky (Berger and Jansen, 1994; Mudelsee and Schulz, 1997; Raymo et al., 1997). From then on, large amplitudinal climate cycles dominated, influenced by the orbital eccentricity cycle.
The study site lies at the crossroads of three distinct oceanographic realms in the South Atlantic: (1) the Benguela Upwelling System, (2) the South Atlantic subtropical gyre and (3) the northern Angolan tropical waters. Sediments at Walvis Ridge contain evidence of variability in these three oceanographic realms, associated water masses, and upwelling conditions in response to climate cycles in the past. The planktonic foraminiferal assemblages in these sediments from Core T89-40 allow us to document changes in surface and subsurface hydrography.

Most studies in this region are restricted to the last 500 ky, the ‘known’ late Pleistocene ice-age world (Schmidt, 1992; Little et al., 1997; Giraudeau et al., 2001; Chen et al., 2002; Peeters et al., 2004; West et al., 2004) when the large amplitudinal climate cycles were already present. The present study uses planktonic foraminiferal assemblages extending back to 1.1 million years.

The foci of this study are to examine (1) the evidence of cycles in nutrient-rich, upwelling water conditions versus the nutrient-poor, subtropical gyre conditions above the core site during the MPT, when the average climate state evolved towards large amplitudinal cycles with large ice sheets during glacial and small ice sheets during interglacials over the last 600-700 ky compared with small amplitudinal cycles in the previous period; (2) shifts in the position of the Angola-Benguela Front under the changing boundary conditions as in (1) during the MPT; (3) changes in subsurface, deep thermocline waters in the same time interval; (4) the influence of Indian Ocean surface waters in the area during the same time interval and (5) the appearance and exit levels of specific planktonic foraminiferal species as a response to the changes in climate change in the last 1.1 million years.

**Oceanographic setting**

Modern hydrography of the eastern South Atlantic is well described by several authors (Shannon, 1985; Duncombe Rae, 1991; Peterson and Stramma, 1991; Weeks and Shillington, 1994; Lutjeharms, 1996; Shannon and Nelson, 1996) (Figure 5.1). The region is influenced by the position of the South Atlantic subtropical gyre and the oceanic branch of the Benguela Current. The shape of the basin and the general atmospheric circulation, SE trade winds and westerlies, set up the gyre and the South Atlantic Anticyclone.

The upwelling intensity and offshore penetration of upwelling waters is related to wind stress. The northernmost cell with extensive seaward penetration of upwelled water is at Walvis Bay, 22°S 14°E (Lutjeharms and Meeuwis, 1987; Lutjeharms and Stockton, 1987; Lutjeharms et al., 1991).
On Walvis Ridge, seasonal variations in temperature and stability of the water column are influenced by the strength and position of the coastal upwelling off Namibia and the subtropical gyre. During the late winter and spring, a nearly homogenous water column has developed due to westward advection of cool, nutrient-rich waters from the coastal upwelling and
filamentous mixing area. The highest surface water temperatures are reached during summer and autumn, induced by a more southern and eastward location of the atmospheric South Atlantic Anticyclone and subtropical gyre (Levitus, 1982; Lutjeharms and Meeuwis, 1987; Lutjeharms and Stockton, 1987). The opposing directions of the Benguela Coastal Current and the Angola Current result in a convergence between 14° and 17°S, the Angola-Benguela Front (ABF) (Shannon and Nelson, 1996). The front is strongest in the upper 50 m and its average width is about 200 km, but may extent to a distance of 1000 km from the coast (Meeuwis and Lutjeharms, 1990). Its location and extent are linked to the South Atlantic Anticyclone (Shannon et al., 1987; Meeuwis and Lutjeharms, 1990) and in tune with Southern Ocean ice fields (Howard and Prell, 1992; Jansen et al., 1996). During austral summer and autumn, when the South Atlantic Anticyclone moves southward, the flow of the warm Angola Current is at its maximum, and the ABF is located farthest south and is widest at this time. During austral winter and early spring, when the South Atlantic Anticyclone moves northward, the ABF also shifts to the north, becoming narrower and weaker (Meeuwis and Lutjeharms, 1990).

Three types of central water masses are found in the subsurface waters of this region: South Atlantic Central Water, Eastern South Atlantic Central Water and Western South Atlantic Central Water (Figure 5.1). Highly-saline, oxygen-poor subsurface waters are found as far south as 17°S at a depth of 100 to 500 m and are related to the distribution of South Atlantic Central Water (Mohrholz et al., 2001; Mohrholz et al., 2008) also identified as Tropical Atlantic Water (Giulivi and Gordon, 2006), pseudo-aged Western South Atlantic Central Water (Poole and Tomczak, 1999) or oxygen depleted Angola Gyre type South Atlantic Central Water (Mohrholz et al., 2008). Eastern South Atlantic Central Water is advected, well ventilated, with the Benguela Current from its source region in the Agulhas Retroflection region (Mohrholz et al., 2001; Giulivi and Gordon 2006). The distribution of Eastern South Atlantic Central Water is strongly linked to Indian Ocean Central Water (Poole and Tomczak, 1999; Mohrholz et al., 2008) and therefore to inter-ocean transfer. Western South Atlantic Central Water is related to the subtropical gyre. The ABF also acts as a front between the different types of central water, South Atlantic Central Water north of ABF and a mixture of South Atlantic Central Water and Eastern South Atlantic Central Water south of it (Mohrholz et al., 2008). Both types of central waters ascend in the upwelling cells and flow onto the central Benguela shelf. If the South Atlantic Central Water ascends in the north at Cape Frio (17°S), it advects polewards (Monteiro et al., 2006).
Materials and Methods

This study is based on variability in planktonic foraminifera assemblages and stable oxygen isotopes in a 16.26 m long piston core, Core T89-40, recovered from a water depth of 3073 m situated at 21°36’S, 6°47’E (Figure 5.1). The sediments of Core T89-40 consist of white calcareous ooze with rare contributions of siliceous material. A total number of 193 planktonic foraminifera samples was studied at a sampling interval of 5 to 10 cm, depending on the sedimentation rates. Aliquots of at least 300 specimens (using an Otto microsplitter) were completely picked in the size range between 150 and 600 μm, mounted on Chapman slides, identified and counted. In Table 5.1 the abundance statistics of all recorded species are listed.

Table 5.1
Minimum, maximum, and average percentages of planktonic foraminifera at Core T89-40.

