

# BERICHTE

aus dem Fachbereich Geowissenschaften  
der Universität Bremen

No. 148

Kinkel, H.

**LIVING AND LATE QUATERNARY COCCOLITHOPHORES  
IN THE EQUATORIAL ATLANTIC:  
RESPONSE OF DISTRIBUTION AND PRODUCTIVITY PATTERNS  
TO CHANGING SURFACE WATER CIRCULATION**

Berichte, Fachbereich Geowissenschaften, Universität Bremen, No. 148,  
183 pages, Bremen 2000



ISSN 0931-0800

The "Berichte aus dem Fachbereich Geowissenschaften" are produced at irregular intervals by the Department of Geosciences, Bremen University.

They serve for the publication of experimental works, Ph.D.-theses and scientific contributions made by members of the department.

Reports can be ordered from:

Gisela Boelen

Sonderforschungsbereich 261

Universität Bremen

Postfach 330 440

**D 28334 BREMEN**

Phone: (49) 421 218-4124

Fax: (49) 421 218-3116

e-mail: [boelen@uni-bremen.de](mailto:boelen@uni-bremen.de)

Citation:

Kinkel, H.

Living and late Quaternary Coccolithophores in the equatorial Atlantic Ocean:

response of distribution and productivity patterns to changing surface water circulation.

Berichte, Fachbereich Geowissenschaften, Universität Bremen, No. 148, 183 pages, Bremen, 2000.

## Der Zweifler

Immer wenn uns

Die Antwort auf eine Frage gefunden schien  
Löste einer von uns die Schnur der alten  
Aufgerollten chinesischen Leinwand, so daß sie  
herabviel und  
Sichtbar wurde der Mann auf der Bank, der  
So sehr zweifelte.

Ich, sagte er uns  
Bin der Zweifler, ich zweifle, ob  
die Arbeit gelungen ist, die eure Tage verschlungen hat.  
Ob was ihr gesagt, auch schlechter gesagt, noch für  
einige  
Wert hätte.  
Ob ihr es aber gut gesagt und euch nicht etwa  
Auf die Wahrheit verlassen habt, dessen was ihr gesagt  
habt.  
Ob es nicht vieldeutig ist, für jeden möglichen Irrtum  
Tragt ihr die Schuld. Es kann auch eindeutig sein  
Und denn Widerspruch aus denn Dingen entfernen; ist es  
zu  
eindeutig?  
Dann ist es unbrauchbar was ihr sagt. Euer Ding ist  
dann  
leiblos.  
Seid ihr wirklich im Fluß des Geschehens?  
Einverstanden mit  
Allem was wird? Werdet ihr noch? Wer seid ihr? Zu  
wem  
Sprecht ihr? Wem nützt es was ihr da sagt? Und  
nebenbei:  
Läßt es euch auch nüchtern? Ist es am morgen zu lesen?  
Ist es auch angeknüpft an Vorhandenes? Sind die Sätze,  
die  
Vor euch gesagt sind benutzt, wenigstens widerlegt? Ist  
alles  
belegbar?  
Durch Erfahrung? Durch welche? Aber vor allem  
Immer wieder vor allem anderen: wie handelt man  
Wenn man glaubt, was ihr sagt? Vor allem: wie handelt  
man?

Nachdenklich betrachten wir mit Neugier den  
zweifelnden  
Blauen mann auf der Leinwand, sahen uns an und  
Begannen von vorne.

*Berthold Brecht*



---

## Preface

The enhanced burning of fossil fuels since the industrial revolution and other manmade activities, lead to an increase in the atmospheric CO<sub>2</sub> content measured at time series stations, as Mauna Loa, Hawaii (Keeling et al., 1996). Though still under debate, it is believed, that the rise of CO<sub>2</sub> and other gases (e.g. methane) can cause a green house effect, leading to a global warming. Yet the consequences of this process are not fully understood and the magnitude of global warming, predicted by models, need further evaluation. Looking back in earth history large changes in atmospheric CO<sub>2</sub> contents are documented in gas bubbles captured in the ice caps of both hemispheres, which are linked to the last two major glaciation cycles (Barnola et al., 1987). The investigation of ultra high resolution marine records show that changes from full glacial to full interglacial conditions were abrupt, occurring within a few decades, rather than on longer time scales (Broecker, 1997). This points out how sensitive our global climate system was and is, even without the massive interference of mankind.

Coccolithophores do not only record these climatic changes in the form of their well preserved fossil assemblages, which form a large part of the carbonate sediments covering the ocean floor, in addition they may produce various direct climate feedbacks due to their biogeochemical and optical behaviour (Westbroek et al., 1993).

This study was carried out within the Special Research Project (Sonderforschungsbereich, SFB) 261 "The South Atlantic in the Late Quaternary: Reconstruction of material budget and current systems" at the University Bremen, funded by the German Science Foundation. The interdisciplinary approach of this project enabled to discuss the coccolithophore data acquired in this study within a larger context.

For reasons of consistent presentation English is used in every part. All data presented here are archived in the PANGAEA database at the Alfred Wegener Institute for Polar and Marine Research (<http://www.pangaea.de>).

---



---

## Table of contents

Preface	
Table of contents	
<b>Part I</b> <i>Introduction : 1. Investigation history and biology of coccolithophores</i>	1
1.1 Historical Background	1
1.2 Coccolith formation	2
1.3 Function of coccoliths	4
1.4 Coccolithophore ecology and biogeography	5
1.5 Coccolithophores and Global Biogeochemical Cycles	6
<i>Introduction : 2. Purpose of this study</i>	10
2.1 Coccolithophores as paleoceanographic proxies in the equatorial Atlantic	10
2.2 (Paleo)oceanography of the equatorial Atlantic	11
2.2 The use of coccoliths as proxies for carbonate dissolution	13
2.2 The micropaleontological and organic geochemical record of coccolithophores	13
3. References	15
<b>Part II</b> <i>Publications</i>	21
1. Baumann, K.H., Cepek, M. and Kinkel, H. (in press) Coccolithophores as indicators of ocean water masses, surface water temperature, and paleoproductivity - examples from the South Atlantic. In: Fischer G., Wefer G. (eds), Proxies in paleoceanography. Springer-Verlag Berlin Heidelberg	21
2. Kinkel, H., Baumann, K.-H. and Cepek, M. (in press) Coccolithophores in the equatorial Atlantic Ocean: response to seasonal and Late Quaternary surface water circulation. Marine Micropaleontology	61
3. Kinkel H., Dittert N., and Henrich R. (subm) Calcareous plankton record of the Equatorial Atlantic: A 300 kyrs record of climate feedback, productivity and dissolution. submitted to: Paleogeography, Palaeoclimatology, Palaeoecology	93
4. Dittert N., Baumann K.-H., Bickert T., Henrich R., Huber R., Kinkel H., and Meggers H. (in press) Carbonate dissolution in the deep ocean: Methods, quantification and paleoceanographic application. In: Fischer G., Wefer G. (eds), Proxies in paleoceanography. Springer-Verlag Berlin Heidelberg	117
5. Kinkel, H., Baumann, K.-H., Cepek, M., Müller, P.J. and Rühlemann, C. Comparison of coccolithophore numbers and alkenone concentrations in Late Quaternary sediments from the South Atlantic. to be submitted	157
<b>Part III</b> <i>Conclusions and perspectives</i>	173
<b>Part IV</b> <i>Appendix</i>	178
Taxonomy	178
Plates	180
Danksagung (Acknowledgements)	183

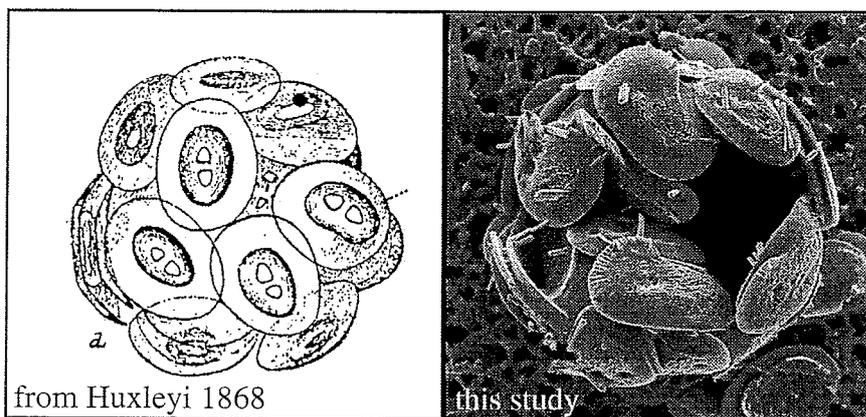
---



## I. Introduction

### 1.1 Historical Background

When Christian Gottfried Ehrenberg observed the first coccoliths in chalk samples from the island Rügen in the Baltic Sea more than 160 years ago, he believed they were of inorganic origin (Ehrenberg, 1836). In subsequent publications Ehrenberg described those ovoid minerals names as "calcareous morpholite" and "Crystalldrusen" and he was still convinced that they were rather concretions, than microfossils. More than 20 years later it was the biologist Thomas H. Huxley, who gave the name coccoliths to the "very curious rounded bodies" he saw when he examined seafloor samples, that were recovered from the North Atlantic during soundings for the first Trans-Atlantic telegraph cable in 1858 (Dayman, 1858). The first coccospheres were described almost simultaneously by G.C. Wallich and H.C. Sorby in 1861 (Wallich et al., 1861). It was also Sorby, who suggested that coccoliths were of organic origin contradicting the statements of Huxley, who, in accordance with Ehrenberg, believed coccoliths were concretions (Sorby, 1861).



*Helicosphaera carteri*

Fig.I.1 The left drawing shows what Huxley called a coccosphere of the "loose type", from the *Cyclops* samples recovered from the North Atlantic in 1857. For comparison there is a SEM picture of *Helicosphaera carteri*, from plankton samples of the equatorial Atlantic.

From the observation, that coccospheres and foraminifers occurred in highest abundances in the same samples, and sometimes were found attached to foraminifera shells and looked a little bit like juvenile globigerinids, Wallich (1861) concluded, they were larvae of foraminifera. However, the different optical properties of coccolith and foraminiferal calcite, lead Sorby (1861) to the conclusion that coccospheres were independent organism groups.

In the following years the most important studies on coccolithophores were performed by Murray and Blackmann during the famous cruises of the HMS Challenger, including the first descriptions of the interior of the cells and a rough biogeographical zonation (Murray and Blackmann, 1898). Additionally they observed for the first time the simple reproduction by

fission and elucidated the interlocking of coccoliths, which they interpreted as a defensive armor.

