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Calcareous plankton dissolution pattern and coccolithophore assemblages during the last 600 kyr at ODP Site 1089 (Cape Basin, South Atlantic): paleoceanographic implications

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Abstract

Coccolithophore assemblages at ODP Site 1089 in the southern Cape Basin (~41°S) were used to reconstruct surface-water conditions for the late Quaternary (Marine Isotope Stages (MIS) 1–15) in a region of strong hydrographic gradients in the southeast Atlantic. Stratigraphic control was provided by oxygen isotope stratigraphy and calcareous nannofossil events that are thought to be synchronous over a broad range of latitudes. The greatest coccolith abundances occurred at glacial terminations and, to a lesser degree, during glacial stages. Conversely, coccolithophores were the least abundant during the transition between interglacial to glacial stages, when calcium carbonate dissolution was strong. With the exception of these intervals, coccolith preservation is moderate to good, allowing study of the assemblages. The total abundance of coccolithophores and calcium carbonate variations at Site 1089 result both from variations in dissolution and carbonate production. During terminations, for example, the greatest calcium carbonate concentrations occurred at the same time as a moderate-to-poor preservation of coccoliths and foraminifers. Carbonate production was relatively high during these intervals. However, during terminations IV and V, maxima in carbonate production in the ocean were linked to high-dissolution processes at Site 1089. This trend is not observed for terminations I, II and III [Hodell et al., Earth Planet. Sci. Lett. 192 (2001) 109–124]. The interval from MIS 9 to 13 is coincident with high abundances of highly calcified species such as *Gephyrocapsa caribbeanica*. Here we discuss the contribution of this ubiquitous species to the production of calcium carbonate and their paleoecological significance. Except for occasional coccolith-barren intervals during interglacial periods, subtropical coccolith species were present continuously at ODP Site 1089 during the late Pleistocene. This suggests that the Polar Front has been south of Site 1089 for the last 600 kyr.

Keywords: Southern Ocean; Pleistocene; calcareous nannofossils; biostratigraphy; isotope stratigraphy; paleoceanography; calcium carbonate dissolution; Ocean Drilling Program

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1. Introduction and objectives

The sector comprising the Cape Town and Agulhas basins is an important region for global heat transport because warm waters from the Indian Ocean are transported to the Atlantic via the Agulhas Current (Gordon, 1986; Broecker, 1987, 1991; Gordon et al., 1992; Wefer et al., 1996; Berger and Wefer, 1996; Lutjeharms, 1996). Changes in the position of frontal systems, mainly linked to Polar Front dynamics, may have affected the interbasinal transport of surface waters. Micropaleontological and biochemical data from the region are scarce because of the limited number of cores available. Hiatuses and low sedimentation rates in this region have also hampered paleoceanographic studies (Flores et al., 1999). During ODP Leg 177, a late Pleistocene sequence with high sedimentation rates (Hodell et al., 2001, 2002) and abundant calcareous nannofossils was recovered. The position of Site 1089 between the Subtropical Front (STF) and the Subantarctic Front (SAF) (Fig. 1) makes this site ideal for monitoring the movements of the frontal boundary and the influences on plankton communities. Different coccolithophore assemblages are associated with different surface-water characteristics (McIntyre and Bé, 1967; Winter and Martin, 1990; Winter et al., 1994; Roth, 1994) and hence provide a tool for mapping the spatial and temporal variations in ancient surface-water masses. In previous studies, coccolithophore communities have been used to reconstruct surface-water temperatures and salinities during the Pleistocene (McIntyre, 1967; CLIMAP project members, 1976), and surface-water masses (Geitzenauer et al., 1977; Roth, 1994). In addition, the study of the production and preservation of coccolithophorids, as calcium carbonate producers, provides important information about the marine carbonate system and its relationship to the global carbon cycle (e.g. Hodell et al., 2001).

The goals of this study were: (1) to establish a high-resolution calcareous nannofossil stratigraphy for the Pleistocene; (2) to reconstruct changes in the paleoenvironment and water mass distribution by analysis of coccolithophore assemblages; (3) to reconstruct the frontal dynamics at Site 1089 during the late Pleistocene; and (4) to assess the relative importance of production and dissolution in controlling the calcium carbonate content at Site 1089.

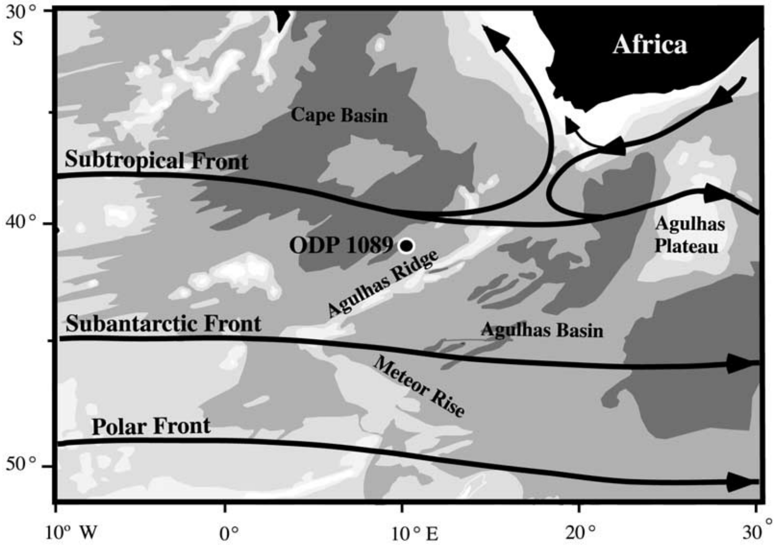

Fig. 1. Location of ODP Site 1089 used in this study and main oceanographic features. Arrows depict the surface-ocean circulation pattern (after Peterson and Stramma, 1991). Distal warm filaments from the Agulhas Current retroflection may reach as far as the core location (Lutjeharms, 1996). The sea floor below 2000 m is gradually shaded in steps of 1000 m.

2. Site location and oceanographic settings

ODP Site 1089 is situated in the southern Cape Basin off Southwest Africa, just north of the Agulhas Ridge (40°56.2′S, 9°53.6′E) at a water depth of 4620 m. ODP Site 1089 is located on a sediment drift and is marked by high sedimentation rates, averaging ~15 cm/kyr during the Pleistocene (Shipboard Scientific Party, 1999). The Pleistocene sediments are mainly calcareous nannofossil ooze with variable terrigenous components. Details about the sedimentological and physical properties of ODP Site 1089 are described in the Leg 177 Initial Reports (Shipboard Scientific Party, 1999). ODP Site 1089 has a continuous sedimentary record for the latest Pleistocene (Hodell et al., 2001).

ODP Site 1089 is located in Subantarctic waters, south of the modern position of the STF and north of the SAF (Peterson and Stramma, 1991) (Fig. 1). Currently, a marked drop in temperature, from 14.2°C north of the STF (Lutjeharms and Valentine, 1984) to 8.4°C south of the STF (Lutjeharms, 1981) can be observed. The area between the STF and SAF is defined as the Subantarctic Zone (SAZ), and is characterized by average surface-water temperatures of 6.7°C, salinities of 34.2‰, and surface-water oxygen concentrations of 6.63 ml/l. However, warm eddies or filaments coming from the Agulhas Current retroflection area are a habitual feature in the area (Lutjeharms et al., 1991).