<table>
<thead>
<tr>
<th>species</th>
<th>minimum</th>
<th>maximum</th>
<th>average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biorbulina bilobata Blow, 1956</td>
<td>0.00</td>
<td>0.63</td>
<td>0.04</td>
</tr>
<tr>
<td>Globigerina bulloides d’Orbigny, 1826</td>
<td>0.96</td>
<td>26.25</td>
<td>13.40</td>
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<tr>
<td>Globigerina falconensis Blow, 1959</td>
<td>0.00</td>
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<td>0.22</td>
</tr>
<tr>
<td>Globigerinella calida (Parker), 1962</td>
<td>0.00</td>
<td>0.92</td>
<td>0.03</td>
</tr>
<tr>
<td>Globigerinella digita (Brady), 1879</td>
<td>0.00</td>
<td>1.47</td>
<td>0.17</td>
</tr>
<tr>
<td>Globigerinella siphonifera (d’Orbigny), 1839</td>
<td>0.00</td>
<td>7.32</td>
<td>2.44</td>
</tr>
<tr>
<td>Globigerinina glutinata Egger, 1893</td>
<td>0.00</td>
<td>12.03</td>
<td>5.97</td>
</tr>
<tr>
<td>Globigerinita uvula (Ehrenberg), 1861</td>
<td>0.00</td>
<td>1.39</td>
<td>0.21</td>
</tr>
<tr>
<td>Globigerinoides conglobatus (Brady), 1879</td>
<td>0.00</td>
<td>0.64</td>
<td>0.02</td>
</tr>
<tr>
<td>Globigerinoides ruber white (d’Orbigny), 1839</td>
<td>0.52</td>
<td>17.36</td>
<td>6.01</td>
</tr>
<tr>
<td>Globigerinoides ruber pink (d’Orbigny), 1839</td>
<td>0.00</td>
<td>3.78</td>
<td>0.22</td>
</tr>
<tr>
<td>Globigerinoides sacculifer (Brady), 1877</td>
<td>0.00</td>
<td>5.21</td>
<td>0.66</td>
</tr>
<tr>
<td>Globigerinoides tenellus Parker, 1958</td>
<td>0.00</td>
<td>9.21</td>
<td>2.16</td>
</tr>
<tr>
<td>Globorotalia cavernula (Bé), 1967</td>
<td>0.00</td>
<td>0.50</td>
<td>0.02</td>
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<tr>
<td>Globorotalia crassaformis s.l. (Galloway and Wissler), 1927</td>
<td>0.00</td>
<td>4.83</td>
<td>0.94</td>
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<td>Globorotalia crassaformis cf. viola Blow, 1969</td>
<td>0.00</td>
<td>2.99</td>
<td>0.27</td>
</tr>
<tr>
<td>Globorotalia crassaformis cf. hessi (Bolli and Premoli-Silva), 1973</td>
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<td>3.54</td>
<td>1.06</td>
</tr>
<tr>
<td>Globorotalia hexagona (Natland), 1938</td>
<td>0.00</td>
<td>0.49</td>
<td>0.02</td>
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<tr>
<td>Globorotalia hirsuta (d’Orbigny), 1839</td>
<td>0.00</td>
<td>1.08</td>
<td>0.08</td>
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<tr>
<td>Globorotalia inflata (d’Orbigny), 1839</td>
<td>3.97</td>
<td>32.97</td>
<td>17.76</td>
</tr>
<tr>
<td>Globorotalia menardii (d’Orbigny), 1826</td>
<td>0.00</td>
<td>10.00</td>
<td>0.59</td>
</tr>
<tr>
<td>Globorotalia menardii + Globorotalia tumida</td>
<td>0.00</td>
<td>10.00</td>
<td>0.67</td>
</tr>
<tr>
<td>Globorotalia scitula (Brady), 1882</td>
<td>0.00</td>
<td>2.07</td>
<td>0.57</td>
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<tr>
<td>Globorotalia theyeri Fleischer, 1970</td>
<td>0.00</td>
<td>0.88</td>
<td>0.01</td>
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<tr>
<td>Globorotalia truncatulinoides right (d’Orbigny), 1839</td>
<td>0.00</td>
<td>8.35</td>
<td>1.73</td>
</tr>
<tr>
<td>Globorotalia truncatulinoides left (d’Orbigny), 1839</td>
<td>0.00</td>
<td>12.78</td>
<td>2.60</td>
</tr>
<tr>
<td>Globorotalia tumida (Brady), 1877</td>
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<td>3.39</td>
<td>0.08</td>
</tr>
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<td>Globoturborotalita rubescens (Hofker), 1956</td>
<td>0.00</td>
<td>1.04</td>
<td>0.09</td>
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<td>Neogloboquadrina dutertrei (d’Orbigny), 1839</td>
<td>0.00</td>
<td>5.49</td>
<td>0.21</td>
</tr>
<tr>
<td>Neogloboquadrina pachyderma right (Ehrenberg), 1861</td>
<td>3.69</td>
<td>68.73</td>
<td>35.07</td>
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<tr>
<td>Neogloboquadrina pachyderma left (Ehrenberg), 1861</td>
<td>0.00</td>
<td>38.21</td>
<td>5.35</td>
</tr>
<tr>
<td>Orbulina universa d’Orbigny, 1839</td>
<td>0.00</td>
<td>4.57</td>
<td>1.53</td>
</tr>
<tr>
<td>Orbulina universa + Biorbulina bilobata</td>
<td>0.00</td>
<td>4.80</td>
<td>1.57</td>
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<tr>
<td>Puliennatina obliquiloculata (Parker and Jones), 1865</td>
<td>0.00</td>
<td>2.65</td>
<td>0.19</td>
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<tr>
<td>Sphaeroidinella dehiscens (Parker and Jones), 1865</td>
<td>0.00</td>
<td>0.39</td>
<td>0.01</td>
</tr>
<tr>
<td>Turborotalita quinqueloba (Natland), 1938</td>
<td>0.00</td>
<td>7.71</td>
<td>0.84</td>
</tr>
</tbody>
</table>

sample size 187 903 446.65
Oxygen isotope measurements (Figure 5.2) were conducted on the planktonic foraminifera species *Globigerinoides ruber* white (250-350 μm) and left- and right-coiled *Globorotalia truncatulinoides* (300-400 μm). The first set of measurements were performed using a Finnigan MAT 251 mass spectrometer and associated ‘Kiel’ carbonate preparation system in Bremen University. The second set was measured using a Finnigan MAT 252 mass spectrometer with...

**Figure 5.2**
Downcore distribution of oxygen isotopes of *G. ruber* white (250-350 μm; black line), *G. truncatulinoides* left-coiled (300-400 μm; blue line) and *G. truncatulinoides* right-coiled (300-400 μm; red line), fragmentation index (FI = # fragments/(# whole specimen + # fragments)) and the ratio of planktonic and benthic foraminifera (PB = p/(p+b)). Glacial periods are shaded grey. Numbers refer to marine isotopic stages.

Oxygen isotope measurements (Figure 5.2) were conducted on the planktonic foraminifera species *Globigerinoides ruber* white (250-350 μm) and left- and right-coiled *Globorotalia truncatulinoides* (300-400 μm). The first set of measurements were performed using a Finnigan MAT 251 mass spectrometer and associated ‘Kiel’ carbonate preparation system in Bremen University. The second set was measured using a Finnigan MAT 252 mass spectrometer with...
the ‘Kiel’ carbonate preparation system at the Institute of Earth Sciences at Vrije Universiteit Amsterdam. About 20 specimens were used for each measurement. Tests of conical \textit{G. truncatulinoides} were crushed and c. 30 mg was measured. Compressed specimens were only used when indicated.

The preservation state of the shells of foraminifera is good. Shells, however, show minor signs of dissolution in certain intervals as indicated by dissolution indices like fragmentation index (FI) and plankton/benthos ratio (PB) (Thunell, 1976), but the assemblages were not affected to the extent that dissolution has distorted the primary signal. Both dissolution indices are shown in figure 5.2. The strongest dissolution occurred at 490 ky (MIS 13) and 950 ky (MIS 26).