During the early years of the twentieth century numerous studies were addressed to coccolithophores biology and taxonomy. This includes such fundamental findings, as the first description of the nucleus by Ostensfeld (1900), or the recognition of the flagella by Lohmann (1902). It was also Lohmann who introduced the term "nannoplankton", for phytoplankton, that is small enough to pass through the mesh of a normal plankton net (45-60  $\mu\text{m}$ ). In the early decades of the twentieth century most living species were described and systematic work established first taxonomic classification schemes.

After Bramlette and Riedel (1954) demonstrated the biostratigraphic use of calcareous nanofossils, the initiation of the Deep Sea Drilling Project (DSDP) and the following Ocean Drilling Project (ODP), lead to the establishment of a precise nanofossil stratigraphy (e.g. Perch-Nielsen, 1985; Bown, 1998), which is used extensively in commercial drilling as well.

The availability of the Transmission Electron Microscope (TEM) since the mid 50s and Scanning Electron Microscopy (SEM) since the late 60s early 70s improved the illustration and studies of coccolith fine structures extremely and became as standard procedure in coccolithophore investigations.

In the late 60s a finer biogeographic zonation of coccolithophores was set up by McIntyre and Bé (1967). Since it was observed, that these zonations changed during the climatic cycles of the Late Quaternary (McIntyre, 1967), coccolithophores were successfully applied as a paleoceanographic tool (Dudley et al., 1980; Molino et al., 1982).

The focus of scientists to global climate change on present and past time scales, gave further drive to coccolithophore studies. The large variety of biogeochemical reactions, which are involved in various feedback mechanisms to global climate, draw the attention from small scale processes, e.g. coccolith formation (Westbroek et al., 1989) and molecular geochemistry (Volkman et al., 1980) to global scale satellite studies (Holligan et al., 1983; Holligan and Balch, 1991).

## 1.2 Coccolith formation:

Coccolith formation has extensively been studied in *Emiliania huxleyi*, the most common coccolithophore species in the world ocean, which can be cultured under controlled laboratory conditions (see (Westbroek et al., 1993)).

Coccoliths are formed intracellularly in a special vascular system, consisting of a coccolith vesicle (cv) and a reticular body (rb) see Fig.1.2. Within this vacuolar system a highly complex polysaccharide is encountered. The main task of this polysaccharide is to inhibit calcite formation as long as  $\text{CaCO}_3$  is in solution, but it will stimulate it, when it is bound to a solid substrate. When the coccolith is completed, it is transported through the cell membrane to the outside, where it forms the extracellular coccolith cover.

---

Laboratory experiments proved that coccolith formation is a very rapid process in *Emiliania huxleyi*, with one new coccolith being formed every two hours (Westbroek et al., 1989). Somewhat different seems to be the formation of holococcoliths, that are composed of a number of single crystalloliths. Those forms are easily dissolved and therefore are almost exclusively observed in water samples, to a much lesser degree in sediment traps and are very rare in the sedimentary record. More recently numerous combinations between heterococcoliths and holococcoliths have been observed on living coccolithophores, suggesting that holococcoliths are formed during a different life-stage within the cell cycle.

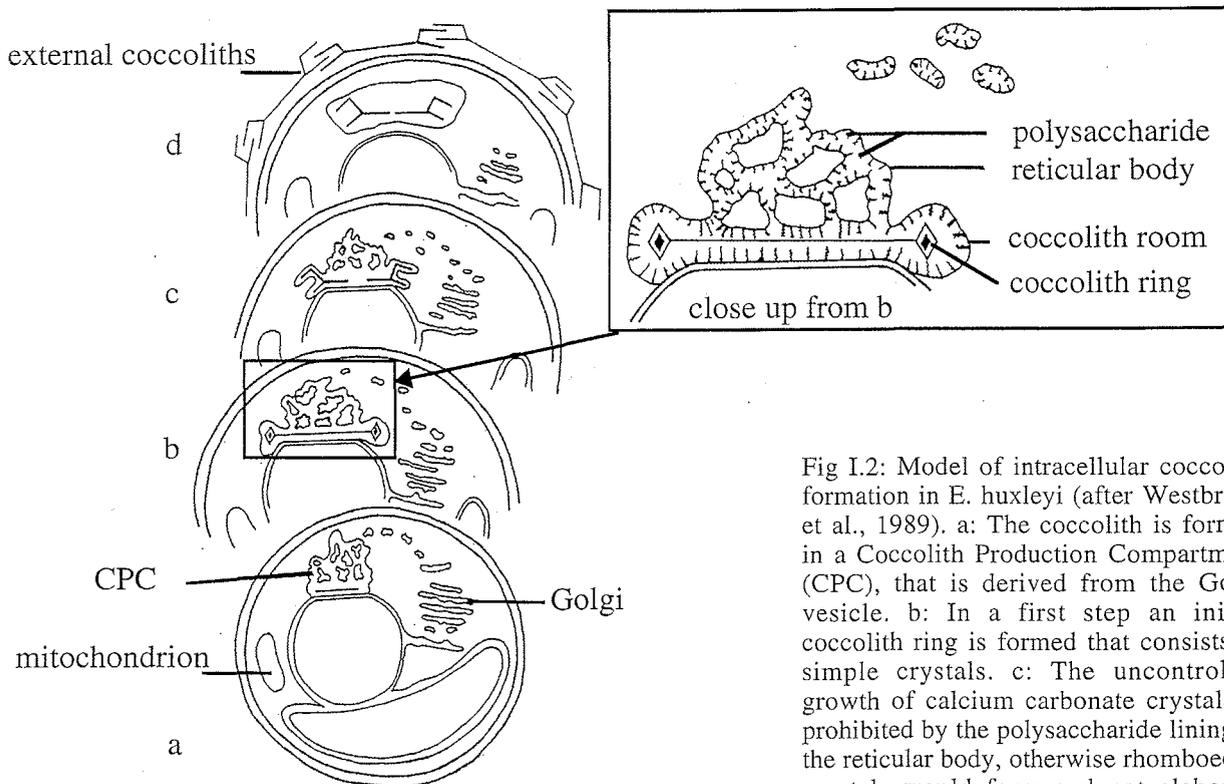


Fig I.2: Model of intracellular coccolith formation in *E. huxleyi* (after Westbroek et al., 1989). a: The coccolith is formed in a Coccolith Production Compartment (CPC), that is derived from the Golgi vesicle. b: In a first step an initial coccolith ring is formed that consists of simple crystals. c: The uncontrolled growth of calcium carbonate crystals is prohibited by the polysaccharide lining of the reticular body, otherwise rhomboedral crystals would form and not elaborate coccoliths. d: After the completion of this process the coccolith is extruded through the cell membrane.

There are various hypothesis about the usefulness of coccolith formation from biogeochemical and functional point of views. A number of studies emphasize, that coccolithophores may form coccoliths, to utilize the  $\text{CO}_2$  from the calcification process for photosynthesis (Nimer et al., 1992; Sikes and Fabry, 1994; Nimer and Merrett, 1995). Coccolithophores would therefore be insensitive to  $\text{CO}_2$  limitation, a process that affects other phytoplankton (e.g. diatoms), because only about one percent of the carbonate available in the surface waters is  $\text{CO}_2$ , whereas most appears as bicarbonate ( $\text{HCO}_3^-$ ), which can be used for calcification or has to be transformed by enzymatic processes (RUBISCO) intracellular, to be utilized during photosynthesis (Raven and Johnston, 1991, 1994).

A number of coccolithophores do not produce calcitic scales at all and are only surrounded by a sphere of organic plates. This is sometimes observed in species that usually calcify as well,

however it is not clear, whether this is due to different life cycles or other unknown reasons (Pienaar, 1994).

### 1.3 Function of coccoliths

Besides the biogeochemical function of removing surplus calcium, which acts toxic to cells (see below), there are only speculations about the functional use of coccoliths for coccolithophores (Young, 1994). Although coccolithophores are ingested by zooplankton, it is very likely, that the coccosphere acts as a protection against grazing pressure. Recently it was shown, that grazing by copepods was indeed less efficient on *E. huxleyi*, than on other phytoplankton groups, like diatoms, which would favor the development of large coccolithophore blooms (Njstgaard et al., 1994; Njstgaard et al., 1996; Wolfe et al., 1997).

Moreover, the formation of a coccoliths may enable a control on the sinking or flotation of the sphere keeping the coccosphere in the preferred position within the photic zone. The light-regulating function of coccoliths is a very elegant explanation for the depth zonation, which is observed for living coccolithophores ( see 1.4), and can be applied for paleo-reconstructions of the nutricline, discussed in Chapter II. Reflection of sunlight by coccoliths does not only alter the albedo of the surface ocean, and therefore makes coccolithophore blooms visible to satellite sensors, it also increases the temperature in surface waters (Holligan et al., 1993).