Deep water in the Cape Basin consists mainly of Circumpolar Deep Water (CDW), which enters the basin from the south (temperature = 0.7°C, salinity = 34.68‰, oxygen concentration = 4.2 ml/l and silica concentration = 125 μM) (Reid et al., 1977; Mantyla and Reid, 1983). The CDW can be distinguished from the North Atlantic Deep Water (NADW) in this region by the low concentrations of dissolved silica of the NADW (about 12 μM; Orsi et al., 1995). As discussed by Hodell et al. (2001), carbonate saturation in the Cape Basin decreases with depth conversely to an increase in the content of dissolved silica. The saturation horizon is associated with the boundary between the NADW and CDW, located at ca. 4000 m water depth.

3. Methods

3.1. Coccolith preparation and estimation of absolute abundance

Coccolith slides were prepared using the technique of Flores and Sierro (1997). Coccolithophore analyses were made at 1250× magnification using a polarized light microscope. Coccolith counts were performed in random visual fields on slides on which the coccoliths were homogeneously distributed. For each slide, a predetermined mass of sediment was taken. This procedure allows calculation of the number of coccoliths per gram of sediment. Nannofossil accumulation rates (NAR; coccoliths/(cm^2 kyr)) were calculated following the procedure described in Mayer et al. (1992): the number of coccoliths per gram was multiplied by the dry density and the linear sedimentation rate. Bulk densities were taken from the report given by the Shipboard Scientific Party (1999), and linear sedimentation rates were calculated using the oxygen isotope stratigraphy of Hodell et al. (2001, 2002). In addition, relative coccolith abundances of some species were also calculated and compared with fluctuations in NAR.

To obtain relative abundances, about 300 coccoliths larger than 3μm were counted per slide in a varying number of fields of view. Coccoliths smaller than 3μm were counted separately in the same number of fields of view. Rare species were counted in additional fields of view. In addition, routine scanning electron microscope (SEM) analyses were performed to evaluate the preservation of calcareous nannofossils in selected samples.

The slides analyzed are deposited in the Micropaleontological Collections at the University of Salamanca.

3.2. Preservation of coccoliths and foraminifers

Differential preservation of coccoliths at Site 1089 varies considerably. Most of the samples show a good-to-moderate degree of preservation, but severe dissolution also occurred, leading to coccolith-barren intervals at some levels (Fig. 2).

Differential dissolution is often visible on the

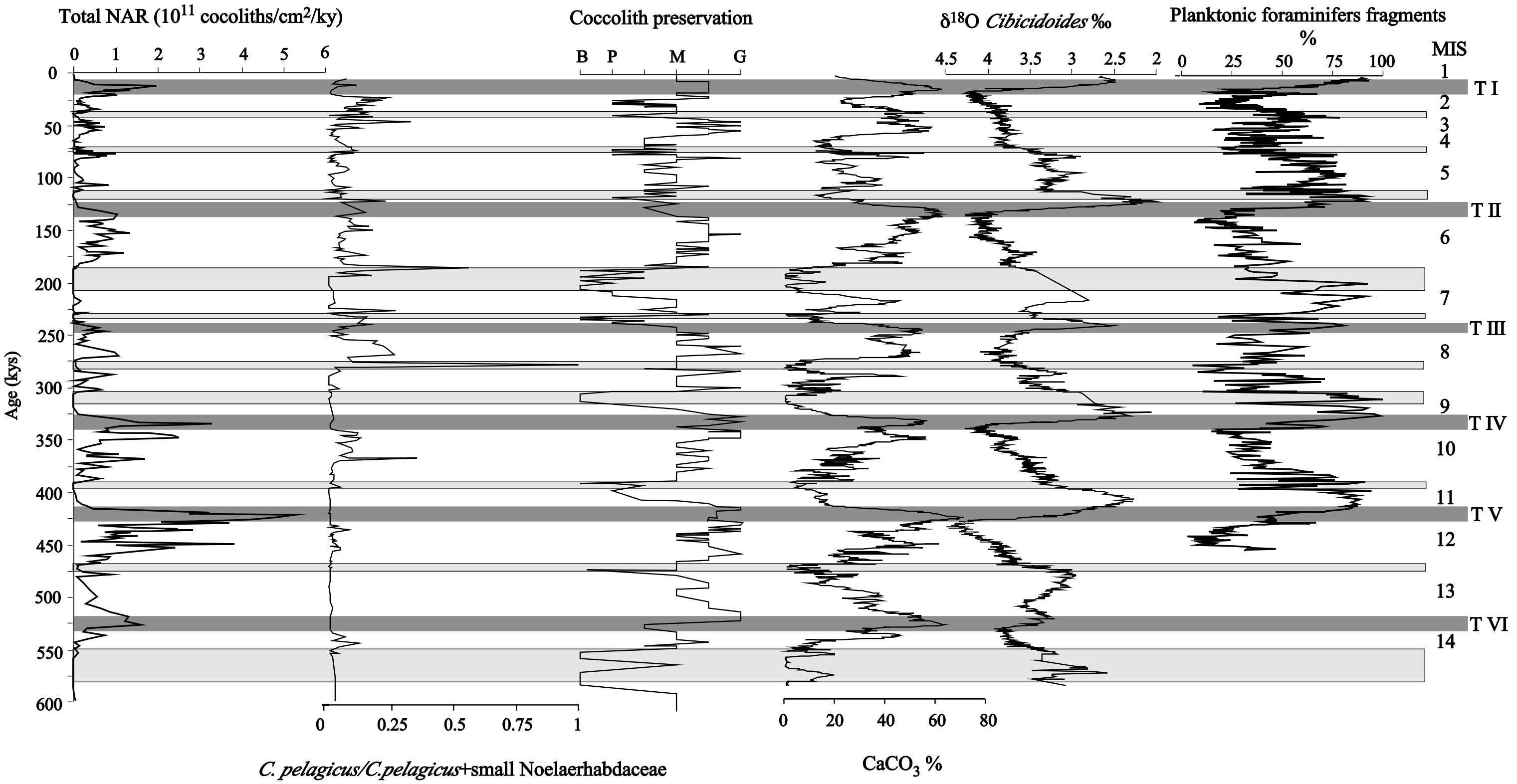

Fig. 2. Total accumulation rate of coccoliths (NAR, nannofossil accumulation rate), percentage of total calcium carbonate, planktonic foraminifer fragmentation and oxygen isotope record at ODP Site 1089. Shaded bands represent high-dissolution intervals. MIS, marine isotope stage; T, termination.

rims of the placoliths of *Gephyrocapsa muellerae* and *Emiliania huxleyi* or in the central area of syracosphaerids and pontosphaerids. However, species ranging from less dissolution-resistant to delicate (e.g. small delicate placoliths and caneoliths) are encountered throughout. Small specimens of *E. huxleyi* and 'small' *Gephyrocapsa*, which have lost their bridge, are difficult to distinguish by light microscopy. In such cases SEM was used to identify species. Overgrowth is not significant but etching was occasionally observed in the central area of *Coccolithus pelagicus* and *Gephyrocapsa oceanica*. Such observations on differential preservation were quantified in each sample, and four preservational categories were distinguished:

Good (G): little or no evidence of dissolution and/or secondary overgrowth of calcite, with fully preserved diagnostic characters.

Moderate (M): dissolution and/or secondary overgrowth with partially altered primary morphological characteristics. Despite this, nearly all specimens can be identified at species level.

Poor (P): severe dissolution, fragmentation, and/or secondary overgrowth. Primary features destroyed; many specimens cannot be identified at species and/or at generic level.

Barren (B): absence of coccoliths.

Two additional categories between good and moderate, and between moderate and poor, with intermediate features, were introduced to refine the pattern (Fig. 2).

Reworked calcareous nannofossils from the Miocene and Pliocene were observed, but remained at less than 0.01% throughout.