The discrimination between the species \textit{Neogloboquadrina dutertrei} and \textit{Neogloboquadrina pachyderma} follows Martin and others (pers. comm. Brown University, August 1993; see also Ufkes and others (2000)). \textit{Globigerinoides sacculifer} with or without a sac-like chamber were lumped. \textit{Globorotalia menardii} and \textit{Globorotalia tumida} were also lumped together. \textit{Orbulina universa} includes \textit{Bi-orbulina bilobata} morphotypes. \textit{Globorotalia crassaformis} includes morphotypes like \textit{G. crassaformis cf. hessi} and \textit{G. crassaformis cf. viola}. Morphological variation of \textit{Globorotalia truncatulinoides} was studied qualitatively with the exception of the downcore distribution pattern of left-coiled versus right-coiled abundances.

A principal component analysis was performed on the data set of percentages of species. Species with maximum percentages less than 2 % (Table 5.1) were excluded from further discussions. We used the SYSTAT program (Wilkinson 1989) to calculate the principal components based on a correlation matrix. A varimax rotation has been applied to maximize the variance in factor loadings (Parker and Arnold 1999).

A Pearson correlation matrix has been calculated to illustrate changes in mutual correlations between the principal components, relative abundance of left- and right-coiled \textit{G. truncatulinoides}, oxygen isotopes of \textit{G. ruber} white ($\delta^{18}O_{rw}$) and both dissolution indices; plankton-benthos ratio and fragmentation index. We used consecutive time-windows of 400 ky. An additional time window, 961-1078 ky, is added to illustrate the mutual relationships prior to the Mid-Pleistocene Transition. By varimax definition the correlation between the principal components for the entire core will be zero. Principal components marked by incidental extreme scores will strongly affect the results and will therefore be omitted in the discussion. A confidence level of 95% is derived from critical values for correlation coefficients (Table 25 in Rohlf and Sokal, 1981).
We employed time-series analysis (band-pass filter synthesis approach using Analyseries; Paillard et al., 1996) to partition each record into its dominant frequency components in the 41- and 100-ky bands. This makes it possible to examine the influence of the two major orbital cycles, separately, on the SE-Atlantic oceanography (Imbrie et al., 1993). This is achieved by applying an appropriate band-pass filter, using, in our case a Gaussian filter. We extracted the filter components from the records (scores of the samples) of the principal components associated with the 41-ky (precession; central frequency= 0.024 cycles/ky; bandwidth= 0.001 cycles/ky), and 100-ky (precession; central frequency= 0.01 cycles/ky; bandwidth= 0.001 cycles/ky) band-pass filters.

Stratigraphy - Stable isotopes

The stratigraphy is based on the oxygen isotope profiles of *G. ruber* white (every 5 to 10 cm, 180 samples, Figure 5.2) and *G. truncatulinoides* (left- and right-coiling morphotypes; 95 samples, unevenly distributed along the core). The oxygen isotope stratigraphy of Core T89-40 was visually correlated with the benthic oxygen isotope record of ODP Site 659 to obtain an age model. In ODP Site 659 Tiedemann and others (1994) followed the isotope timescale of Shackleton and others (1990). After alignment, the average sedimentation rate was calculated with an average value of about 1.5 cm/ky.

The down-core distribution of $\delta^{18}$O of *G. ruber* white ($\delta^{18}$Orw; 250-350 μm) shows visual glacial-interglacial cyclicity related to eccentricity, since 900 ky. Heaviest values of $\delta^{18}$Orw are found at Marine Isotopic Stages (MIS) 22, 16, 12, 10, 8 and MIS 2 (Figure 5.2). The downcore profiles of $\delta^{18}$O of *G. truncatulinoides*, left- and right-coiled (crushed conical specimens; 300-400 μm), show a similar pattern as the profile of $\delta^{18}$Orw (Figure 5.2). The oxygen isotope records of *G. truncatulinoides* (and especially of left-coiled *G. truncatulinoides*) show their heaviest values at MIS 22, 12 and 10. MIS 22 appears as the first marked glacial period with substantial cooling of the (sub) surface waters during the last 1.1 million years.

Results

Here, we examine the relative abundances of the main planktonic foraminiferal species of Core T89-40, which are shown in figure 5.3. Further, the results of the principal component analysis have been used to reduce the number of faunal parameters (Figure 5.4; Table 5.2). A Pearson correlation matrix has been calculated to illustrate changes in mutual correlations.
Figure 5.3
Oxygen isotope stratigraphy, relative abundances of the main species (maximum > 2 %). Glacial periods are shaded grey. Numbers refer to marine isotopic stages. The asterisks’ in oxygen isotope curve mark the presence of *G. hexagona*.
Figure 5.3
continued
The results of the band-pass filters at orbital frequencies of the main faunal reflectors and oxygen isotope time series are shown in figure 5.5.

**Planktonic foraminiferal assemblage distribution**

**Main contributors**

In Core T89-40 the planktonic foraminiferal fauna is dominated by 3 species, in order of abundance: right-coiled *Neogloboquadrina pachyderma*, *Globorotalia inflata* and *Globigerina bulloides*. Together they represent on average 65% of the faunal assemblage.

Right-coiled *N. pachyderma* is abundantly present throughout the core. The relative abundance curve shows a long-term trend with high values (with peak abundances over 50%) during the periods 550 to 266 ky and 980 to 847 ky. Minima of about 3-9% are found in the periods 405 to 395 ky and 333 to 323 ky. *Globorotalia inflata* shows relative abundance trends that are mainly opposite of right-coiled *N. pachyderma*. Higher values (with peak abundances over 24%) are recorded during the periods 1010–950 ky, 805-690 ky, 390-320 ky and around 85 ky.

High abundances of *G. bulloides* occur throughout the entire record with maxima during MIS 2, 6, 8, 10, 15, 28 and MIS 30. In general, minima (< 10%) are recorded during interglacial periods.

**Other important contributors**

Incidental relatively high contributions are supplied by *Globigerinoides ruber* white, left-coiled *N. pachyderma*, *Globigerinita glutinata*, left and right-coiled *Globorotalia truncatulinoides*, and *Globorotalia menardii*.

*Globigerinoides ruber* white as well as other warm species (*G. sacculifer*, *G. tenellus*, *G. siphonifera*, *Globigerinoides ruber* pink and *G. falconensis*) generally have their highest abundances during interglacials. Whereas *G. ruber* white shows somewhat higher abundances in the lower half of the core (1078-550 ky; on average 7% versus 5% in the upper half of the core), *G. tenellus* and *G. falconensis* are more abundant in the upper half of the core (11-500 ky). *Globigerinella siphonifera* is abundant during interglacial periods with maxima up to 6%. Suppressed peaks of *G. siphonifera* are recorded from 880 to 490 ky (MIS 21 – MIS 13) with maxima up to about 3%.

Left-coiled *N. pachyderma* shows extremely high peaks (> 20%) during specific interglacials, at the top of MIS 31 and at the base of MIS 11 and MIS 9. Abundances of less than 20% of this species are related to MIS 5 and glacial periods.
Although fairly well abundant, on average 6 %, *G. glutinata* does not show a specific frequency pattern.