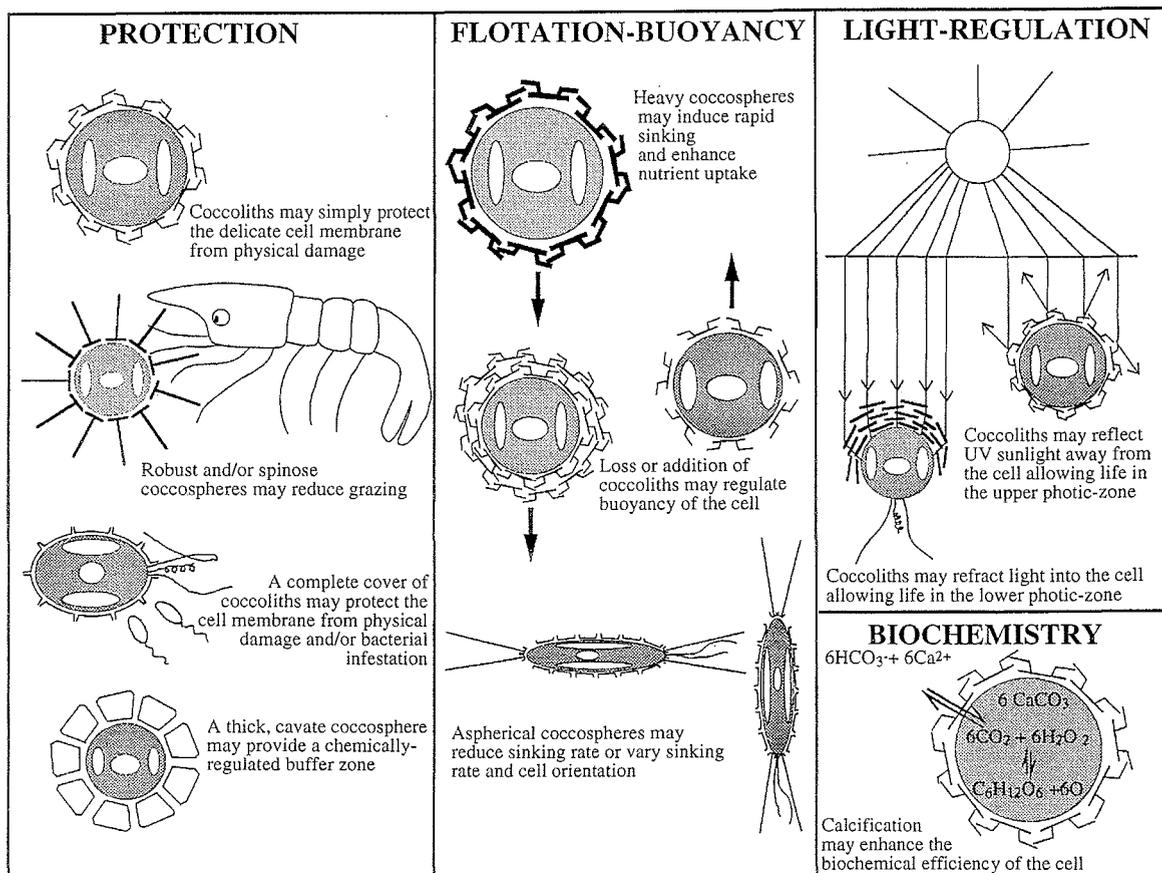


Fig. I.3 Schematic cartoon of possible coccolith functions (from Bown, 1998)

#### 1.4 Coccolithophore ecology and biogeography

A certain temperature dependence of coccolithophores has been noticed early and a rough biogeographic zonation scheme was set up by (McIntyre and Bé, 1967). Subsequently, the modern biogeographic distribution and changes in those patterns during the last glaciation proved to be consistent with other paleoceanographic proxies and thus indicated the capability to reconstruct climatic changes with coccolithophores. *Coccolithus pelagicus* for example is only abundant in waters with temperatures below 14 °C and it dominates the Arctic surface waters in the Norwegian Greenland Seas (Samtleben et al., 1995). It was never recorded in any of the samples examined in this study. Nevertheless there are various indications that temperature is not the dominating factor for the biogeographic distribution of coccolithophores, most clearly demonstrated by the broad temperature range (1-31°C) that is tolerated by *E. huxleyi* (McIntyre et al. 1970). Similar broad tolerances are observed for salinity, with occurrences of *E. huxleyi* reported from the hypersaline Red Sea (41 ppt) (Winter et al., 1979) as well as from the brackish Black Sea (11ppt)(Morozova-Vodyanitskaya and Belogorkaya, 1957; Hay and Honjo, 1989). It seems obvious, that there must be other mechanisms, that influence the observed distribution patterns in coccolithophores. Ecological strategies are likely to enable certain species to adapt to different temperature, nutrient, light and or energy regimes. Usually all these limiting or driving factors are independent from each other, and therefore we can not apply simple relationships.

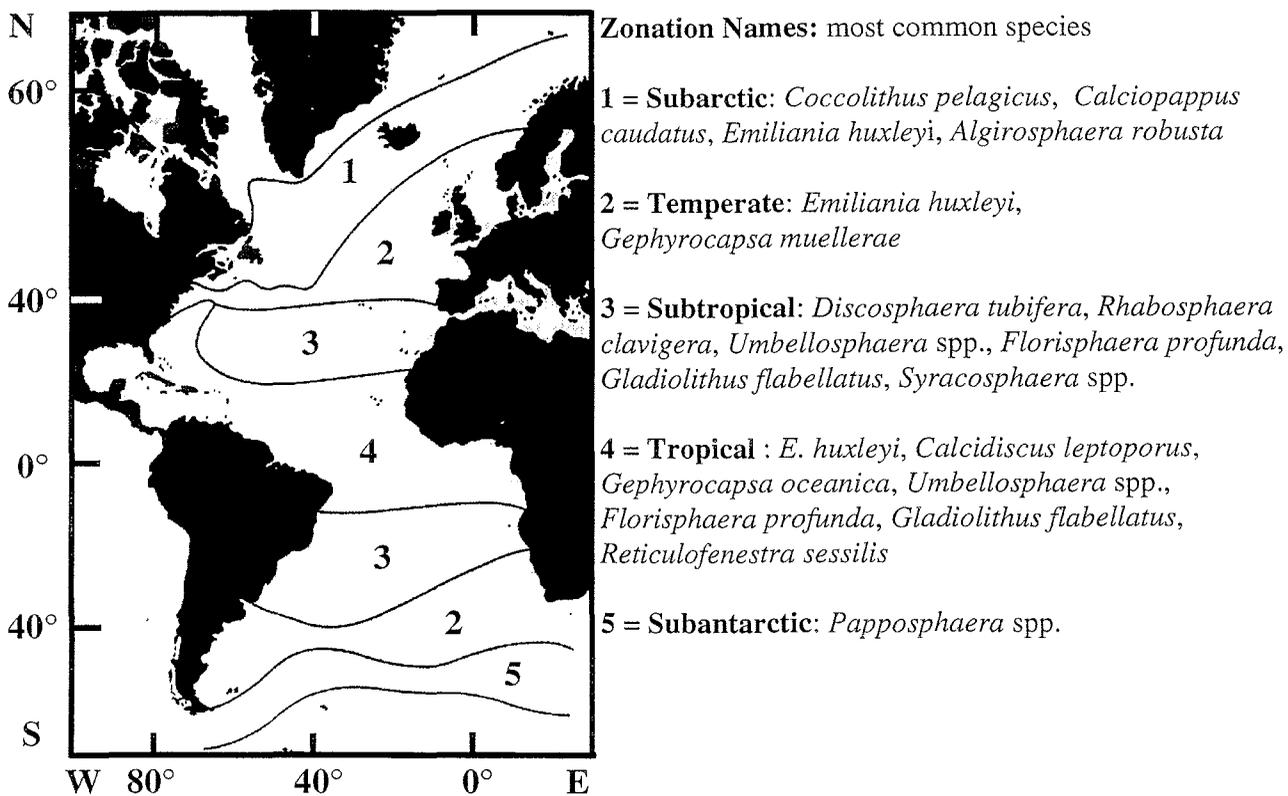


Fig.I.4: Biogeographic zonation of living coccolithophores in the Atlantic Ocean (after Winter et al., 1994)

In chapter II.2 Fig. 9 a very simple model is presented, in which the most important factors controlling the occurrence of coccolithophores in the equatorial Atlantic are summarized. It seems apparent, that nutrient availability due to the depth of the nutricline / thermocline seems to be the most important factor in this area. But both temperature and light intensity are coupled to the nutricline and thermocline depth, which demonstrates the complexity of such a simple model. Nevertheless, it seems to be possible to distinguish three different ecological groups of coccolithophores all adapted to characteristic environments. The first group includes placolith bearing species, which dominate the coastal areas and upwelling systems. They appear to have an affinity to higher nutrient levels, to which they react with increasing growth rates, sometimes leading to large scale blooms. (Hulburt, 1983) interpreted coccolithophore plankton samples in terms of an ecological concept, that distinguishes phytoplankton groups due to their ability in utilizing nutrients, mainly expressed in growth rates. His findings stated that *E. huxleyi* and *Gephyrocapsa oceanica* are the only species that are able to react to increased nutrient levels with higher growth rates, whereas all the other species do not. Therefore these two groups do not compete with each other and if any other group would exist, it would live in the deeper parts of the ocean. This third group, does exist indeed and includes the so called floriform species (*Florisphaera profunda* and *Gladiolithus flabellatus*) and a few other taxa (e.g. *Algirosphaera* spp.). Coccolithophores of this group are adapted to lower light intensities, maybe by refracting light into their cells (see Fig. I.3), and preferably dwell in the lower photic zone (80-200 m), where they benefit from higher nutrient concentrations.

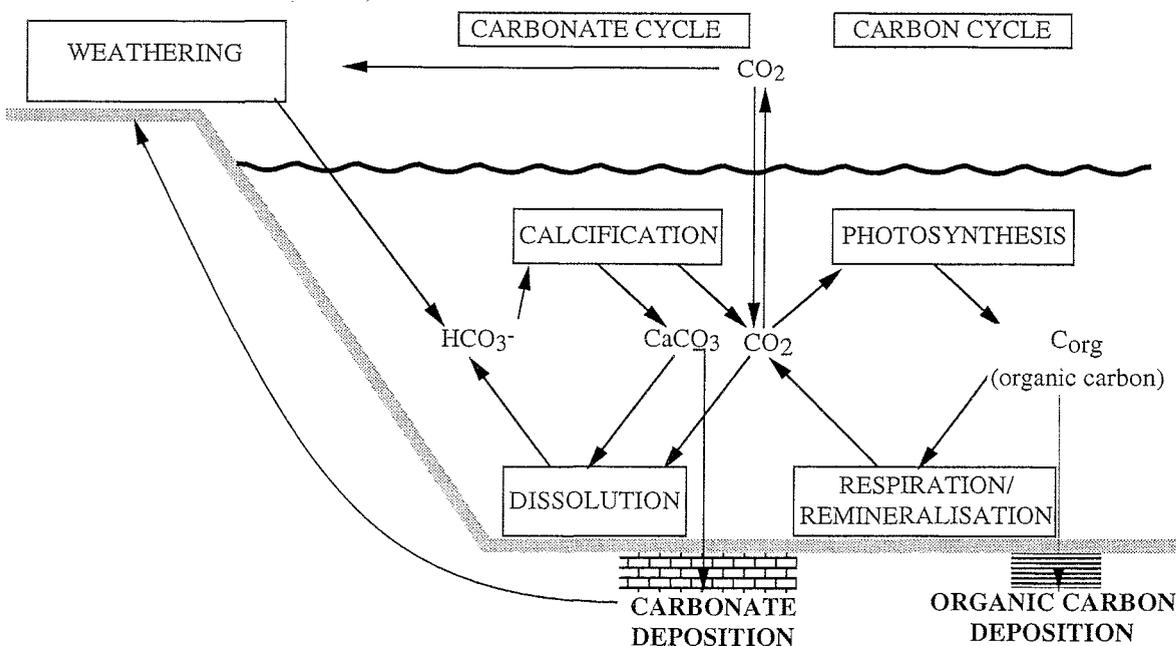
### 1.5 Coccolithophores and the Global Biogeochemical Cycles