Samples from Marine Isotope Stages (MIS) 8–12 were wet-sieved at 62 and 150 μm and the > 150 μm fraction was analyzed in order to obtain a fragmentation index from the planktonic foraminifers. Samples were split to approximately 300 specimens and the percentage of fragmented-to-intact foraminiferal shells was calculated.

3.3. Calcium carbonate content and oxygen isotope analysis

Techniques and data concerning total calcium carbonate and oxygen isotope records are described in Hodell et al. (2001). Site 1089 was sampled at 5-cm intervals, resulting in a temporal resolution of approximately 350 yr. Total calcium carbonate contents were estimated (in %) with a precision of ±1%. Oxygen isotopes were measured in tests of *Cibicidoides wuellerstorfi* and *Cibicidoides kullenbergi* from the > 150 μm fraction. However, intense dissolution and the scarcity of benthic foraminifers during MIS 7 preclude a continuous benthic oxygen isotope record (Hodell et al., 2001, 2002). Accordingly, between 185 and 220 kyr was obtained by adding 0.6‰ to the $\delta^{18}O$ values of *Globigerina bulloides* (Figs. 2–4).

4. Taxonomic concept of coccolithophores

Most of the species identified in this study belong to the family Noelaerhabdaceae (reticulofenestrids including the genera *Emiliania*, *Pseudoemiliania*, and *Gephyrocapsa*) (Thierstein et al., 1977; Pujos-Lamy, 1977; Wei, 1993; Raffi et al., 1993; Weaver and Thomson, 1993; Flores et al., 1999, 2000) (Figs. 5 and 6). A complete list of the taxa is given in the Appendix. For the gephyrocapsids, we adopted the concept of Raffi et al. (1993) and the morphological terminology used here is summarized in Flores et al. (1999, 2000). *Calcidiscus leptoporus* is mainly represented by specimens smaller than 5 μm, which comprise the 'small' morphotype of Knappertsbusch et al. (1997), although larger specimens also occur occasionally.

Species observed in low proportions were grouped at genus level (Figs. 7 and 8). *Syracosphaera* consists mainly of *S. pulchra*, with few *S. anthos*. *Umbilicosphaera* is dominated by *U. sibogae*, whereas *Ceratolithus cristatus* is the most significant species of the genus *Ceratolithus*. Other, less abundant species are listed in the Appendix.

5. Stratigraphy

5.1. Age model and stable isotope record

For the present study, age assignments are based on Hodell et al. (2001, 2002). These authors

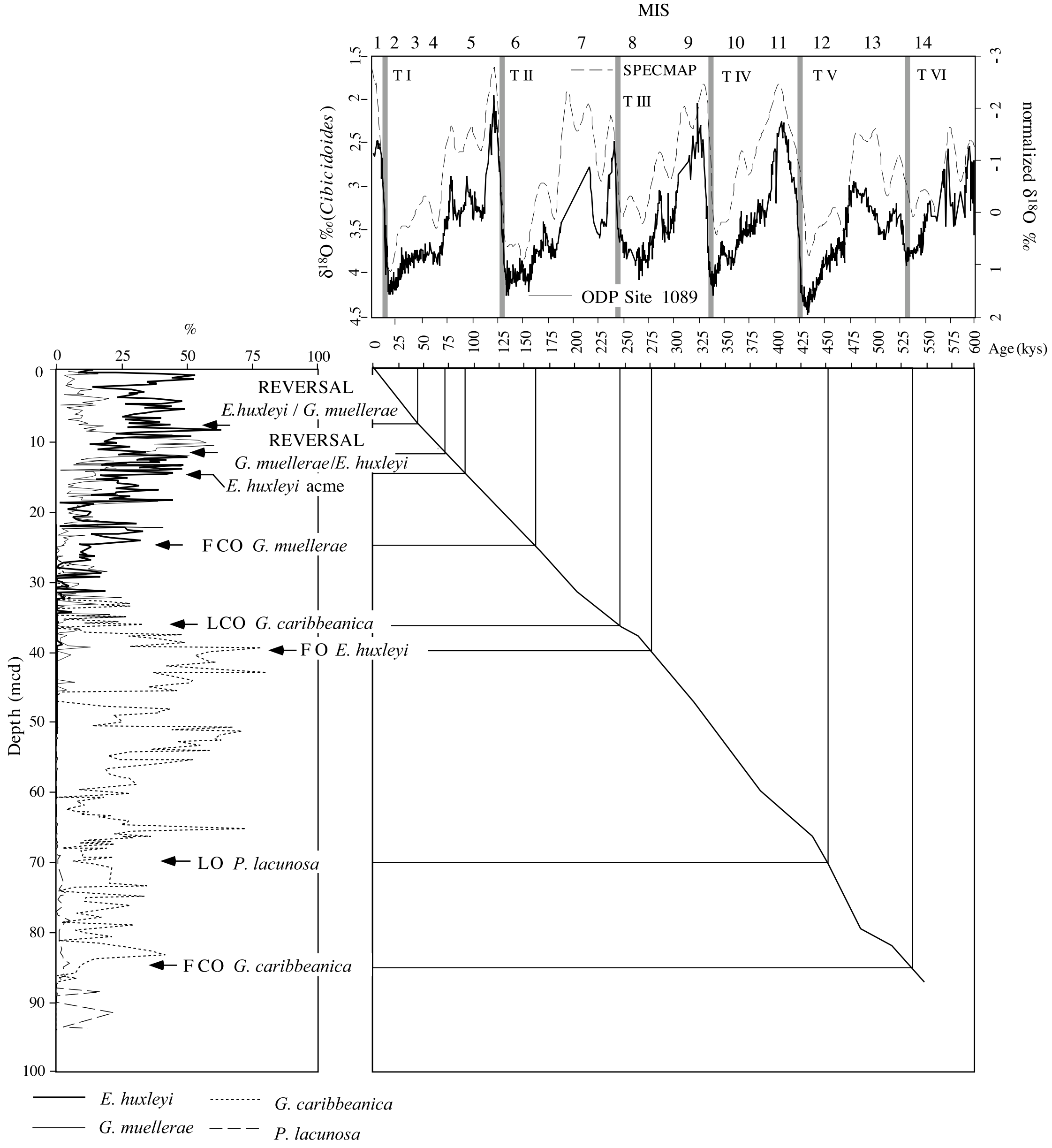

Fig. 3. Composite depth (mcd) vs. age (kyr) and calcareous nannofossil biostratigraphic events at ODP Site 1089, and their relationship with the oxygen isotope curve (after Hodell et al., 2001, 2002). The isotope data were obtained from the benthic foraminifer *Cibicidoides*, except for MIS 7, where planktonic foraminifers were analyzed. NAR, nannofossil accumulation rate; FO, first occurrence; LO, last occurrence; FCO, first common occurrence; LCO, last common occurrence; T, termination. Coccolith preservation: B, Barren; P, Poor; M, Moderate; G, Good (see text for definition).

describe a high-resolution oxygen isotope record correlated to the SPECMAP time scales of Martinson et al. (1987) and Imbrie et al. (1984) (included in Figs. 2 and 3). Sample ages in our study were obtained by linear interpolation on composite depths (Shipboard Scientific Party, 1999), which allowed us to calibrate several calcareous nannofossil events for this location.