Left- and right-coiled *G. truncatulinoides* alternate generally during glacial and interglacial periods during the last 600 ky. Most remarkable is the near-absence of left-coiled *G. truncatulinoides* between 960-610 ky, albeit some minor peaks of less than 4 % at 800, 877, 905 and 936 ky are present. More compressed, flat morphotypes, both left- and right-coiled, are found since 343 ky in Core T89-40, starting with extremely rare to a few percentages of the *G. truncatulinoides* population since 185 ky to over 50 % during the last glacial maximum.

*Turborotalita quinqueloba* is recorded mainly during glacial periods during the last 500 ky.

Although not very abundant, *G. crassaformis* shows a distinct distribution pattern. In the lower part of the core, prior to 400 ky, *G. crassaformis* shows an average abundance of about 1.6 %. From 400 ky on its relative abundance diminishes down to an average of 0.3 %. *Globorotalia crassaformis* cf. *viola* is only present prior to 490 ky.

*Globorotalia hexagona*, an expatriate from the Indian Ocean (Bé and Hutson 1977; Peeters et al., 2004), is found very scarcely during interglacial periods mainly since MIS 11, although a single occurrence in MIS 17 has been found.

**Statistical analysis**

To reduce the number of faunal parameters and to obtain meaningful quantitative environmental interpretations, we applied a principal component analysis (Systat). The first four components of the principal component analysis explain about 45 % of the total variance. A natural drop in eigenvalues is recorded between principal component 4 (PC 4) and principal component 5. To discriminate the major components they are listed with increasing rank (Table 5.2).

The first principal component, PC 1, is positively dominated by the presence of the warm surface water species *G. sacculifer*, *G. siphonifera*, *G. ruber* pink, *P. obliquiloculata*, *G. falconensis*, *G. ruber* white and *G. tenellus*, whereas right-coiled *N. pachyderma* dominates the weaker negative values. The time-series of the PC 1 scores in Core T89-40 reveal a distinct glacial-interglacial pattern, particularly during the last 600-700 ky (Figures 5.4 and 5.5).

*Globorotalia crassaformis* and *G. ruber* white largely dominate the positive values of the second principal component (PC 2), whereas *O. universa* and *T. quinqueloba* account for the negative scores. PC 2 largely mimics the
downcore distribution pattern of *G. crassaformis*. Scores denote a diminishing trend since 400 ky. In general, high scores are found during interglacials especially during the past 500 ky. However, some glacial maxima are noticed at 524, 888, 968 and 1005 ky.

Positive values of the third principal component (PC 3) are dominated by right-coiled *N. pachyderma* and to a minor extent *G. bulloides* (Table 5.2), whilst negative values of PC 3 are controlled by high abundances of left-coiled *N. pachyderma*, *G. menardii* and *N. dutertrei*. During MIS 9, 11 and 31 strong negative scores of PC 3 are noticed.

Positive scores of PC 4 are dominated by *G. inflata* and *G. bulloides*, while negative scores are dominated by a single species, right-coiled *N. pachyderma*. Like *G. inflata*, PC 2 shows minimum scores during the periods MIS 12-14 and MIS 21-27. Maximum scores are reached during MIS 5, 9, 11, 26, 28 and 30. Relatively high glacial and interglacial scores are reached during the period 560-830 ky.

### Table 5.2
Loadings of the attributing species to the principal components, their variance explained, and eigenvalue. To emphasize the main attributing species loadings over 0.5 are in bold. The principal component analysis was calculated after a correlation matrix of species with a maximum > 2 % and a varimax rotation.
The downcore distribution of the oxygen isotope stratigraphy and the 4 principal components; the maximum daily insolation at 65°N at June 21st (BSI) using the Berger 1978 solution (Analyseries; Berger, 1978; Paillard et al., 1996). Glacial periods are shaded grey. Numbers refer to marine isotopic stages. PC 1 depicts subtropical gyre waters versus upwelling filaments from the Benguela Upwelling System. PC 2 reflects the change in position of the Angola-Benguela Front (ABF): positive values represent southward shifts of the Angola-Benguela Front. Strong negative values of PC 3 reflect extreme upwelling events indicated by peaks of left-coiled *N. pachyderma*, whereas positive values of PC 3 point to more normal upwelling conditions. PC 4 points to the upwelling intensity. A decrease in upwelling intensity, positive values, are also affected by a southward shift of the Angola-Benguela Front. The line thickness of the arrows corresponds to the main loading of the principal components. The dashed lines denote peaks in PC 1 during MIS 1, 5, 21, 25 and 31, which match the maxima in insolation.
The results of the band-pass filter records of the time-series of Core T89-40, using 100-ky and 41-ky filters, are shown in figure 5.5. The results of the LR04 benthic stable oxygen isotope stack (Lisiecki and Raymo, 2005), using the same frequencies, are also shown for reference. Benthic stable isotope records

**Figure 5.5**
Overview of the 100-ky and 41-ky band-pass filter results: the oxygen isotope records of LR04, of *G. ruber* white; right–coiled *G. truncatulinoides*, left–coiled *G. truncatulinoides*, the relative abundances of right- and left-coiled *G. truncatulinoides* and all principal components. The Mid-Pleistocene Transition period (MPT) is shaded in grey.

**Band-pass filter records and orbital periodicities**

The results of the band-pass filter records of the time-series of Core T89-40, using 100-ky and 41-ky filters, are shown in figure 5.5. The results of the LR04 benthic stable oxygen isotope stack (Lisiecki and Raymo, 2005), using the same frequencies, are also shown for reference. Benthic stable isotope records
are used to illustrate global ice volume changes during the Mid-Pleistocene Transition.

Filtered oxygen isotope profiles and orbital periodicities – timing of Mid-Pleistocene Transition

The filtered LR04 benthic stable oxygen isotope stack after application of the 100-ky filter, shows the previously noticed increase in amplitude of the 100-ky cycle throughout the Mid-Pleistocene Transition (e.g. Clark et al., 2006). The high amplitude glacial-interglacial cycles were well established by about 600-700 ky. The filtered Core T89-40 stable oxygen isotope profiles records are similar to the LR04 record using the 100-ky filter. The filtered output of all oxygen isotope curves after application of the 41-ky filter shows diminishing influence of the 41 ky frequency since about 600-700 ky.

Filtered G. truncatulinoides relative abundance profiles and orbital periodicities

The filtered records of relative abundance data of both coiling morphotypes of G. truncatulinoides, after application of the 100-ky filter, show presence of the 100-ky periodicity throughout the record. The filtered right-coiled G. truncatulinoides record shows the largest increase towards high amplitude cycles in the last 600-700 ky of all the analyzed records, suggesting a strong response of right-coiled G. truncatulinoides to eccentricity cycles in this interval. It is interesting to note that a phasing shift occurred in these two G. truncatulinoides records. They roughly covary prior to 400 ky, while they are in anti-phase since 250 ky.