The global carbon cycle is one of the topics that many scientific disciplines have turned their attention to, since a possible greenhouse warming by increased release of CO<sub>2</sub> by combustion of fossil fuels since the industrial revolution, was suggested. For geologists this topic became even more relevant, when a close relation between atmospheric CO<sub>2</sub> contents and global temperature was detected in ice cores from Antarctica and Greenland (Barnola et al., 1987; Barnola et al., 1995). Although the combustion of fossil fuels have elevated atmospheric CO<sub>2</sub> contents, clearly documented in the Mauna Loa CO<sub>2</sub> record, the whereabouts of approximately 25% of the released CO<sub>2</sub> remains unknown (Keeling et al., 1996). The oceans form large sinks and reservoirs for CO<sub>2</sub>, and within the oceans it is the coccolithophores that are likely to play an important part in atmosphere-ocean exchange of CO<sub>2</sub>, as they are widely distributed all over the oceans and fix CO<sub>2</sub> in both organic and inorganic carbon. Coccolithophores and planktic foraminifera form the largest part of the pelagic carbonate production, with lesser contribution due to pteropods and calcareous dinoflagellates (Milliman, 1993).

Coccolithophores may be small in size, but they occur in huge numbers in the surface layers of the oceans, sometimes in blooms with cell densities larger than a million cells per liter. These blooms are features large enough to be traced from spaceshuttles and satellites. It is obvious,

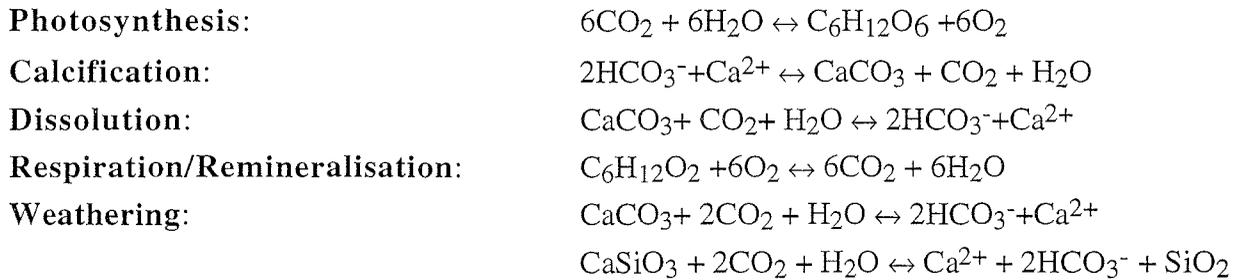
---

that the high reflectance in blooms of this size significantly alter the ocean albedo and reduce the capacity of the oceans to receive energy from solar radiation. Since satellites became equipped with ocean colour and radiation sensors in the 70's, coccolithophore blooms have been monitored continuously on a global scale (Brown and Yoder, 1994). The classified coccolithophore blooms reach an annual area of 1.4 million km<sup>2</sup>. This might even be a minimum estimation as it only considers cloud free areas. The balance, that distinguishes if coccolithophores, and especially the large blooms they form, act as a sink or source for atmospheric CO<sub>2</sub> is the ratio between calcification and photosynthesis. Nevertheless, as blooms often occur in remote areas, there are still limited numbers of investigations within a bloom, and it is not completely clear, if coccolithophorid blooms act as a sink or a source of CO<sub>2</sub> (Robertson et al., 1994; van der Wal et al., 1994; Tyrrell and Taylor, 1995). However, taking into account the various culture and mesocosm studies, predominantly carried out on *E. huxleyi*, it appears, that coccolithophores act as a slight sink in respect to atmospheric CO<sub>2</sub>. Calcification of marine organisms is believed to be a biotic response to calcium toxicity which evolved around 600 million years ago, when calcium concentrations in the sea increased rapidly (Degens, 1989). Calcification was more or less restricted to benthic communities through the entire Paleozoic until pelagic carbonate production by planktic organisms took off at an enormous rate around the Triassic/Jurassic boundary (Degens, 1989). Recently a few authors tried to budget the global calcium carbonate production, ending up with different numbers and thus contradicting implications for the global carbon cycle (Milliman, 1993; Wollast, 1994). Yet there are no reliable estimations on the relative contribution of different organism groups to the global calcium carbonate production, but it is estimated that about 40-60% of the total marine carbonate production is due to coccoliths (Wollast, 1994).



**Fig. I.5:** Schematic drawing of the carbon and carbonate cycle and the processes involved in the production and dissolution. The reactions involved in this processes are listed on the following page.

The chemical reactions involved in the carbon and carbonate cycle outlined in Fig. I.5:

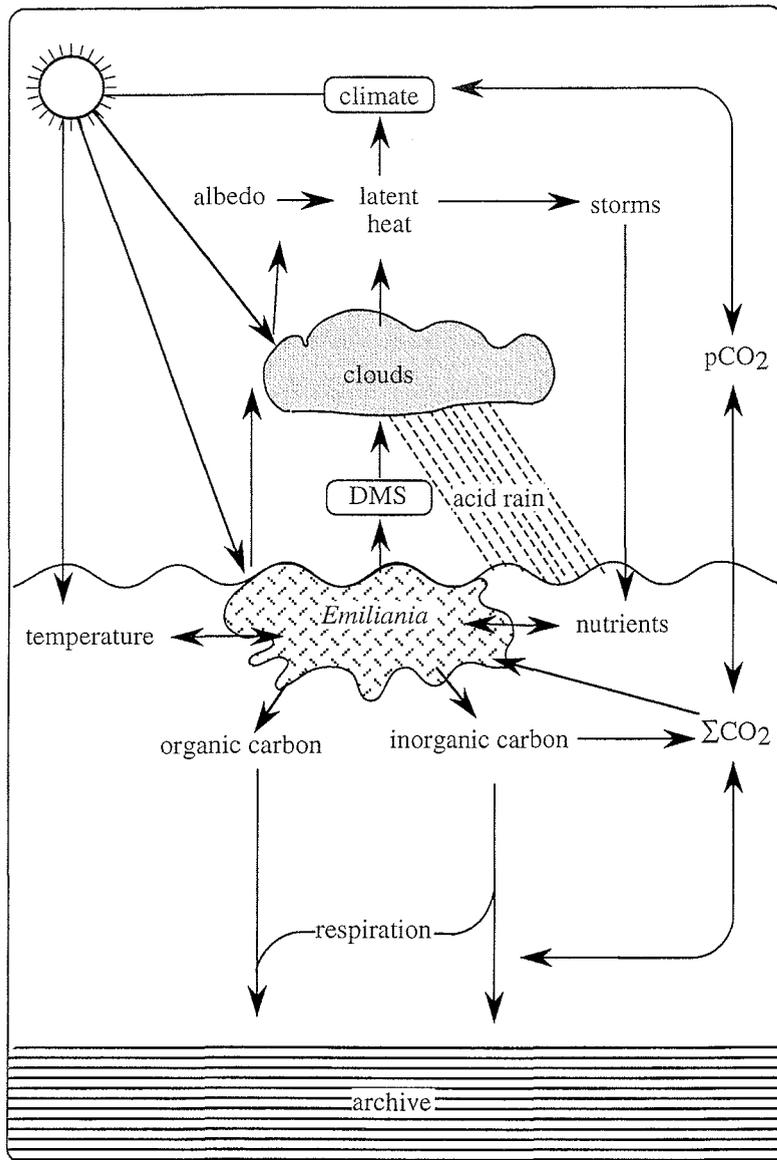


It was and still is commonly accepted, that calcification of marine organisms acts as a major source for  $\text{CO}_2$ . Therefore all calcification by marine organisms is called the "carbonate pump" that counteracts the "biological pump" in which all organisms are combined that draw down  $\text{CO}_2$  from the atmosphere by converting it during photosynthesis into organic matter. The assumption, that calcification is a source for  $\text{CO}_2$  is based on equations for inorganic carbonate precipitation, and might hold true for some calcifying organisms, but most likely not for coccolithophores. Calcification and photosynthesis occur intracellular in coccolithophores, and theoretically it seems possible, that coccolithophores possess the ability, to supply their own  $\text{CO}_2$  for photosynthesis via calcification. The aspect of an intracellular source of  $\text{CO}_2$  for photosynthesis is of particular interest, as it was shown, that phytoplankton growth can be limited by the availability of dissolved  $\text{CO}_2$  in seawater (Raven, 1993; Riebesell et al., 1993). This effect that especially effects organic or siliceous phytoplankton, can be detoured by coccolithophores, as they produce their own  $\text{CO}_2$  via bicarbonate consumption during calcification and not through the relatively slow diffusive uptake of dissolved  $\text{CO}_2$ . Bicarbonate is the predominant form of dissolved  $\text{CO}_2$  in sea water (about 98%) and therefore seems not to be limiting at all. However, recent results seem to indicate that coccolithophores only might use there intracellular  $\text{CO}_2$  source under very limiting  $\text{CO}_2$  conditions in culture studies (Nimer et al., 1997).

It became essential to know, to what extent coccolithophores utilize bicarbonate or free  $\text{CO}_2$  for photosynthesis, since an increasing number of studies are focused on the reconstruction of paleo  $\text{CO}_2$  concentrations, by measuring compound specific stable isotopes in coccolithophore biomarkers (Jasper et al., 1994; Bidigargare et al., 1997).

Some coccolithophores, *E. huxleyi* and *G. oceanica*, synthesize a number of unusual specific biomarkers, the so called long-chain alkenones (Volkman et al., 1980). Although the physiological function of these compounds remain unclear, the ratio between the diunsaturated and triunsaturated  $\text{C}_{37}$  alkenones, the so called  $U_{37}^K$  index, is highly correlated with sea surface temperature (SST) (Prah and Wakeham, 1987). Therefore these compounds can be used for the reconstruction of past sea surface temperatures, and have been established as a powerful paleoceanographic proxy (e.g. Schneider et al., 1996; Müller et al., 1998). Furthermore these compounds could be used for reconstructing the paleo-productivity of coccolithophores (Villanueva et al., 1997; Schubert et al., 1998). However, there is still little information about

the relationship between coccolithophore and biomarker production (Conte et al., 1995; Müller et al., 1997). This is discussed in detail in Chapter II.5 where the biomarker and coccolithophore records of the alkenone producing species during the Late Quaternary are compared.



modified after Westbrook, 1995

Fig.I.6: Model of the biogeochemical impact of an *Emiliani huxley* bloom on the carbon and carbonate cycle and its possible feedback on climate.