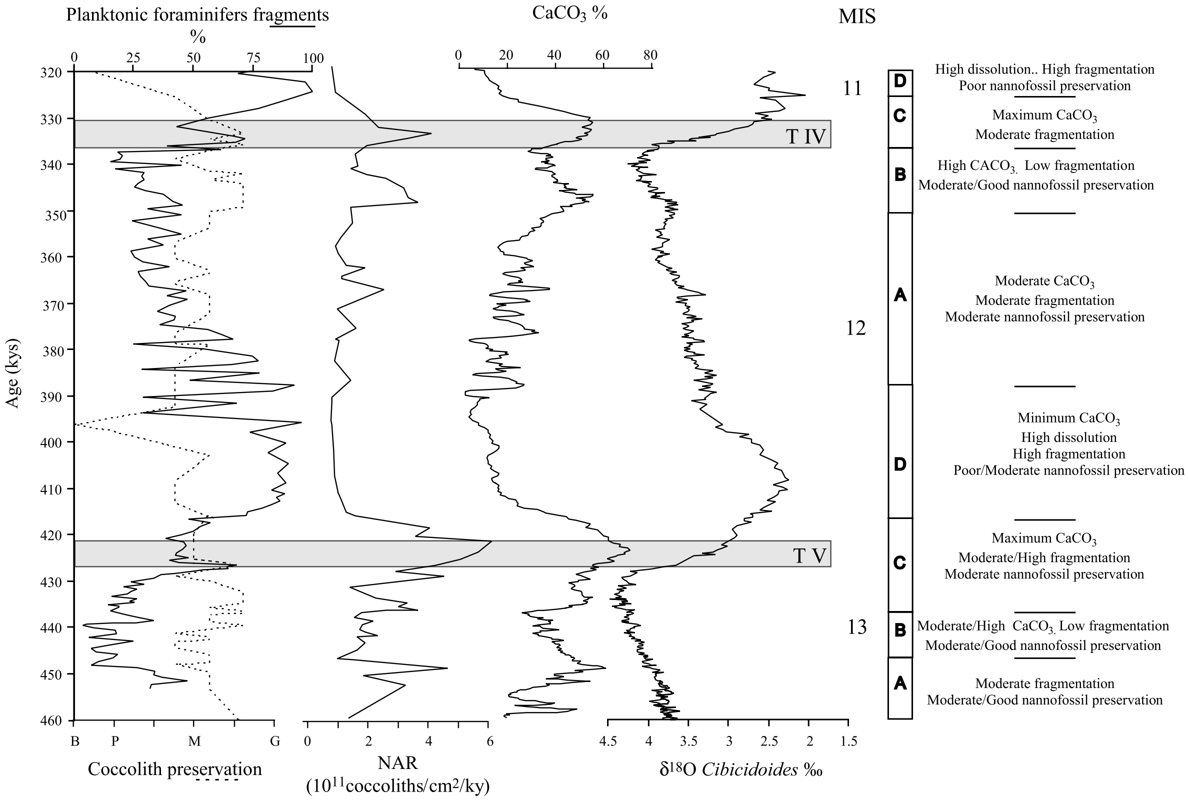

Fig. 4. Planktonic foraminifer fragmentation, coccolith accumulation rate, percentage of total calcium carbonate and oxygen isotope record between MIS 9 and 12. Detail of preservation vs. abundances in the calcium carbonate and coccolith record at ODP Site 1089. T, termination.

5.2. *High-resolution calcareous nannofossil stratigraphy*

In the upper part of the core at Site 1089, the following calcareous nannofossil events were calibrated to the SPECMAP timescale:

A well-defined reversal in *Emiliania huxleyi–Gephyrocapsa muellerae* was found at 8.6 mcd (meters of composite depth), at an age close to 45 kyr. This coincides with the results of Thierstein et al. (1977) in Cores V19-240 and V22-174 at MIS 2 and 3. Flores et al. (1997) observed the same event in the Mediterranean cores and estimated an age of 47 kyr (MIS 3). Wells and Okada (1997) reported a similar trend during MIS 2 for DSDP Site 594. Another reversal in dominance from *Gephyrocapsa muellerae* to *Emiliania huxleyi* (Fig. 3) was observed close to 12 mcd, at the base of MIS 4 (at an age close to 65 kyr). This event was initially identified by Thierstein et al. (1977) at the same age, both in low- and high-latitude sites in the ocean.

A relative increase in the proportion of *E. huxleyi* occurs at 14.8 mcd (85 kyr) and is interpreted as the base of the *E. huxleyi* acme zone (Thierstein et al., 1977). This is a diachronous and confusing event that is difficult to recognize in certain areas of the ocean (Jordan et al., 1996; Gartner, 1977; Novacyzk and Baumann, 1992; Flores and Marino, 2002).

The first common occurrence (FCO) of *G. muellerae* is found at 25 mcd (165 kyr; Table 1). This event has been reported previously by Flores et al. (1999, 2000) in MIS 6.

During MIS 7 (base) an important decrease occurs in the abundance of *Gephyrocapsa caribbeanica* (last common occurrence (LCO)) (Figs. 3 and 4), similar to the observations of Pujos-Lamy

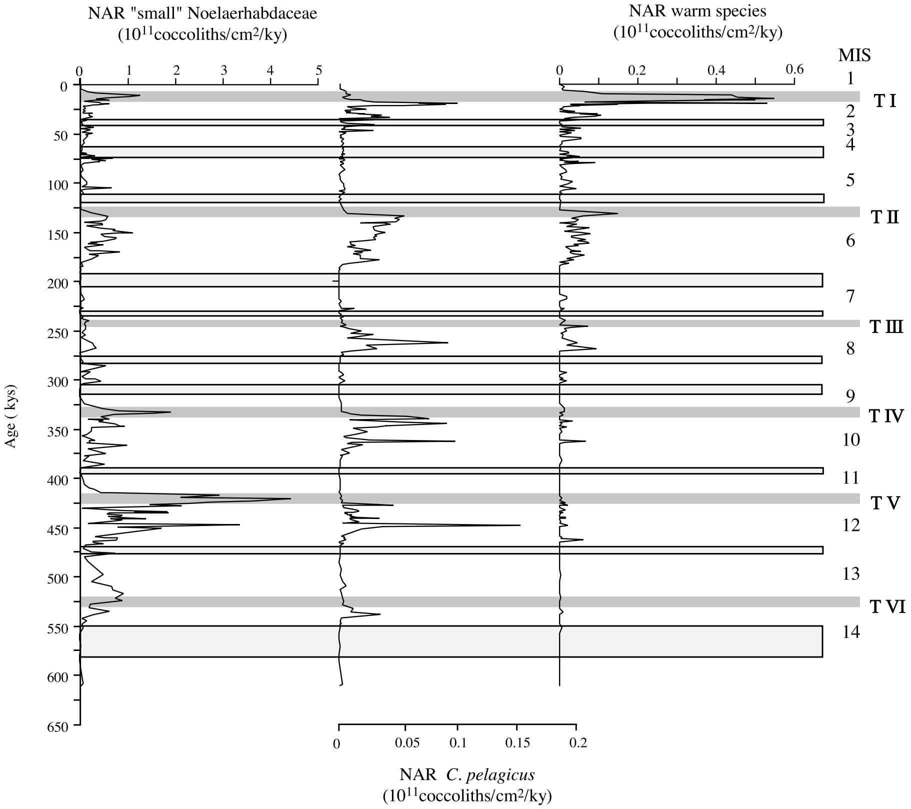

Fig. 5. Accumulation rates (NAR, nannofossil accumulation rate) of high productivity, cold (*Coccolithus pelagicus*) and warm coccolithophore indicators at ODP Site 1089. Shaded bands represent high-dissolution intervals. MIS, marine isotope stage. T I to T VI, terminations I–VI

(1977), Giraudeau and Pujos (1990), Weaver and Thomson (1993), Bollmann et al. (1998), Flores et al. (2000) and Flores and Marino (2002).