The filtered records of both left- and right-coiled G. truncatulinoides, after application of the 41-ky filter, show a persistent influence of the 41-ky cycle throughout the record, where the right-coiled G. truncatulinoides record shows a slight decrease in amplitude between 800 and 400 ky and the left-coiled G. truncatulinoides record shows increased amplitudes from 650 to 250 ky. The two 41-ky filter outputs are out of phase.

Filtered records of principal component scores and orbital periodicities

The filtered records of PC 1, PC 2 and PC 4, after application of the 100-ky filter, show a shift from low to high amplitude cycles mostly around 600-700 ky, although the shift in PC 4 occurred much earlier at around 1000 ky. These results are similar to those of the filtered oxygen isotope records, although the filtered record of PC 3 doesn't show much of cyclicity in the 100-ky frequency band. The 100-ky filtered output records of PC 1 and PC 4 are in phase during the last 600 ky, whilst they are in anti-phase in the interval 1078-850 ky.
The filtered record of PC 1 shows a decreased influence of the 41-ky cycle during the Mid-Pleistocene Transition, whilst the filtered record of PC 2 shows a small increase in dominance of the 41-ky cycle around 600 ky. The filtered record of PC 3 record shows increased influence of 41-ky cycles between 200-700 ky. Maximum amplitudes of the 41-ky filtered output of PC 4 are noticed in the lower part of the core, in the interval 1078-800 ky.

Discussion

In this study, we aim to document changes in fossil planktonic foraminiferal assemblages in Core T89-40. These changes suggest regional oceanographic responses in the SE Atlantic to climate development during the Mid-Pleistocene Transition, a period of distinct changes in climate cyclicity and cooling of the SE Atlantic during glacial periods (e.g. Jahn et al., 2003; Schefuß et al., 2004; this study). Variability in surface water distribution during the past million years is schematically depicted in figure 5.6.

Principal components as reflectors of surface water masses

Variability in the downcore distribution of planktonic foraminifera is summarized with the two principal components, which describe the influence of the major oceanic realms in the surface waters. Here, especially the regional ecology of planktonic foraminifera is used in order to obtain an accurate characterization of the principal components.

PC 1 reflects warm water species, which dwell mainly in warm, oligotrophic surface waters of the subtropical SE-Atlantic gyre (Schmidt, 1992; Ufkes and Zachariasse, 1993; Ufkes et al., 1998) and/or northern Angolan waters (Oberhänsli et al., 1992; Ufkes et al., 1998), versus the negative values of right-coiled N. pachyderma. Today, right-coiled N. pachyderma is found in the nutrient-rich coastal upwelling waters (van Leeuwen, 1989; Oberhänsli et al., 1992; Schmidt, 1992; Giraudieu, 1993; Ufkes and Zachariasse, 1993; Little et al., 1997; Ufkes et al., 1998; Ufkes et al., 2000). PC 1 reflects the movements of the South Atlantic Anticyclone.

Scores of PC 2 reflect species variation on either site of the Angola-Benguela Front (ABF). Today, G. crassaformis flourishes in subsurface waters north of the ABF (van Leeuwen, 1989; Oberhänsli et al., 1992; Kemle-von Mücke and Oberhänsli, 1999), in the South Atlantic Central Water (Figure 5.7) and Equatorial Undercurrent, where it is associated with oxygen minima (Jones, 1967; Oberhänsli et al., 1992; Kemle-von Mücke and Oberhänsli, 1999). Local oxygen minima are found north of the ABF as well as the shelf waters offshore.
Namibia (Shannon and Nelson, 1996). *Globigerinoides ruber* white is recorded in the subtropical gyre as well as the tropical waters north of the ABF. In these tropical waters *G. ruber* white shows high abundances during summer (Oberhänsli et al., 1992) when the most southern position of the ABF is reached (Meeuwis and Lutjeharms, 1990). *Orbulina universa* and *T. quinqueloba* are found in temperate to cold waters with high food levels of the Benguela Upwelling System (BUS), south of the ABF (van Leeuwen, 1989; Giraud, 1993; Kemle-von Mücke and Hemleben, 1999).

Positive loadings of PC 3 are dominated by right-coiled *N. pachyderma* and *G. bulloides*. As right-coiled *N. pachyderma* reflects moreover the upwelling cells, *G. bulloides* is found further offshore than right-coiled *N. pachyderma* in the less fertile and warmer waters of the filaments (Oberhänsli et al., 1992; Schmidt, 1992; Giraud, 1993; Pflaumann et al., 1996; Ufkes et al., 2000). Negative scores controlled by left-coiled *N. pachyderma*, *G. menardii* and *N. dutertrei* dominate the downcore distribution of PC 3. Today, the combination of right-coiled *N. pachyderma* and *G. bulloides* can be found in upwelling and associated filament waters. *Neogloboquadrina dutertrei* and *G. menardii* thrive in (sub)tropical areas (Fairbanks et al., 1982; van Leeuwen, 1989; Ufkes et al., 1998), in the BUS they are most likely reseeded from the Indian Ocean (Charles and Morley, 1988; Giraud et al., 2001; Peeters et al., 2004) suggesting increased interocean exchange. The assemblage of left-coiled *N. pachyderma* and warm water species *G. menardii* and *N. dutertrei*, however, is unknown in the modern BUS environment or subtropical gyre. The left-coiled *N. pachyderma*, thrives in highly eutrophic, upwelling conditions, has its origin in the Southern Ocean, and has been injected into the BUS during the course of the Quaternary (Darling and Wade, 2008). Darling and Wade (2008) show that in the BUS left-coiled *N. pachyderma* represents a relict population marked by the *N. pachyderma* Type V and Type VI genotypes. Ufkes and others (2000) suggested that the left coiling peaks (> 20 %) represent periods with strong coastal upwelling and subsequently transport offshore without filamentous mixing towards the location of Core T89-40. We interpret variability in PC 3 to reflect extreme meridional and seasonal zonal changes in hydrography, where *G. menardii* and *N. dutertrei* would reflect the summer season and left-coiled *N. pachyderma* winter upwelling.

PC 4 is controlled by *G. inflata* and *G. bulloides* on one hand and right-coiled *N. pachyderma* on the other hand. The downcore distribution of PC 4 is largely influenced by the abundance patterns of *G. inflata*. *Globorotalia inflata* is found offshore at the transition of the subtropical gyre and the Benguela Oceanic Current and the Benguela upwelling filaments (Schmidt, 1992; Giraud, 1993; Ufkes and Zachariasse, 1993; Little et al., 1997; Ufkes et al.,
1998; Ufkes et al., 2000) as well as frontal zones like the ABF (Ufkes et al., 1998), reflecting vertical mixing. Apart from upwelling filaments, *G. bulloides* is also recorded in frontal zones like the ABF (Ufkes et al., 1998). Based on the biogeographies of these species PC 4 appears to reflect the BUS upwelling intensity. A less extensive upwelling area as well as a more southern position of the ABF may induce reduced intensity reflected by positive PC 4 scores.