Despite organic and inorganic carbon, coccolithophores produce a third important compound, dimethylsulfoniopropionate (DMSP), which will be reduced to dimethylsulfide (DMS) outside the cell. Therefore coccolithophores are also influencing the global sulfur cycle (Charlson, 1987). DMS is one of the most important cloud condensation nuclei (CCN) in the atmosphere over the open oceans, and therefore coccolithophores and cloud formation seem to be linked together, especially when a lot of DMS is released over a bloom area.

DMSP and its oxidation products are not only involved in cloud forming, it also seems to keep away unpleasant predators from below. Wolfe et al 1997, found out that DMS released in the guts of zooplankton that fed on *E.huxleyi*, had a toxic effect and grazing on *E. huxleyi* was reduced. In the oceans zooplankton then might turn to another phytoplankton food source, e.g. diatoms, that do not produce DMS (Njstgaard et al., 1996).

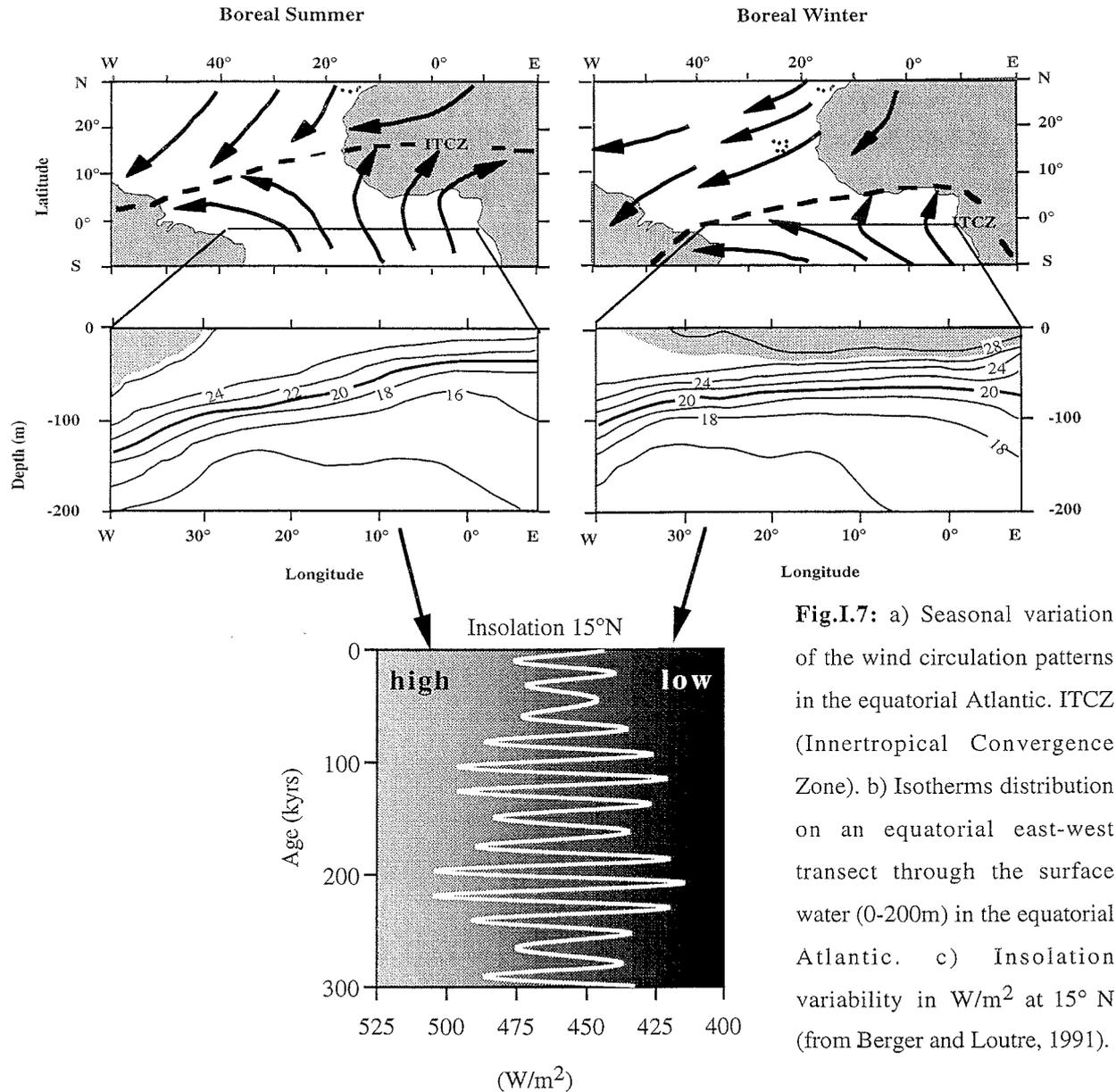
## **2. Purpose of this study**

### 2.1 Coccolithophores as paleoceanographic proxies in the Equatorial Atlantic

The study was carried out to investigate the ecological factors that control the composition of coccolithophore assemblages in recent and Late Quaternary sediments from the equatorial Atlantic as well as their absolute numbers, which should provide information on the productivity of this algae. Composition of coccolithophore assemblages and their sedimentation is controlled by the hydrographic conditions in the photic zone and therefore are coupled to the surface water circulation patterns.

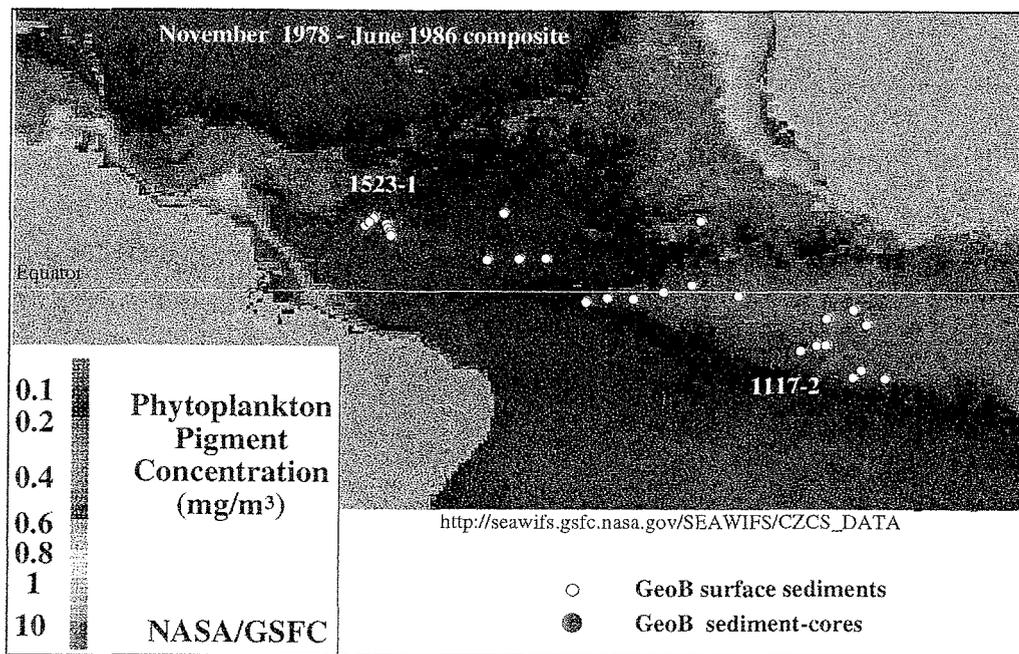
Although the equatorial Atlantic has been the focus of numerous paleoceanographic investigations (McIntyre et al., 1989; deMenocal et al., 1993; Wefer et al., 1996) there is relatively little information on the living and fossil coccolithophore assemblages. This is especially puzzling since a set of papers by Barbara Molfino and Andrew McIntyre, who used the relative abundance of the deep dwelling coccolithophore species *Florisphaera profunda* to reconstruct precessional driven nutricline dynamics in the equatorial Atlantic (Molfino and McIntyre, 1990; Molfino and McIntyre, 1990; McIntyre and Molfino, 1996), are among the most cited, and lead to similar investigations in other ocean areas (Ahagon et al., 1993; Okada and Matsuoka, 1996; Beaufort et al., 1997). However, the lack of quantitative data and information on other species of the coccolithophore assemblages remained in the equatorial Atlantic emphasized the need for further investigations in this area. The refined biogeographical distribution of coccolithophores in both water samples and surface sediments of the equatorial Atlantic compiled during this study gives further support for the application of coccolithophores in paleoceanographic studies. The application of quantitative counting techniques enabled us to test if changes in the relative abundance of certain key species as *F. profunda* is reflected in the total coccolithophore productivity measured as coccoliths per gram sediment or coccolith accumulation rates. In general coccolithophore productivity in the equatorial Atlantic is related to the upwelling intensity today and during the late Quaternary. This is reflected by coccolithophore cell densities in the surface water masses, where highest numbers are found within the equatorial upwelling, almost exclusively formed by *Emiliana huxleyi*. This species, together with *Calcidiscus leptoporus* is found in highest relative and absolute abundances under the equatorial upwelling zone. In the oligotrophic areas the living coccolithophore communities are dominated by *Umbellosphaera tenuis* and *Umbellosphaera irregularis*, which occur in relatively low cell densities in the upper photic zone, whereas the lower photic zone (LPZ) is in general dominated by *Florisphaera profunda* and *Gladiolithus flabellatus*. Since *Umbellosphaera tenuis* and *Umbellosphaera irregularis* are very fragile forms they become strongly dissolved on their way through the water column, leading to an strong increase in the relative abundance of the LPZ taxa in sediments underlying oligotrophic water masses.