The first occurrence (FO) of *E. huxleyi*, dated by Thierstein et al. (1977) at 268 kyr (MIS 8), was found at 39 mcd (271 kyr).

The last occurrence (LO) of *Pseudoemiliania lacunosa* is well-calibrated at MIS 12 (Thierstein et al., 1977) and could be identified in Site 1089 at 447 kyr (Fig. 3 and Table 1). Very close to this event, at the top of MIS 14, we identified the FCO of *G. caribbeanica* (540 kyr), equivalent to the progressive increase in *Gephyrocapsa* sp. D observed by Matsuoka and Okada (1990) at ODP Site 709.

The nannofossil events identified and the ages

Table 1
Calibration (age) of the most significant coccolithophore biostratigraphic events at ODP Site 1089

Nannofossil event	mcd	age (kyr)
Reversal *E. huxleyi*/*G. muellerae*	8.57	44
Reversal *G. muellerae*/*E. huxleyi*	11.93	65
E. huxleyi acme (base)	14.81	85
FCO *G. muellerae*	25.49	165
LCO *G. caribbeanica*	36.31	249
FO *E. huxleyi*	39.07	271
LO *P. lacunosa*	69.27	447
FCO *G. caribbeanica*	85.17	540

FO, first occurrence; LO, last occurrence; FCO, first common occurrence; LCO, last common occurrence; mcd, meters of composite depth (after Shipboard Scientific Party, 1999).

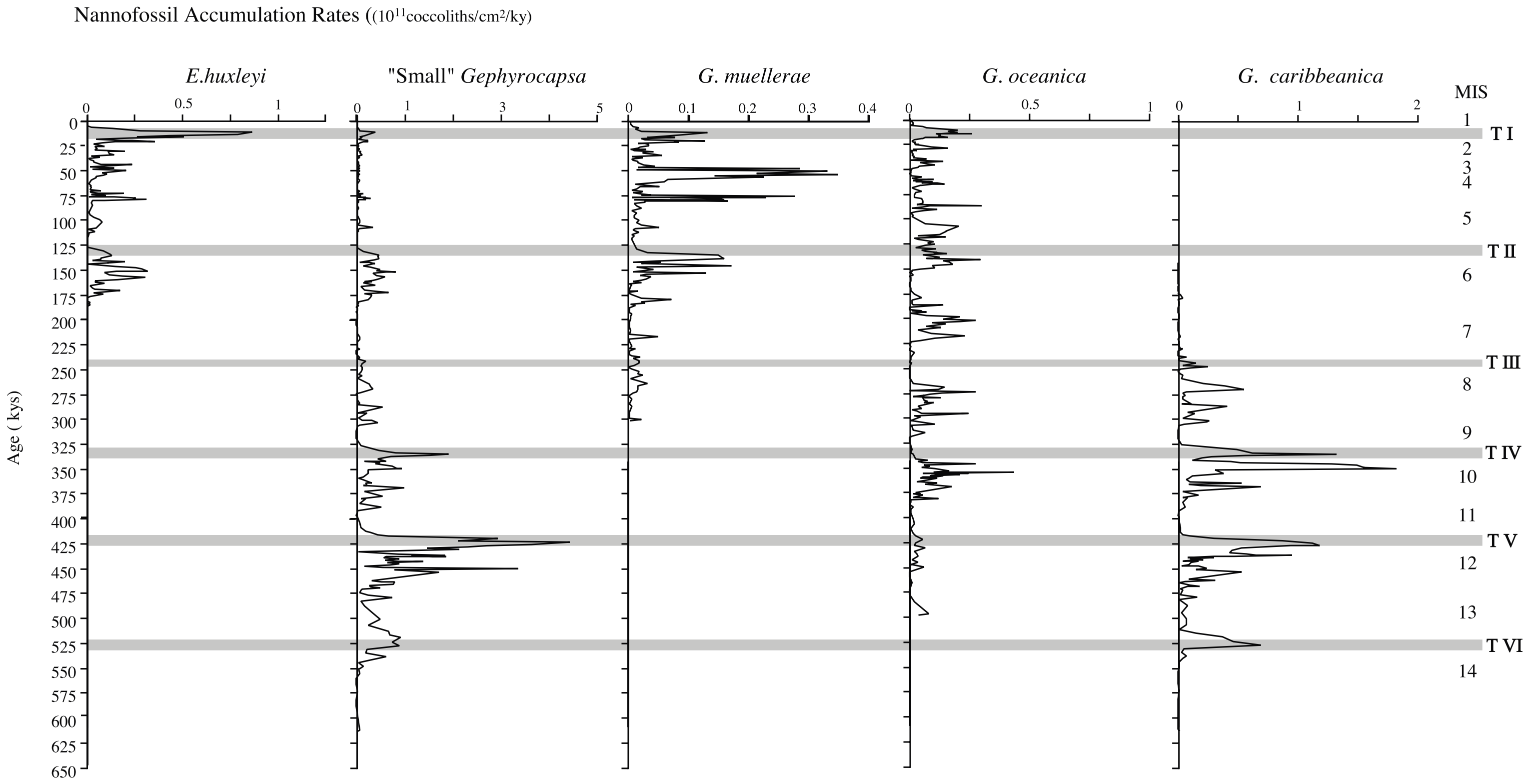

Fig. 6. Accumulation (NAR, nannofossil accumulation rate) rate of the most significant Noelaerhabdaceae species at ODP Site 1089. T I to T VI, terminations I–VI.

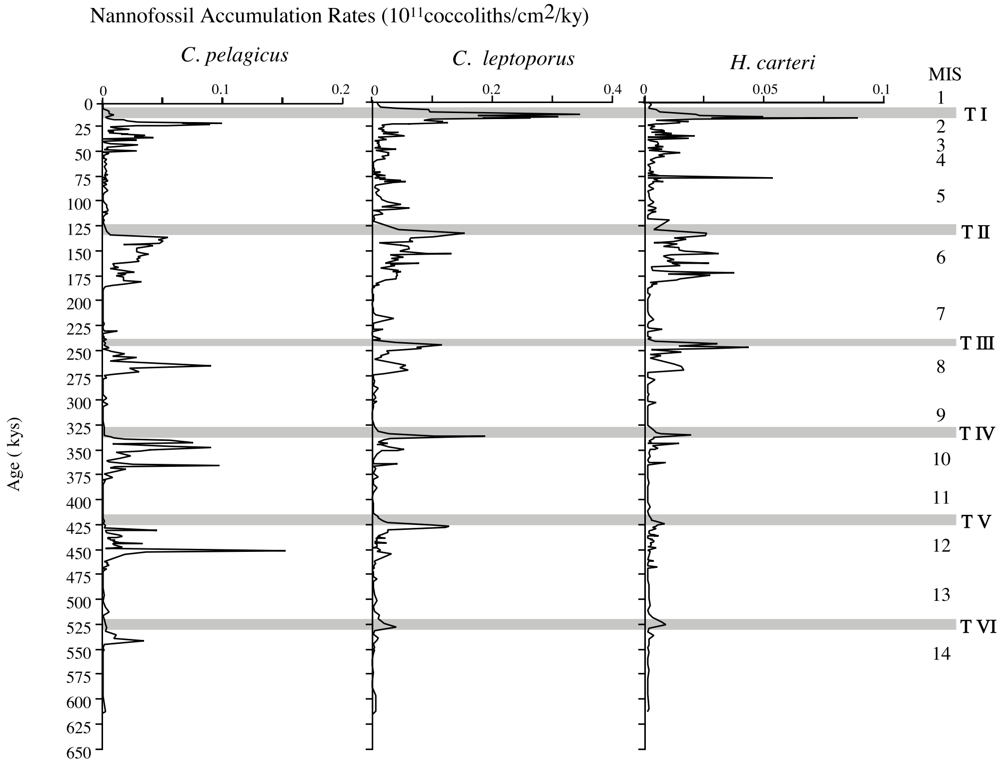

Fig. 7. Accumulation rate (NAR, nannofossil accumulation rate) of the most significant species at ODP Site 1089. T I to T VI, terminations I–VI.

assigned are shown in Fig. 3 and Table 1. Additional information and the precise abundances of the most significant species are shown in Figs. 6–8.