Changes in surface water mass distribution during the past million years

The largest variability in the dataset of planktonic foraminiferal counts is by definition described by the PC 1 and PC 2 outcomes. The time-series of the PC 1 and PC 2 scores in Core T89-40 reveal a distinct glacial-interglacial pattern, particularly during the last 600-700 ky (Figures 5.4 and 5.5). Maximum peaks of PC 1 and PC 2, characterized by oligotrophic species such as *G. sacculifer*, *G. siphonifera*, *G. ruber* and *G. crassaformis*, represent periods of maximum extension of the SE Atlantic subtropical gyre waters and southward shifts of the Angola-Benguela Front (ABF), while troughs of PC 1 and PC 2, characterized by eutrophic species, represent periods of influence of Benguela Upwelling.

### Table 5.3

Pearson correlation variability in time; 400-ky time windows in steps of 200 ky as well as the period prior to the Mid-Pleistocene Transition (> 961 ky); principal components PC 1, PC 2 and PC 4, percentages of *G. truncatulinoides* right-coiled (trunc-r), *G. truncatulinoides* left-coiled (trunc-l), oxygen isotopes of *G. ruber* white ($\delta^{18}$Orw), 21 June insolation at 65°N (BSI), plankton-benthos ratio (PB = p/(p+b)) and fragmentation index (FI) in steps of 400 ky. Bold numbers represent correlation coefficients significantly different from zero using a 95 % confidence level.
System (BUS) upwelling filaments and/or influence of cool waters from the south. Since 600 ky, obliquity also had a strong impact on PC 2 as shown by increasing numbers of *O. universa* and *T. quinqueloba*, which are more subject to influence from southern cold waters.

The regular patterns of cyclicity in the PC 1 and PC 2 records suggest that insolation patterns driven by orbital cycles somehow controlled the (sub)surface ocean conditions in the S. Atlantic. The maximum peaks of PC 1 and PC 2, concur with periods of maxima in 21 June insolation at 65°N (Boreal Summer Insolation), although this relationship is less clear for PC 2 in the early part of the record prior to 600 ky (Figure 5.4; Table 5.3). Noteworthy are the large maximum peaks of PC 1 in MIS 1, 5, 21, 25 and 31, matching the maxima in insolation.

It appears from the PC 1 and PC 2 records that during maxima in Boreal Summer Insolation the South Atlantic Anticyclone shifted southeastwards in the southern hemisphere, which resulted in a more eastern extent of the subtropical gyre and a more southern ABF at the expense of the BUS. These southeastwards shifts of the South Atlantic Anticyclone resulted in warm, oligotrophic waters above the core site at the same time when the southern polar fronts shifted southwards (Becquey and Gersonde, 2002; Marino et al., 2009), when maximum sea surface temperatures occurred in the Southern Ocean and Equatorial Atlantic (Schneider et al., 1996) and when Indian Ocean Agulhas waters entered the SE Atlantic (Peeters et al., 2004). These relationships occurred through the entire record, although the peaks of PC 1 were rather subdued during the period 400-800 ky (Figure 5.4), which suggests that eastward expansion of the subtropical gyre was probably hindered by a strong southward shift of the ABF. Figure 5.6b shows the suggested position of the ABF during early part of this period. There is some evidence for this in other records from the literature, for instance proxy temperature records indicate a large temperature gradient across the ABF (Marlow et al., 2000; Jahn et al., 2003; Schefuß et al., 2004).

The largest shifts of the subtropical gyre at the expense of the BUS occurred during transitions of glacial to interglacial periods and thus preceded the full interglacial conditions by several thousand years as indicated by minima in δ¹⁸O. This relationship of SE-Atlantic warming before full interglacial conditions as described by minima in ice volume has been described before (Schneider et al., 1996; Peeters et al., 2004). In Core T89-40 scores of PC 1 show that these periods of early warming during deglaciations, perfectly in phase with Boreal Summer Insolation, were already present before and during the Mid-Pleistocene Transition.
Figure 5.6
Schematic distribution of surface water masses in time, glacial and interglacial setting in 3 time windows: ‘late Pleistocene state’; post Mid-Pleistocene Transition (MPT) - 0-600 ky; Mid-Pleistocene Transition (MPT) - 600-900 ky; pre Mid-Pleistocene Transition (MPT) - > 900 ky. The small panels show the main principal component orientation as well as the dominant coiling direction in G. truncatulinoides during each time window.
Abbreviations: ABF – Angola Benguela Front; STC– SubTropical Convergence; SAF – Subantarctic Front; PZ – Polar Front; right-coiled; post Mid-Pleistocene Transition G. truncatulinoides left-coiled; pre Mid-Pleistocene Transition G. truncatulinoides left-coiled. The line thickness of the arrows and ellipses reflect wind strength and upwelling intensity. The positions of the South Atlantic frontal systems are inferred from Becquey and Gersonde (2002).
Although there is an obvious relationship of S. Atlantic paleoceanographic change and Boreal Summer Insolation, unless the age model based on tuning contains basic flaws, the causal mechanism of how northern Hemisphere climate change has been transferred to the south is difficult to envisage at this stage, and is beyond the scope of this paper, but perhaps the warm sea surface temperature conditions in the S. Atlantic during periods of high Boreal Summer Insolation may have been amplified by the repeated occurrence of the Atlantic- and/or Benguela Niños. Today, during such an Atlantic- and/or Benguela Niño higher sea surface temperatures in the eastern equatorial Atlantic occur due to a relaxation of trade winds in the western part of the equatorial Atlantic and/or stronger westerly winds along the equator (Rouault et al., 2007). As a result low-nutrient, low-oxygen, warm Angolan waters flow southwards into the BUS (Shannon, 1986; Monteiro et al., 2006). Modern Benguela Niño events are part of interannual variations (Rouault et al., 2007). Repeated Benguela Niño-like conditions may have contributed to warming of the SE Atlantic, explaining the high scores of PC 2 and PC 4 (Figure 5.6). These high scores of PC 2 suggest that the ABF resided further to the south than during the last 400 ky (see also Jansen et al., 1996). Prior to MIS 12, oxygen

**Figure 5.7**

Schematic vertical distribution of water masses at the 8°E transect (after Mohrholz et al., 2001) and nearby (Poole and Tomczak, 1999) and the distribution of G. truncatulinoides and G. crassaformis within the central waters before and after the Mid-Pleistocene Transition (MPT). Prior to the Mid-Pleistocene Transition left-coiled G. truncatulinoides is aligned to G. crassaformis, which is restricted to the oxygen-depleted South Atlantic Central Water, whereas since the Mid-Pleistocene Transition left-coiled G. truncatulinoides is found further south associated with Eastern South Atlantic Central Water. Abbreviations: ABF - Angola-Benguela Front; SACW - South Atlantic Central Water; WSACW - Western South Atlantic Central Water; ESACW - Eastern South Atlantic Central Water; AAIW - Antarctic Intermediate Water; G - G. truncatulinoides right-coiled; ☀ - post MPT G. truncatulinoides left-coiled; ☀ - pre MPT G. truncatulinoides left-coiled.
isotopes of ODP Site 1082 (21°S) (Jahn et al., 2003) imply that the ABF may have shifted as far south as 21°S.