## 2.2 (Paleo)oceanography of the of the equatorial Atlantic



The surface water oceanography of the equatorial Atlantic is characterized by the westward flowing South Equatorial Current (SEC) and the eastward flowing South Equatorial Counter Current (SECC), the North Equatorial Current (NECC) and the Equatorial Undercurrent (EUC). Maps of the surface water circulation are presented in the following chapters. The westward flow of the SEC is mainly controlled by the intensification of westward directed tradewinds in boreal spring in the western tropical Atlantic (Philander and Pacanowski, 1986). This causes a massive transport of warm surface waters from the eastern tropical Atlantic, one of the major pathways of oceanic heat transport to the northern hemisphere within the Atlantic. As a result of the wind induced westward flow of the SEC, the thermocline is uplifted in the eastern tropical Atlantic and a corresponding deepening is observed in the western tropical Atlantic (Fig I.7). The seasonal uplift of the thermocline is at its maximum in boreal summer,

and causes an elevated nutrient flux in the eastern sector, which results in a productivity increase within the photic zone. Besides thermocline uplift, additional nutrient flux to the photic zone results from the a wind driven equatorial divergence and shear mixing between the EUC and the SEC. During boreal autumn the thermocline has returned to its pre-upwelling state. More recently a comprehensive summary between the physical ocean dynamics and the observed phytoplankton response in the Equatorial Atlantic was given by (Monger et al., 1997). The equatorial upwelling system is of major importance to global carbon production, not due to the amount of carbon produced per area, but due to the fact that this production takes place in a much larger area than in the high productivity zones of coastal upwelling areas or in high latitudes (Longhurst, 1993).



**Fig. I.8:** Composite picture of the phytoplankton pigment concentrations in the equatorial Atlantic derived from the Coastal Zone Color Scanner and the distribution of surface sediments samples (white dots) and sediment cores (red dots) investigated in this study.

This seasonal cycle in the surface water circulation of the equatorial Atlantic is an analogon for long-term variations by the precessional component of orbital forcing (Fig.I.7c) (Molfinio and McIntyre, 1990). Perihelion centered on boreal winter (December) is equivalent to maximum divergence, while perihelion centered on boreal summer is equivalent to minimum divergence (McIntyre et al., 1989). The driving force behind this system is the seasonal and long-term variation of insolation over the North African continent. (Weisberg and Tang, 1987). The intensified heating of the African continent during June perihelion causes an uplift of air and relative low pressure in this region. As a result, a monsoonal effect is caused with meridional winds from the south.

### 2.3 The use of coccoliths as proxies for carbonate dissolution

Due to their small size, delicate ultrastructure, and complex sedimentation processes, relatively little work was done on coccolith dissolution as compared to planktic foraminifera, most likely due to the small size of coccoliths, which limits ultrastructure investigations that can be carried out on planktic foraminifera. Nevertheless a simple relationship, the *Calcidiscus leptoporus* - *Emiliana huxleyi* - dissolution index (CEX)(Dittert et al., in press), was established in this study, to determine the effect of carbonate dissolution on calcareous nannoplankton assemblages. This method corroborates the bulk parameters (carbonate content) and a foraminifera ultrastructure dissolution index along three different depth transects across the lysocline, and even can separate between carbonate dissolution in the open ocean and at the continental margin. However, it has to be stated that this method has a limited use since one of the two species, *Emiliana huxleyi*, has a limited geological record extending back approximately 270 ka (Thierstein et al., 1977) and already decreases in abundance in sediments older than the last glacial interval, due to its evolutionary development and not carbonate dissolution.

### 2.4 The micropaleontological and organic geochemical record of coccolithophores



C<sub>37:2</sub>: Heptatriaconta - 15E, 22E-dien-2-one

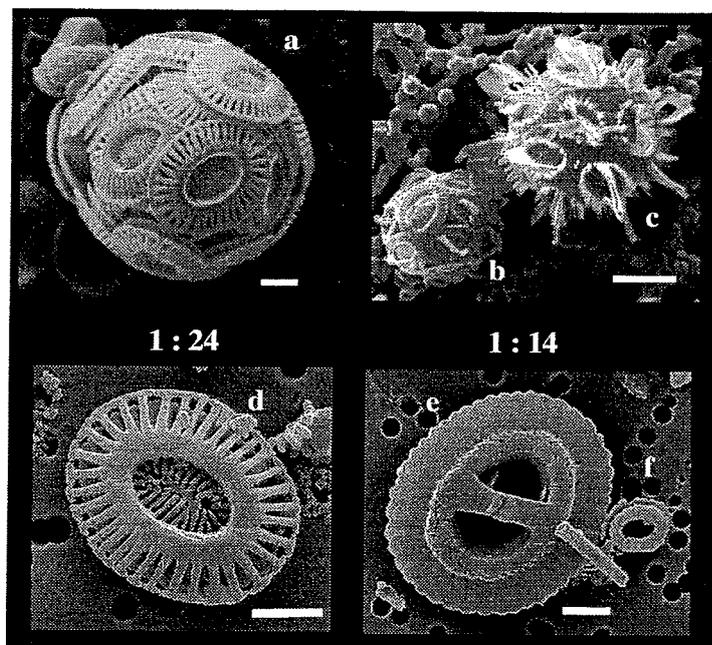


C<sub>37:3</sub>: Heptatriaconta - 8E, 15E, 22E-trien-2-one

**Fig. I.9:** Structure and abbreviated notations of the two most abundant long-chain alkenones found in sediments (after de Leeuw et al. (1980))

Besides the classical micropaleontological approach, coccolithophores can although be studied by organic geochemical methods, since they produce a set of unsaturated long-chain ketones, so called alkenones (Fig. I.9), which are specific for certain haptophyte algae. *Emiliana huxleyi* and *Gephyrocapsa oceanica* are the only two species, that are known to produce these biomarkers in the modern open ocean (Volkman et al., 1980; Volkman et al., 1995). There is strong evidence that other species of the Genus *Gephyrocapsa* produce these biomarkers as well (Marlowe et al., 1990; Müller et al., 1997), which is of major importance for the application of the alkenone based temperature reconstruction ( $U_{37}^k$ -index) in sediments that predate the first

occurrence of *Emiliana huxleyi*. The calibration of the  $U_{37}^{k'}$ -index, which expresses the ratio between di- and triunsaturated  $C_{37}$  alkenones, against sea surface temperature has recently been demonstrated on a global set of surface sediments and emphasized the use of this method as a powerful paleoceanographic proxy (Müller et al., 1998). Only a few studies used absolute concentrations of alkenones as a proxy for past coccolithophore productivity (Prah1 et al., 1993; Villanueva et al., 1997; Schubert et al., 1998).



**Fig. I.10:** Living coccospheres of *Emiliana huxleyi* (a), *Gephyrocapsa ericsonii* (b) and *Gephyrocapsa ornata* (c) from the equatorial Atlantic. Coccoliths of *Emiliana huxleyi* (d), *Gephyrocapsa oceanica* (e) and *Gephyrocapsa ericsonii* (f) from sediment samples in the equatorial Atlantic. The numbers indicate the ratios that were used to calculate the real cell numbers from the counts of single coccoliths in the sediments and are based on averaged coccolith per cell counts carried out on the plankton samples in this study. All scales are 1µm.

Within the present study an approach was applied, which combines quantitative coccolith counts and absolute alkenone concentrations to decipher the changes in past coccolithophore productivity. It became obvious that we have to consider coccosphere cell counts rather than coccolith counts, since the ratio of coccoliths per cell varies for different species (see Fig. I.10) and the amount of biomarkers is related to the amount of cells rather than the numbers of the coccoliths.

#### 4. References:

- Ahagon, N., Tanaka, Y. and Ujiie, H., 1993. *Florisphara profunda*, a possible nannoplankton indicator of late Quaternary changes in sea-water turbidity at the northwestern margin of the Pacific. *Mar. Micropaleontol.* 22, 255-273.
- Barnola, J. M., Anklin, M., Porcheron, J., Raynaud, D., Schwander, J. and Stauffer, B., 1995. CO<sub>2</sub> evolution during the last millenium as recorded in Antarctic and Greenland Ice. *Tellus* 47, 264-272.
- Barnola, J. M., Raynaud, D., Korotkevich, Y. S. and Lorius, C., 1987. Vostok Ice Core Provides 160,000-year Record of Atmospheric CO<sub>2</sub>. *Nature* 329, 408-414.
- Beaufort, L., Lancelot, Y., Camberlin, P., Cayre, O., Vincent, E., Bassinot, F. and Labeyrie, L., 1997. Insolation cycles as a major control of Equatorial Indian Ocean Primary Production. *Science* 278, 1451-1454.
- Berger, A. and Loutre, M. F., 1991. Insolation values for the climate of the last 10 million years. *Quaternary Science Review* 10, 297-317.
- Bidigargare, R. R., Fluegge, A., Freeman, K. H., Hanson, K. L., Hayes, J. M., Hollander, D., Jasper, J. P., King, L. L., Laws, E. A., Milder, J., Millero, F. J., Pancost, R., Popp, B. N., Steinberg, P. A. and Wakeham, S. G., 1997. Consistent fractionation of <sup>13</sup>C in nature and the laboratory: Growth-rate effects in some haptophyte algae. *Global Biogeochem. Cycles* 11, 279-292.
- Bown, P. R., 1998. *Calcareous nannofossil stratigraphy*. Chapman & Hall, London, 314 pp.
- Bramlette, M. N. and Riedel, W. R., 1954. Stratigraphic value of discoasters and some other microfossils related recent coccolithophores. *J. Paleont.* 28, 385-403.
- Broecker, W. S., 1997. Thermohaline Circulation, the Achilles Heel of our climate system: will man made CO<sub>2</sub> upset the current balance? *Science* 278, 1582-1588.
- Brown, C. W. and Yoder, J. A., 1994. Coccolithophorid blooms in the global ocean. *J. Geophys. Res.* 99, 7467-7482.
- Charlson, R. J., Lovelock, J.E., Andrae, M.O. & Warren, S.G., 1987. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature* 326, 655 -661.
- Conte, M. H., Thompson, A., Eglinton, G. and Green, J. C., 1995. Lipid biomarker diversity in the coccolithophorid *Emiliania huxleyi* (Prymnesiophyceae) and the related species *Gephyrocapsa oceanica*. *J. Phycol.* 31, 272-282.
- Dayman, J., 1858. *Deep Sea Soundings in the North Atlantic Ocean Between Ireland and New Foundland, made in HMS Cyclops*. London, Eyre and Spottiswoode
- Degens, E. T., 1989. *Perspectives on Biogeochemistry*. Springer, Berlin, Heidelberg, New York, 423 pp.
- deMenocal, P. B., Ruddiman, W. F. and Pokras, E. M., 1993. Influences of high and low latitude processes on african terrestrial climate: Pleistocene eolian records from Equatorial Atlantic Ocean Drilling Program Site 663. *Paleoceanography* 8, 209-242.
-