6. Results and discussion

6.1. Coccolith preservation versus production

According to the Shipboard Scientific Party (1999), for the interval investigated, calcareous nannofossils are the dominant component of the carbonate fraction. The accumulation of coccolithophores is mainly controlled by three processes: production, dissolution (including alteration during settling) and dilution (not considered here). High coccolith concentrations in the sediments may be the result of high coccolithophore productivity in surface waters or to low coccolith dissolution in water or at the sediment/water interface, or both. Conversely, low coccolith accumulation may result from low surface-water productivity or high dissolution. The highest coccolithophore accumulation and the highest calcium carbonate content occurred towards glacial periods and terminations, whereas minimum values are recorded in interglacial stages. As reported by Hodell et al. (2001), this pattern is consistent with an ‘Indo-Pacific’ type of carbonate stratigraphy. The carbonate preservation spike during terminations may reflect a redistribution of alkalinity and dissolved inorganic carbon (DIC) in the ocean (‘carbonate compensation’) (Broecker and Peng, 1987; Sigman and Boyle, 2000). Also, the carbonate signal in glacial and interglacial episodes may represent a lag in response to sea-level changes, where the lysocline controls the balance between riverine carbonate input and marine carbonate loss through burial (‘steady-state’ model).

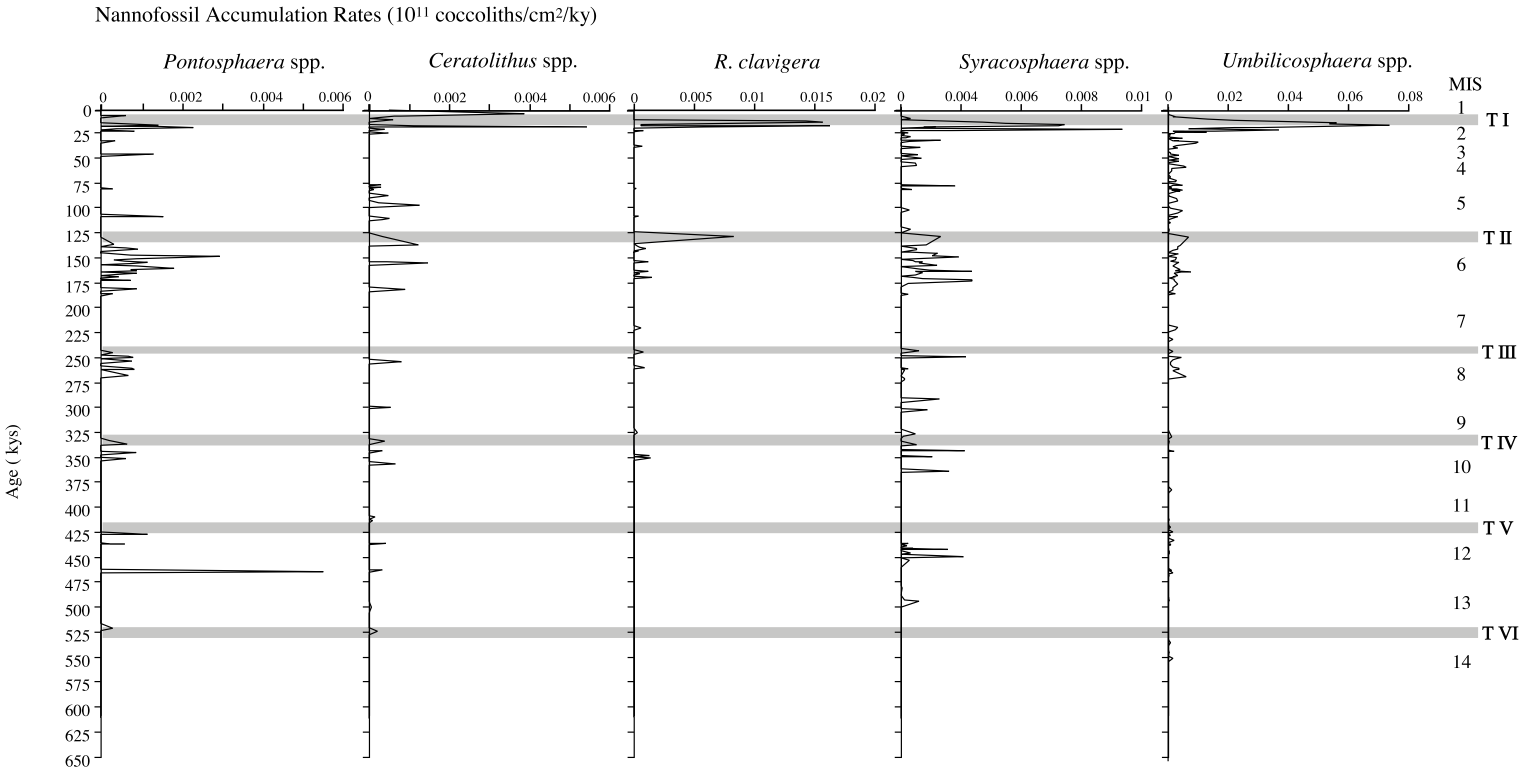

Fig. 8. Accumulation rate (NAR, nannofossil accumulation rate) of rare coccolithophore species at ODP Site 1089 T I to T VI, terminations I–VI.

Although dissolution seems to play an important role in the calcium carbonate record, detailed analysis of the coccolithophore assemblages reveals that processes other than dissolution may also have affected the accumulation patterns of these autotrophic algae during the late Pleistocene. In this sense, during intervals with strong dissolution coccolithophore assemblages were affected and, consequently, their paleoecological significance is hidden. This is especially significant in the intervals devoid of coccoliths. However, the rest of the intervals show degrees of coccolith preservation that are between moderate and good, allowing comparisons of the abundances of different taxa for paleoecological approaches. Studying planktonic foraminifers at ODP Site 1090 (3° south of Site 1089), Becquey and Gersonde (2002) commented that, although the carbonate dissolution record exhibits high variability during the Pleistocene, it can be shown that surface-water temperature estimates as obtained by foraminiferal census were not significantly biased. Another important feature to take into account is the ratio between dissolution-resistant vs. less resistant species. *Coccolithus pelagicus* is constituted by robust coccoliths, resistant to dissolution (Roth and Berger, 1975; Roth, 1994). The ratio between this species and other, less resistant ones, such as small placoliths during interglacials, suggests that dissolution did not substantially affect the assemblages.

Barren intervals are observed at the end of interglacials, close to the transition to glacials, following an orbital pattern (Milankovitch-related) (Fig. 2). During these warm periods, the position of the SPF was far more to the south than the present-day location of Site 1089 (Becquey and Gersonde, 2002; Cortese and Abelmann, 2002), in the SAZ, where coccolithophores are always present. This means that the intervals devoid of coccoliths are not ecological but preservational.