During glacial periods, species such as left- and right-coiled *N. pachyderma* and *T. quinqueloba* were thriving in the relatively cool waters above the Walvis Ridge. There is no evidence of warming periods in association with boreal insolation peaks during glacial periods. The glacial boundary conditions may have prevented warming events to occur, and the BUS conditions prevailed, or the time resolution in Core T89-40 was not high enough. Most likely Antarctic sea-ice expansion reinforced the southern hemisphere meridional temperature gradients and forced the southern hemisphere oceanic and atmospheric frontal zones to move equatorward (Howard and Prell, 1992; Schneider et al., 1996; Stuut et al., 2004) and subsequently pushed the Intertropical Convergence Zone northwards (Mix and Morey, 1996).

Although the BUS conditions prevailed during glacial periods, the highest numbers of left-coiled *N. pachyderma*, a polar species, occurred during interglacials MIS 9, 11 and 31. These peaks of left-coiled *N. pachyderma* resulted in the high negative scores of PC 3 (Figures 5.3 and 5.4). Ufkes and others (2000) explained that these unusual interglacial BUS conditions were caused by extreme zonal winds, resulting in strong upwelling and contour jet like currents, which transported the upwelled waters offshore. During MIS 11 and 9, the peaks of left-coiled *N. pachyderma* were preceded by extreme meridional shifts of ocean frontal systems yielding from increased percentages of subtropical species by about 6 ky (Ufkes et al., 2000).

The left-coiled *N. pachyderma* was accompanied surprisingly by *N. dutertrei* and *G. menardii* in the PC 3 scores. Today, the latter species are (sub)tropical in origin, and they are certainly not associated with core upwelling cells. The co-occurrence of the polar and (sub)tropical species can only be explained by strong seasonality of the BUS with strong upwelling in winter/spring and stratification in summer, and at the same time a connection to the Indian Ocean must have existed. The presence of *G. menardii* during these particular interglacials MIS 9, 11 and 31 can be explained only by extensive inter-ocean transfer of (sub)surface waters of the Agulhas Current, because during each glacial period *G. menardii* disappeared from the Core T89-40 record, just like anywhere else in the Atlantic (Ericson and Wollin, 1968).

Reseeding of *G. menardii* from the Indian Ocean is the most important factor in its distribution, like in the near-coastal SE Atlantic (Charles and Morley, 1988; Giraudeau et al., 2001). During the period 1085-1055 ky, also ODP Site 1090, located at 43°S (about 2° south of Subtropical Convergence), experienced the influence of subtropical waters yielding from calcareous nannofossil assemblages (Maioranoa et al., 2009). Thus the high scores of PC 3 at lowermost
end of the core (1078 ky - 1073 ky) represent an early phase of inter-ocean exchange prior to the Mid-Pleistocene Transition (MPT).

The increased productivity, induced by upwelling, in the BUS and the westward extension of the upwelling filaments is reflected by negative scores of PC 4, high abundances of right-coiled *N. pachyderma*. The PC 4 time-series show a pattern with highly productive waters occur during glacial periods, but only after the MPT ended when large amplified glacial-interglacial cycles started (Figure 5.6a). In contrast prior and during the MPT, however, we notice a non-analogue situation: increased productivity during warm periods as well as a diminishing productivity during the cool season (Figures 5.4, 5.5 and 5.6c; Table 5.3). This reversed relationship shows that a change occurred in nature and source of productive waters. The change in relationship between the extent of the subtropical gyre (PC 1) and productivity (PC 4) coincides with a change in the nature of marine production at the onset of the 100-ky cyclicity (at 650 ky) noticed by Schefuß et al. (2005): from a runoff dominated marine production to one mainly influenced by wind-driven coastal and oceanic upwelling due to increased trade winds. Increased productivity has also been generated by southward transport of terrigenous material until 800 ky as reported by Durham et al. (2001).

Two pronounced periods of enhanced productivity as indicated by negative scores of PC 4 are noticed from 910-830 ky and from 530-400 ky. The period 910-830 ky is related to increased upwelling induced by strong trade winds – an intensified Benguela Current (Durham et al., 2001). Another period of enhanced productivity, from 530-400 ky, may be related to the upwelling of more nutrient rich waters due to a shoaling of Antarctic Intermediate Water (Oberhänsli 1991; Ufkes et al., 2000). These two periods of enhanced upwelling are likely to be related to the 400-ky cyclicity of the northern and southern hemisphere, which alternate in trade wind intensity.

**Subsurface water mass distribution - changes in biogeography of left-coiled**

*G. truncatulinoides*

Left- and right-coiled *G. truncatulinoides* make up a minor contribution to the total planktonic foraminiferal assemblage, but their distribution patterns (Figures 5.3 and 5.8) and oxygen isotope profiles (Figure 5.2) may give insights into the history of the subsurface water masses over the course of the Quaternary. There are two issues about the *G. truncatulinoides* patterns which may relate to climate development during the Mid-Pleistocene Transition (MPT) and over the course of the Quaternary: the exit of left-coiled *G. truncatulinoides* at 960 ky (MIS 26), onset of a near absence period until about 600 ky and the...
appearance of an interval with regular cycles of alternating dominance of left-to right-coiled specimens which follow the climate cycles. This may suggest paleoecological changes affecting the distribution of left-coiled *G. truncatulinoides*. 

**Figure 5.8**

The maximum daily insolation at 65°N at June 21st (BSI) using the Berger 1978 solution (Analyseries; Berger, 1978; Paillard et al., 1996); the downcore distribution of the relative abundances of left- and right-coiled *G. truncatulinoides*, their coiling ratio (left/(left +right)) and oxygen isotopes of *G. ruber* white (250-350 μm). Left-coiled *G. truncatulinoides* shows a near absence during the period 960-610 ky. The dashed lines denote high percentages of right-coiled *G. truncatulinoides*, which match the maxima in insolation. Glacial periods are shaded grey. Numbers refer to marine isotopic stages.
Today, left-coiled specimens are mainly found south of 30°S (Bé and Tolderlund, 1971; Kemle-von Mücke and Hemleben, 1999) and as north as 23°S on the Namibian shelf (Giraudeau, 1993). Surface sediment studies by Niebler and Gersonde (1998) indicate an offshore increase in abundance of right-coiled *G. truncatulinoides*, while left-coiled *G. truncatulinoides*, bounded roughly by the 21°C surface summer isotherm, decreases. Compressed, flat, morphotypes represent relatively deeper cool-subtropical and/or Subantarctic waters of the S. Atlantic, Indian and Pacific Ocean (Healy-Williams et al., 1985; De Vargas et al., 2004). Oxygen isotope data suggest that left- and right-coiled *G. truncatulinoides* are related to subsurface, central water masses at intermediate depths of about 150-500 m (Mulitza et al., 1997; Wilke, 2005; Lončarić et al., 2006). Based on their current biogeography left- and right-coiled *G. truncatulinoides* would thrive in Eastern South Atlantic Central Water and (Western) South Atlantic Central Water, respectively (Figure 5.7a).