- de Leeuw, J. W., van der Meer, F. W., Rijpstra, W. I. C. and Schenck, P. A., 1980. On the occurrence and structural identification of long chain unsaturated ketones and hydrocarbons in sediments In: A. G. Douglas and J. R. Maxwell (Eds), *Advances in Organic Geochemistry* 1979. pp 211-217.
- Dittert, N., Baumann, K.-H., Bickert, T., Henrich, R., Huber, R., Kinkel, H. and Meggers, H., in press. Carbonate dissolution in the deep sea: Methods, Quantification and Paleoceanographic Application In: G. Fischer and G. Wefer (Eds), *Use of Proxies in Paleoceanography: Examples from the South Atlantic*. Springer, Berlin, Heidelberg, pp
- Dudley, W. C., Duplessy, J. C., Blackwelder, P. L., Brand, L. E. and Guillard, R. R. L., 1980. Coccoliths in the Pleistocene - Holocene nannofossil assemblage. *Nature* 285, 222-223.
- Ehrenberg, C. G., 1836. Bemerkung über feste mikroskopische anorganische Formen in erdigen und derben Mineralien. *Bericht. Verh. K. Preuss. Akad. Wiss. Berlin* 84-85.
- Hay, B. J. and Honjo, S., 1989. Particle sources and in the present and Holocene Black Sea. *Oceanography* 2, 26-31.
- Holligan, P. M. and Balch, W. M., 1991. From the ocean to cells: coccolithophore optics and biogeochemistry In: S. Demers (Eds), *Particle Analysis in Oceanography*. 27. Springer, Berlin, Heidelberg, pp
- Holligan, P. M., Fernández, E., Aiken, J., Balch, W. M., Boyd, P., Burkill, P. H., Finch, M., Groom, S. B., Malin, G., Muller, K., Purdie, D. A., Robinson, C., Trees, C. C., Turner, S. M. and van der Waal, P., 1993. A biogeochemical study of the coccolithophore *Emiliania huxleyi* in the North Atlantic. *Global Biogeochem. Cycles* 7, 879 - 900.
- Holligan, P. M., Viollier, M., Harbour, D. S., Camus, P. and Champagne-Philippe, M., 1983. Satellite and ship studies of coccolith production along a continental shelf. *Nature* 304, 339-342.
- Hulburt, E. M., 1983. Quasi K-selected species, equivalence, and the oceanic coccolithophorid plankton. *Bulletin of Marine Research* , 33, 197-212.
- Jasper, J. P., Mix, A. C., Prahl, F. G. and Hayes, J. M., 1994. Photosynthetic  $^{13}\text{C}$  fractionation and estimated  $\text{CO}_2$  levels in the Central Equatorial Pacific over the last 255,000 years. *Paleoceanography* 9, 781-799.
- Keeling, R. F., Piper, S. C. and Heimann, M., 1996. Global and Hemispheric  $\text{CO}_2$  sinks deduced from changes in Atmospheric  $\text{O}_2$  concentrations. *Nature* 381, 218-221.
- Lohmann, H., 1902. Die Coccolithophoridae. *Arch. Protistenk.* 1, 89-165.
- Longhurst, A., 1993. Seasonal cooling and blooming in tropical oceans. *Deep-Sea Research* 40, 2145-2177.
- Marlowe, I. T., Brassell, S. C., Eglinton, G. and Green, J. C., 1990. Long - chain alkenones and alkyl alkenoates and the fossil coccolith record of marine sediments. *Chem. Geol.* 88, 349 - 375.
-

- McIntyre, A., 1967. Coccoliths as paleoclimatic indicators of Pleistocene glaciation. *Science* 158, 1314-1317.
- McIntyre, A. and Bé, A., 1967. Modern Coccolithophoridae in the Atlantic Ocean. I. Placoliths and cyrtholiths. *Deep-Sea-Res.* 14, 561-597.
- McIntyre, A. and Molfino, B., 1996. Forcing of Atlantic Equatorial and Subpolar Millennial Cycles by Precession. *Science* 274, 1867-1870.
- McIntyre, A., Ruddiman, W. F., Karlin, K. and Mix, A. C., 1989. Surface water response of the equatorial Atlantic ocean to orbital Forcing. *Paleoceanography* 4, 19 - 55.
- Milliman, J. D., 1993. Production and accumulation of calcium carbonate in the ocean: Budget of a non steady state. *Global Biogeochem. Cycles* 7, 927 - 957.
- Molfino, B. and McIntyre, A., 1990. Nutricline Variation in the equatorial Atlantic coincident with the Younger Dryas. *Paleoceanography* 5, 997 - 1008.
- Molfino, B., Kipp, N. G. and Morley, J. J., 1982. Comparison of Foraminiferal, Coccolithophorid and Radiolarian Paleotemperature Equations: Assemblage Coherency and Estimate Concordancy. *Quat. Res.* 17, 279 -313.
- Molfino, B. and McIntyre, A., 1990. Precessional Forcing of Nutricline Dynamics in the Equatorial Atlantic. *Science* 249, 766-769.
- Monger, B., McClain, C. and Murtugudde, R., 1997. Seasonal phytoplankton dynamics in the eastern tropical Atlantic. *J. Geophys. Res.* 102, 12,389-12,411.
- Morozova-Vodyanitskaya, N. V. and Belogorkaya, E. V., 1957. Oznachenii kokkolitoforid i osobenno pontosfery v plaktone Chernogo morya (On the importance of coccolithophorids and particular Pontosphaera in the Plankton of the Black Sea). *Trud. Sevastopol. Biol. Stants.* 9, 14-21.
- Müller, P. J., Cepek, M., Schneider, R. and Ruhland, G., 1997. Alkenone and coccolithophorid changes in Late Quaternary sediments from the Walvis Ridge: Implications for the alkenone paleotemperature method. *Paleogeogr., Paleoclimatol., Paleoecol.* 135, 71-96.
- Müller, P. M., Kirst, G., Ruhland, G., von Storch, I. and Rosell-Melé, A., 1998. Calibration of the alkenone paleotemperature index  $U_{37}^{k'}$  based on core-tops from the eastern South Atlantic the global ocean (60°N-60°S). *Geochim. Cosmochim. Acta* 62, 1757-1772.
- Murray, G. and Blackmann, V. H., 1898. On the Nature of coccospheres and Rhabdospheres. *Phil. Trans. Roy. Soc. B* 190, 427-441.
- Nimer, N. A., Dixon, G. K. and Merret, M. J., 1992. Utilization of inorganic carbon by the coccolithophorid *Emiliana huxleyi* (Lohmann) Kamptner. *New. Phytol.* 120, 153-158.
- Nimer, N. A., Iglesias-Rodriguez, M. D. and Merret, M. J., 1997. Bicarbonate utilization by marine phytoplankton species. *J. Phycol.* 33, 625-631.
- Nimer, N. A. and Merrett, M. J., 1995. Calcification rate in relation to carbon dioxide release, photosynthetic carbon fixation and oxygen evolution in *Emiliana huxleyi*. *Bulletin de l'Institut Oceanographique (Monaco) SPEC. ISSUE* 14, 37-42.
-

- Njestgaard, J. C., Gismervik, I. and Solberg, P. T., 1996. Feeding and reproduction by *Calanus finmarchicus*, and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore *Emiliania huxleyi*. *Mar. Ecol. Prog. Ser.* 147, 197-217.
- Njestgaard, J. C., Witte, H. J., Van-Der-Wal, P. and Jacobsen, A., 1994. Copepod grazing during a mesocosm study of an *Emiliania huxleyi* (Prymnesiophyceae) bloom. *Sarsia* 79, 369-377.
- Okada, H. and Matsuoka, M., 1996. Lower - photic nanoflora as an indicator of the late Quaternary monsoonal paleo - record in the tropical Indian Ocean In: A. M. & R. Whatley (Eds), *Microfossils and Oceanic Environments*. Aberystwyth Press, Aberystwyth, pp 231-245.
- Ostenfeld, C. H., 1900. Über Coccosphaera. *Zool. Anz.* 23, 198-200.
- Perch-Nielsen, K., 1985. Cenozoic calcareous nanofossils In: H. M. Bolli, J. B. Saunders and K. Perch-Nielsen (Eds), *Plankton Stratigraphy*. 1. Cambridge University Press, Cambridge, pp 427-554.
- Philander, S. G. H. and Pacanowski, R. C., 1986. A Model of the Seasonal Cycle in the Tropical Atlantic Ocean. *J. Geophys. Res.* 91, 14192-14206.
- Pienaar, R. N., 1994. Ultrastructure and calcification of coccolithophores In: A. Winter and W. G. Siesser (Eds), *Coccolithophores*. Cambridge University Press, Cambridge, pp 13-38.
- Prahl, F. G., Collier, R. B., Dymond, J., Lyle, M. and Sparrow, M. A., 1993. A biomarker perspective on prymnesiophyte productivity in the northeast Pacific Ocean. *Deep - Sea - Research I* 40, 2061-2076.
- Prahl, F. G. and Wakeham, S. G., 1987. Calibration of unsaturation patterns in long-chain ketone compositions for paleotemperature assessment. *Nature* 330, 367-369.
- Raven, J. A., 1993. Limits on growth rates. *Nature* 361, 209-210.
- Raven, J. A. and Johnston, A. M., 1991. Mechanisms of inorganic-carbon acquisition in marine phytoplankton and their implications for the use of other resources. *Limnol. Oceanog.* 36, 1701-1714.
- Raven, J. A. and Johnston, A. M., 1994. Algal DIC Pumps and Atmospheric CO<sub>2</sub> In: N. E. Tolbert and J. Preiss (Eds), *Regulation of Atmospheric CO<sub>2</sub> and O<sub>2</sub> by Photosynthetic Carbon Metabolism*. Oxford University Press, New York Oxford, pp 184-198.
- Riebesell, U., Wolf-Gladrow, D. A. and Smetacek, V., 1993. Carbon dioxide limitation of marine phytoplankton growth rates. *Nature* 361, 249-251.
- Robertson, J. E., Robinson, C., Turner, D. R., Holligan, P., Watson, A. J., Boyd, P., Fernandez, E. and Finch, M., 1994. The impact of a coccolithophore bloom on oceanic carbon uptake in the northeast Atlantic during summer 1991. *Deep-Sea Research Part I Oceanographic Research Papers* 41, 287-314.
- Samtleben, C., Schaefer, P., Andrulleit, H., Baumann, A., Baumann, K.-H., Kohly, A., Matthiessen, J. and Schroeder-Ritzrau, A., 1995. Plankton in the Norwegian-Greenland
-