A comparison of the degrees of coccolith and foraminifer preservation may help to better understand the calcium carbonate record. The relationship between foraminiferal fragmentation and dissolution is a non-linear function at low carbonate ion concentrations (Le and Shackleton, 1992). During times of severe dissolution, total fragmentation begins to decrease with increasing dissolution because small fragments are completely dissolved at this time. In this study, the fragmentation index was calculated for the whole interval studied, with special attention to the interval from MIS 8 to 12. For the MIS 1–10 interval, maxima in calcium carbonate coincide with low fragmentation index values. One exception is seen during MIS 8, where high calcium carbonate concentrations coincide with marked planktonic foraminiferal fragmentation (Fig. 2). During the early part of glacial cycles MIS 10 and 12, foraminiferal fragmentation changes from high-to-moderate to high, and coccolith preservation from moderate to good, is followed by an interval of low dissolution (good preservation) during the glacial maximum (Fig. 4). The carbonate and coccolith preservation records suggest that maximum dissolution occurred during the transition from interglacial to glacial stages (Fig. 2). Low foraminiferal fragmentation values at times of maximum dissolution may be explained by the artifact described by Le and Shackleton (1992). At the end of glacial maxima in MIS 10 and 12, shortly before the terminations, dissolution started to increase moderately during the early part of the interglacial stage and became very strong at the end of the interglacial period. The low values of foraminiferal fragmentation at times of glacial maxima (MIS 10 and 12) coincide with high coccolith (and calcium carbonate) abundance. However, the preservation maxima in planktonic foraminifers (low fragmentation) and coccoliths are not in phase with the maxima in coccolithophore abundance, as would be expected if coccolith abundance were controlled only by dissolution. Coccoliths and calcium carbonate levels reached their maximum concentrations during terminations IV and V (when relatively high values in the fragmentation index are seen), whereas dissolution was at a minimum during glacial maxima before terminations (Fig. 4). This means that this record was not only controlled by dissolution. However, this pattern is not observed during terminations I, II and III (Hodell et al., 2001), where maxima in calcium carbonate coincide with low planktonic foraminifer fragmentation.

6.2. Coccolithophore assemblages

As discussed, we consider that the coccolithophore assemblages were modified in the high-dissolution intervals, although most of the record offers enough information to reconstruct environmental conditions and reflects the calcium carbonate record. Coccoliths were abundant and well preserved during terminations, and were rare and strongly dissolved during the transition from interglacial to glacial stages (Figs. 2 and 5). The assemblages are mainly constituted by 'small' Noelaerhabdaceae species (*Emiliania huxleyi*+*Gephyrocapsa ericsonii*+*Gephyrocapsa aperta*), whose absolute and relative abundances increased in upwelling areas or episodes of high (paleo)productivity (Wells and Okada, 1997; Flores et al., 1999; Bollmann et al., 1998) (Figs. 5 and 6).

Sea surface-water temperature (SST) is an important factor controlling coccolithophore assemblages. *Gephyrocapsa muellerae* is considered to be a cold form that today inhabits mesotrophic waters (Bollmann, 1997). An increase of this species occurred during MIS 2, 4 and 6. Down-core this species almost disappears. *Gephyrocapsa caribbeanica*, included by Bollmann (1997) under the denomination of GO (*Gephyrocapsa* Oligotrophic), is today considered a warm and oligotrophic morphotype. At Site 1089, this taxon seems to follow a similar pattern to that observed for *G. muellerae*: during the early part of MIS 8 it was frequent, but became less abundant during the upper part of MIS 8 (where *G. muellerae* increased), important peaks being observed during MIS 10, 12 and terminations IV, V and VI (Figs. 6 and 7). This observation allows us to suggest that the same factors (not necessarily SST) may have controlled the abundance of these species in the past. Another open question is the real taxonomic equivalence between the recent and the older morphotypes, not discussed here.

Coccolithus pelagicus is a species traditionally considered as a cold-water indicator (McIntyre and Bé, 1967; Winter et al., 1994), although other authors have associated it with increased productivity (Cachão and Moita, 1995). At Site 1089, the abundance of *C. pelagicus* was highest during glacial periods, and declined before terminations (Figs. 5 and 7). Other species usually related to warm water masses (*Umbilicosphaera* spp., *Rabdosphaera* spp., and *Pontosphaera* spp.; Winter et al., 1994) do not show any clear correlation with the isotope record. The sum of these warm-water indicators is plotted in Fig. 5, where a similar trend as that observed in *C. pelagicus* is seen, although here maximum values occurred during terminations I and II. We suggest that factors other than temperature alone may have influenced the abundance of these species. For example, Giraudeau et al. (1993) observed an increase in this warm species below the thermocline in the Benguela Current, suggesting a closer relationship with nutrient concentrations.

In this region, other frequent species, such as *Calcidiscus leptoporus*, are considered to be warm-water indicators (Gard and Crux, 1991; Flores et al., 1999), relatively abundant in the present-day SAZ (Eynaud et al., 1999). At Site 1089, the maximum values of *C. leptoporus* are recorded during glacial periods and terminations (Fig. 7). A similar pattern to that observed for *C. leptoporus* is seen for *Helicosphaera carteri*, opposite to that of *C. pelagicus*. The parallel distribution observed between *C. leptoporus* and *H. carteri* with the 'small' Noelaerhabdaceae suggests a relationship with high-productivity environments.

Other species, such as *Gephyrocapsa oceanica*, are associated with warm-water conditions (Winter et al., 1994; Flores et al., 1999) and are abundant north of the STC (Eynaud et al., 1999). Bollmann (1997) identified the GE (*Gephyrocapsa* Equatorial) and GL (*Gephyrocapsa* Larger) morphotypes of *G. oceanica*. These morphotypes are associated with equatorial temperate waters and high-productivity waters, respectively. At Site 1089 we counted both morphotypes together, because we observed continuity in size among specimens. At Site 1089 the record of *G. oceanica* does not follow any clear pattern. Minimum values occurred during terminations (both in the late glacial and early interglacial), except for termination I, where the species was abundant. This record is the converse of that of 'small' Noelaerhabdaceae, and is perhaps related to more oligotrophic conditions.

6.3. Coccolithophore paleoecology and frontal systems

The late Pleistocene coccolithophore assemblages at Site 1089 show two trends: First, variations in the abundance of some species, such as *Coccolithus pelagicus*, are linked to glacial–interglacial cycles and are probably temperature-controlled. Hodell (1993) and Howard and Prell (1992) interpreted northward and southward displacements of the APF during glacial and interglacial periods, respectively. Changes in the abundances of cold species could be linked to these processes. The low abundances of *C. pelagicus* during the Holocene and interglacial periods suggest that sea surface temperatures were similar to modern conditions during these intervals. The increase in *C. pelagicus* during glacial periods indicates a cooling of surface waters. However, during glacials and the base of interglacials (with the exception of the coccolith-barren samples), the coccolithophore assemblage is similar, characteristic of the SAZ. Currently, assemblages recorded south of the Polar Front (PF) are monospecific (*Emiliania huxleyi*) (Eynaud et al., 1999), a phenomenon never observed along the core. Although these data must be taken with caution, because they represent only a year's data set, they do suggest assemblages developed north of the SPF. The continuous record of warm-water (subtropical) species (Fig. 5) is consistent with this idea, suggesting that during the last 600 kyr the PF was always situated south of ODP Site 1089 (~41°S) and that it was probably influenced by warm-water eddies or filaments, as today (Lutjeharms, 1996). However, important changes in temperature may have occurred during the period studied: the abrupt decrease in the abundance of *C. pelagicus* observed during terminations I and II, as well as its high abundances during cold periods, are in agreement with the data reported by Cortese and Abelmann (2002) for the same site, where they found important drops in temperature. This characteristic is also maintained for the warmest MIS 9 and 11 and during the coldest MIS 12, although recent data suggest strong fluctuations between glacial and interglacial periods at Site 1090, 3° south of Site 1089, PFZ conditions being reached during MIS 6, 8, 10 and 12 (Becquey and Gersonde, 2002).