The abrupt exit of left-coiled *G. truncatulinoides* in MIS 26, the first issue, occurred at various sites in the S. Atlantic: elsewhere on the Walvis Ridge (Pflaumann, 1988), the western S. Atlantic (Lohmann, 1992) and the western equatorial Atlantic (Cullen and Curry, 1997). The exit at the various locations suggests that this event occurred S. Atlantic wide, which supports the notion that it represents at least a regional exit level. We note that this regional exit level coincided with considerable cooling of surface and subsurface waters as expressed in the stable oxygen isotope records of *G. ruber* white and left- and right-coiled *G. truncatulinoides*, and also with general cooling of surface and subsurface waters as evidenced in the alkenone based temperature record of Site 1084, offshore Namibia (e.g. Marlow et al., 2000). The drop in (sub)surface water temperatures may have been the result of a change in ventilation of subsurface waters and/or deep winter mixing in the equatorial and S. Atlantic during the early MPT period. The correlation with PC 2 suggests that the pre-MPT left-coiled *G. truncatulinoides* may have had a more northern subtropical origin, in contrast to today's left-coiled specimens, which may have a more southern origin (De Vargas et al., 2001), thereby assuming that different left-coiled cryptic species prevailed in the two intervals. Figures 5.6 and 5.7 schematically depict the biogeography of left- and right-coiled *G. truncatulinoides* in time.

The re-entry of left-coiled *G. truncatulinoides* occurred around MIS 15, around 600 ky. From this re-entry level onwards, the relative abundance levels of left-coiled versus right-coiled specimens became perfectly cyclical in tune with the glacial-interglacial cycles. The right-coiled *G. truncatulinoides* preferred the warmer interglacial subsurface waters and the left-coiled *G. truncatulinoides* thrived in the cooler glacial waters as expected considering the modern
distribution of the two coiling types (Bé and Tolderlund, 1971; Giraudieu, 1993; Niebler and Gersonde, 1998; Kemle-von Mücke and Hemleben, 1999). This pattern of amplified left- to right-coiled ratio cycles is perfectly in tune with the climate development during the MPT with enhanced glacial-interglacial cycles (Figure 5.8) with high abundance peaks of right-coiled *G. truncatulinoides* largely in tune with periods of maximum Boreal Summer Insolation (Figure 5.8).

It is interesting to note that the record of left-coiled *G. truncatulinoides* after the re-entry shows an increase in amplitude in the 41-ky filter output (Figure 5.5), suggesting a strong impact of the obliquity cycle in the late Pleistocene after the MPT. Obliquity variability may have had an influence on subsurface water circulation originating from the southern high latitude, and ultimately on the distribution of the modern left-coiling *G. truncatulinoides*.

The re-entry of *G. truncatulinoides*, and subsequent presence during glacial periods concurred with a strong increase in upwelling activity and glacial surface-water cooling after the MPT (e.g. ODP Site 1077, 1082, 1084; (Marlow et al., 2000; Jahn et al., 2003; Schefuß et al., 2004) which in turn enhanced ventilation of deep thermocline and intermediate waters, where *G. truncatulinoides* resides (Lohmann, 1992; Wilke, 2005; Lončarić et al., 2006). This ventilation of the deep thermocline waters was synchronous with enhanced ventilation of deep-water masses beneath the BUS, which caused extinction of certain benthic foraminifera (O’Neill et al., 2007).

The distribution as discussed above suggests that the before and after the MPT left-coiled *G. truncatulinoides* had different ecological habitats with a different origin. This suggests in turn that they were different species with a distinct ecology.

The timing of the re-entry of modern left-coiling *G. truncatulinoides* in the Walvis Ridge record occurred prior to the period of evolution of left-coiled *G. truncatulinoides* and migration in more southern Subantarctic regions between 500 and 200 ky (Kennett, 1968a; 1970; De Vargas et al., 2001). The Subantarctic left-coiled *G. truncatulinoides* was most likely closely related to the S. Atlantic left-coiled *G. truncatulinoides*, or had a common left-coiled ancestor that lived in the Indian Ocean. Both developed in the S. Atlantic and the southern Subantarctic sector in the late Pleistocene after the MPT. During this period a widened ‘Cape gateway’ (Becquey and Gersonde, 2002; Marino et al., 2009) may have enabled the establishment of an Indian Ocean derived Eastern South Atlantic Central Water with implications for gene flow (e.g. Darling et al., 1999), resulting in a habitat for modern left-coiled *G. truncatulinoides*. 
Conclusions

Over the course of the Pleistocene major changes in planktonic foraminiferal distribution, mutual relationships and therefore water mass distribution have been noticed at around 950-900 ky, 600 ky and 400 ky. At Walvis Ridge the Mid-Pleistocene Transition started to emerge at about 950-900 ky and is nearly completed at 600 ky. The latest response of the hydrographical setting to the Mid-Pleistocene Transition is the location of the ABF to its ‘current’ position at 400 ky completing ‘the late Pleistocene state’.

(1) The main cyclicity of the planktonic foraminiferal record, driven by shifts in oligotrophic versus eutrophic water masses, was in tune with glacial-interglacial cyclicity, with maximum influence of warm, oligotrophic waters during periods of maximum Boreal Summer Insolation. However, upwelling intensity (PC 4) does not appear to be steered directly by Boreal Summer Insolation.

(2) These cycles were amplified during the last 600 ky in line with amplified global climate change cycles after the Mid-Pleistocene Transition.

(3) Prior to 800 ky increased upwelling intensity is recorded during warm, interglacial periods opposed to glacial periods during ‘the late Pleistocene state’. The apparent contradiction between PC 1 and PC 4, a concurrent expanding subtropical gyre and Benguela Upwelling System compared to an alternating system today, is due to a relaxation of zonal trade winds during glacial periods prior to 600 ky.

(4) Prior to MIS 12, the Angola-Benguela Front may have shifted as far south as 21°S, higher eastern equatorial sea surface temperatures and Benguela Niño-like conditions may have induced the southward progadation of warm Angolan waters. During this period the Angola-Benguela Front was stronger and probably wider inhibiting the eastward extent of the subtropical gyre during interglacials, especially from 400-800 ky.

(5) In the S. Atlantic the exit of left-coiled G. truncatulinoides occurred synchronously with cooling of deeper waters at 960 ky at the onset of the Mid-Pleistocene Transition.

(6) The re-entry of left-coiled G. truncatulinoides was followed by a cyclic alternation of left- and right-coiled G. truncatulinoides in line with glacial-interglacial cycles since 600 ky.

(7) During the Mid-Pleistocene Transition the correlation of left-coiled G. truncatulinoides with various parameters changed in time suggesting that the ‘recent’ left-coiled morphotype does not represent the one prior the absence period. It has a different biogeography, habitat or even is a different genotype.
Enhanced inter-ocean transfer allowed *G. truncatulinoides* (left-coiled) to occupy new habitats and alter its biogeography and even to evolve into a new species.

(8) Various morphotypes of *G. truncatulinoides* thrive in different central water masses. Prior to 960 ky left-coiled *G. truncatulinoides* is related to the tropical South Atlantic Central Water, north of Angola-Benguela Front, while since 600 ky it is related to more southern central waters; Eastern South Atlantic Central Water. Right-coiled *G. truncatulinoides* continued to thrive in more or less the same water mass, Western South Atlantic Central Water and probably since 600 ky also South Atlantic Central Water.

(9) Strong inter-ocean exchange (Indian Ocean-Atlantic) and a highly productive Benguela Upwelling System are revealed by the unusual co-occurrence of left-coiled *N. pachyderma* and subtropical species *G. menardii* and *N. dutertrei* during MIS 9, 11 and 31.

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