However, as discussed in Section 6.2, the general abundance pattern of the coccolithophore assemblages seems to be controlled by more factors than temperature alone (light, nutrient content, temperature, seasonality, grazing pressure, trace elements, etc.). According to Berger and Wefer (1996) for the region studied, 'to a first approximation, it is seen that wind intensity is perhaps the single most important factor in producing the overall productivity pattern'. 'Small' Noelaerhabdaceae, such as *E. huxleyi* and *Gephyrocapsa* smaller than 3 μm, have been considered as upwelling indicators (Wells and Okada, 1997). The distribution of 'small' Noelaerhabdaceae at Site 1089 over the past 600 kyr can be subdivided into three periods (Fig. 6), as follows.

6.3.1. MIS 1–7

Between MIS 1 and 7 maximum productivity occurred during cold periods, including terminations I and II, which we interpret as a direct influence of the SAF. For this interval, maximum values are seen for *Calcidiscus leptoporus* during terminations. Typical warm-water markers, such as genus *Umbilicosphaera*, although recorded in very low proportions, are related to a high-productivity environment rather than to warm surface-water masses.

6.3.2. MIS 8–11

A different situation prevailed for the interval between MIS 8 and 11. This interval is characterized by the dominance of *Gephyrocapsa caribbeanica*. Species such as *Coccolithus pelagicus*, *C. leptoporus* and *Helicosphaera carteri* show peaks during glacials and terminations. According to Hodell (1993), who studied ODP Hole 704A, MIS 9 and 11 had the lowest $\delta^{18}O$ values of the last 3.2 Ma, indicating unusually high temperatures and a very southerly position of the PFZ in the Southern Atlantic Ocean (such observations are consistent with high coccolithophore level abundances and high calcium carbonate concentrations at this ODP site; Gard and Crux, 1991). However, Hodell et al. (2001) modified this interpretation and found that stage 11 did not have lower $\delta^{18}O$ values than other interglacial stages of the late Pleistocene. At Site 1089 we observed the highest degree of dissolution and a relatively low proportion of cool-water indicators during MIS 9. The southward displacement of the PFZ must have been accompanied by a concurrent southward displacement of the STF (Hodell, 1993; Howard and Prell, 1992). Flores et al. (1999) observed a reduction in subtropical species in this interval, which was dominated by *G. caribbeanica*. However, we cannot confirm a major increase in temperature in the study region. The different concentrations and compositions during MIS 9 and 11 of the calcareous nannoplankton assemblages reflect major paleoceanographic changes (described in the previous section) that are not yet understood but that do coincide with the Mid-Brunhes event, which for MIS 11 resulted in an increased carbonate production (Howard and Prell, 1994; Howard, 1997; Hodell et al., 2000). For this interval, Jansen et al. (1986) reported an intensified atmospheric and oceanic circulation in the Southern Hemisphere, linked to a perturbation due to the orbital eccentricity cycle of 413 kyr. In the same way, Hodell et al. (2000) reported high productivity in the Southern Ocean for this period, which linked upwelling of the CDW lower whole-ocean nutrient inventories, higher gas exchange rates, and/or lowered alkalinity of Antarctic surface waters. Additionally, these authors suggest that MIS 11 was not substantially different from other interglacials at high southern latitudes (except that it was longer in duration). It is interesting to note the development of the relatively 'highly-calcified' coccolithophore species *G. caribbeanica* during this interval (Bollmann et al., 1998; Flores et al., 1999). This micropaleontological event is observed in all oceans at fairly broad latitudes, but it is not certain whether the increase in this taxon represents a biological response to an increase in carbonate ion concentrations in surface waters, or whether the increase contributed to the (global?) production of carbonate at this time; or, as suggested by Bollmann et al. (1998), although not well documented yet, a response to global change in the depth of the thermocline. Thus, the relationship between the present-day and fossil assemblage of the so-called *G. caribbeanica* needs clarification, and does not necessarily respond in the same way to the same factors.

6.3.3. MIS 12–14

During the interval from MIS 12 to 14, we observed maximum coccolithophore production within termination VI. However, it is important to note that gephyrocapsid assemblages may have changed their environmental dependences and preferences through evolutionary processes (Bollmann et al., 1998), and this consequently masks the real meaning of these organisms at this time.

In sum, at Site 1089, for the last 600 kyr, we have observed an increase in the production of coccolithophores during glacials and terminations. This observation agrees with the 'Upwelled Iron Hypothesis' of Latimer and Filippelli (2001), who proposed an increase in nutrients in surface water (including iron) during glacial periods, suggesting a relationship between nutrient supply and coccolithophore production. This will be studied in the near future

7. Conclusions

Coccolithophore assemblage variations and abundances reveal orbital-scale changes in dissolution and surface-water dynamics at ODP Site 1089.

Dissolution partially controlled the coccolithophore flora over the last 600 kyr, with strong dissolution occurring during the latest interglacial and the transition from interglacial to glacial periods. However, with the exception of strongly dissolved intervals, a moderate-to-good degree of preservation in the coccolithophore assemblages allows us to reproduce past surface-water characteristics.

These intervals, sometimes barren in coccoliths, are linked to changes in the position of the lysocline rather than to episodes with restrictions for the development of coccolithophores (ecological). Although we observed variations in the coccolithophore pattern over time, we conclude that the PF was always south of 42°S.

High coccolithophore production was probably the cause of the sharp increases during glacial maxima; these increases may have been driven by increased surface nutrient supplies. During terminations IV and V (episodes of high abundance in calcium carbonate), intervals of moderate to poor preservation are interpreted as episodes of relatively high production.

The dominance of relatively highly calcified *Gephyrocapsa caribbeanica* between MIS 9 and 13 coincides with the high carbonate content observed for this interval. The similar behavior of *G. caribbeanica* and *G. muellerae* (as well as other cold-water indicator species) suggests a change in the ecological conditions of this species over time, and/or taxonomic discrepancies between the present-day and fossil specimens.

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Taxonomic appendix

Calcidiscus leptoporus (Murray and Blackman, 1898) Loeblich and Tappan, 1978

Ceratolithus cristatus Kamptner, 1950

Ceratolithus telesmus Norris, 1965

Coccolithus pelagicus (Wallich, 1877) Schiller, 1930

Emiliania huxleyi (Lohmann, 1902) Hay and Mohler in Hay et al., 1967

Gephyrocapsa caribbeanica Boudreaux and Hay, 1967

Gephyrocapsa muellerae Bréhéret, 1978

Gephyrocapsa oceanica Kamptner, 1943

Gephyrocapsa omega Bukry, 1973

Very small *Gephyrocapsa* (>3 μm)

Gephyrocapsa ericsonii McIntyre and Bé, 1967

Gephyrocapsa aperta Kamptner, 1963

Helicosphaera carteri (Wallich, 1877) Kamptner, 1954

Pseudoemiliania lacunosa (Kamptner, 1963) Gartner, 1969

Pontosphaera multipora (Kamptner, 1948) Roth, 1970

Pontosphaera discopora Schiller, 1925

Syracosphaera pulchra Lohmann, 1902

Syracosphaera anthos (Lohmann, 1912) Jordan and Young, 1990

Umbilicosphaera sibogae (Weber-van Bosse, 1901) Gaarder, 1970

Umbilicosphaera hulburtiana Gaarder, 1970

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