- Sea: From Living communities to Sediment Assemblages - an actualistic approach. Geol. Rundsch. 84, 108 - 136.
- Schneider, R. R., Müller, P. J., Ruhland, G., Meinecke, G., Schmidt, H. and Wefer, G., 1996. Late Quaternary surface temperatures and productivity in the east-equatorial South Atlantic: response to changes in Trade / Monsoon wind forcing and surface water advection. In: G. Wefer, W. H. Berger, G. Siedler and D. Webb (Eds), *The South Atlantic: Present and Past Circulation*. Springer, Berlin, pp 527-551.
- Schubert, C. J., Villanueva, J., Calvert, S. E., Cowie, G. L., von Rad, U., Schulz, H., Berner, U. and Erlenkeuser, H., 1998. Stable phytoplankton community structure in the Arabian Sea over the past 200,000 years. *Nature* 394, 563-566.
- Sikes, C. S. and Fabry, V. J., 1994. Photosynthesis, CaCO<sub>3</sub> Deposition, Coccolithophorids, and the Global Carbon Cycle In: N. E. Tolbert and J. Preiss (Eds), *Regulation of Atmospheric CO<sub>2</sub> and O<sub>2</sub> by Photosynthetic Carbon Metabolism*. Oxford University Press, New York, Oxford, pp
- Sorby, H. C., 1861. On the organic origin of the so called 'crystalloids' of the chalk. *Ann. Mag. Nat. Histor. Ser. 3*, 193-200.
- Thierstein, H. R., Geitzenauer, K. R., Molino, B. and Shackleton, N. J., 1977. Global synchronicity of late Quaternary coccolith datum levels: Validation by oxygen isotopes. *Geology* 5, 400-404.
- Tyrrell, T. and Taylor, A.-H., 1995. Latitudinal and seasonal variations in carbon dioxide and oxygen in the northeast Atlantic and the effects on *Emiliana huxleyi* and other phytoplankton. *Global Biogeochem. Cycles* 9, 585-60.
- van der Wal, P., van Bleijswijk, J. D. L. and Egge, J. K., 1994. Primary productivity and calcification rate in blooms of the coccolithophorid *Emiliana huxleyi* (Lohmann) Hay et Mohler developing in mesocosms. *Sarsia* 79, 401-408.
- Villanueva, J., Grimalt, J. O., Cortijo, E., Vidal, L. and Labeyrie, L., 1997. A biomarker approach to the organic matter deposited in the North Atlantic during the last climatic cycle. *Geochim. Cosmochim. Acta* 61, 4633-4646.
- Volkman, J. K., Barrett, S. M., Blackburn, S. I. and Sikes, E. L., 1995. Alkenones in *Gephyrocapsa oceanica*: Implications for studies of paleoclimate. *Geochim. Cosmochim. Acta* 59, 513-520.
- Volkman, J. K., Eglinton, G., Corner, E. D. S. and Sargent, J. R., 1980. Novel unsaturated straight-chain C<sub>37</sub>-C<sub>39</sub> methyl and ethyl ketones in marine sediments and a coccolithophore *Emiliana huxleyi*. In: A. G. Douglas and J. R. Maxwell (Eds), *Advances in Organic Geochemistry 1979*. Pergamon, Oxford, pp 219-227.
- Wallich, G. C., D., M., S., F. L. and S., F. G., 1861. Remarks on some novel phases of organic life, and on the boring powers of minute annelids, at the great depths in the sea. Reprinted from *Ann. Mag. Nat. Hist., Ser 3*, 8:52-58 3,
-

- Wefer, G., Berger, W. H., Bickert, T., Donner, B., Fischer, G., Kemle-von-Mücke, S., Meinecke, G., Müller, P. J., Mulitza, S., Niebler, H.-S., Pätzold, J., Schmidt, H., Schneider, R. R. and Segl, M., 1996. Late Quaternary surface circulation of the South Atlantic: The stable isotope record and Implications for Heat Transport and Productivity In: G. Wefer, W. H. Berger, G. Siedler and D. Webb (Eds), *The South Atlantic: Present and Past Circulation*. Springer, Berlin, pp 461-502.
- Weisberg, R. H. and Tang, T. Y., 1987. Further studies on the response of the equatorial thermocline in the Atlantic Ocean to seasonally varying trade winds. *J. Geophys. Res.* 92, 3709-3727.
- Westbroek, P., Brown, C. W., van Bleijswijk, J., Brownlee, C., Brummer, G. J., Conte, M., Egge, J., Fernández, E., Jordan, R., Knappertsbusch, M., Stefels, J., Veldhuis, M., van der Waal, P. and Young, J. R., 1993. A model system approach to biological climate forcing. The example of *Emiliana huxleyi*. *Global and Planetary Change* 8, 27-46.
- Westbroek, P., Young, J. R. and Linschooten, K., 1989. Coccolith Production (Biomineralization) in the Marine Alga *Emiliana huxleyi*. *J. Protozool.* 36, 368-373.
- Winter, A., Jordan, R. W. and Roth, P. H., 1994. Biogeography of living coccolithophores in ocean Waters In: A. Winter and W. G. Siesser (Eds), *Coccolithophores*. Cambridge University Press, Cambridge, pp
- Winter, A., Reiss, Z. and Luz, B., 1979. Distribution of living coccolithophore assemblages in the Gulf of Elat ('Aqaba). *Mar. Micropaleontol.* 4, 197 - 223.
- Wolfe, G. V., Steinke, M. and Kirst, G. O., 1997. Grazing-activated chemical defence in a unicellular marine alga. *Nature* 387, 894-897.
- Wollast, R., 1994. The relative importance of biomineralization and dissolution of CaCO<sub>3</sub> in the global carbon cycle In: F. Doumenge (Eds), *Past and Present Biomineralization Processes. Considerations about the Carbonate Cycle*. **13**. *Bulletin de l'Institut océanographique, Monaco, numéro spécial*, Monaco, pp 37-60.
- Young, J. R., 1994. Functions of coccoliths. In: A. Winter and W. G. Siesser (Eds), *Coccolithophores*. Cambridge Academic Press, Cambridge, pp 63-82.

## **Coccolithophores as indicators of ocean water masses, surface-water temperature, and paleoproductivity - examples from the South Atlantic**

Karl-Heinz Baumann, Martin Cepek, and Hanno Kinkel

*FB Geowissenschaften, Univ. Bremen, Postfach 330440, D-28334 Bremen, Germany*

### **Abstract**

The present study was designed to ascertain the significance of coccolithophores as a proxy for paleoceanographic and paleoproductivity studies in the South Atlantic. Literature data is briefly reviewed and new results on the regional distribution of living coccolithophores, their distribution in surface sediments, and their development in the late Quaternary from both the equatorial Atlantic and the eastern South Atlantic are introduced.

The spatial dynamics of living coccolithophores in the surface and subsurface-waters shows considerable variation in cell numbers and distribution patterns. In general, cell densities reached maximal up to  $300 \times 10^3$  coccospheres/l in the equatorial Atlantic whereas up to about  $400 \times 10^3$  coccospheres/l were observed in the eastern South Atlantic. Generally, *Emiliana huxleyi* is the dominant species in the plankton. In addition, *Calcidiscus leptoporus*, *Gephyrocapsa ericsonii*, *Syracosphaera* spp., *Umbellosphaera irregularis*, *U. tenuis*, and holococcolithophores also considerably contribute to the communities. Coccolith assemblages in bottom sediments of the eastern South Atlantic generally reflect the distribution and composition of the living coccolithophore communities within the surface-waters.

Implications from down-core data both for paleoproductivity estimates in the equatorial Atlantic and for variations in sea-surface temperatures in the eastern South Atlantic are discussed. Highest numbers of coccoliths are observed during relatively cold periods and most probably are indicative of relatively nutrient-rich waters. Thus, variations in the coccolithophore assemblages give relative temperature changes. Absolute sea-surface temperatures are determined by alkenone data ( $U_{37}^k$ -index). Nevertheless, the relationship between alkenone-derived SST data and coccolithophore assemblages still is an open question. Abundances of *G. oceanica* fit best to alkenone concentrations, whereas the calibration made by *E. huxleyi* yield the more reasonable SSTs.

## Introduction

Coccolithophores are a major group of marine, unicellular phytoplankton. Their cell surfaces are covered with minute external calcite scales (=coccoliths) bearing a complex ornamentation. These coccoliths form an important part of fine-grained deep-sea sediments and, therefore, are extensively used in biostratigraphic, paleoecologic, and paleoceanographic studies (e.g., McIntyre 1967, Geitzenauer et al. 1977, Roth and Coulbourn 1982, Crux and van Heck 1989, Winter and Siesser 1994). Coccoliths constitute the single most important component of deep-sea sediments and provide key floral, and biomarker signals for interpreting global change in the geological record. In addition, their exceptional fossil record makes them an outstanding biostratigraphic group and gives them unusual potential for testing evolutionary hypotheses (Young *et al.* 1994). Recently, coccolithophores have gained increased attention as they make an important contribution to the oceanic primary productivity. Hence they may provide a good index of open ocean primary productivity (Brummer and van Eijden, 1992). They play a significant role in the CO<sub>2</sub>/O<sub>2</sub> exchange between the ocean and atmosphere and are peculiar because of their combined effects on both, the biological and the carbonate pump. Because of their optical (albedo - masses of detached coccoliths substantially reflect incoming light) and biochemical (dimethylsulfide - which act as a source molecule for cloud nucleation) effects they likely produce an additional feedback to climate change (Westbroek et al. 1993). Some species, such as *Emiliana huxleyi*, contain alkenones, that are long-chained (C<sub>37</sub>-C<sub>39</sub>) di- and tri-unsaturated ketones, first observed by Boon et al. (1978) in Miocene to Pleistocene sediments from the Walvis Ridge. The alkenone ratios are sensitive to the coccolithophores' growth temperatures and, thus, these compounds are potentially useful in the reconstruction of past surface-water temperatures (e.g., Brassell et al. 1986, Prah et al. 1989). Hence, variation in saturation ratios of these alkenones form an important palaeothermometer ( $U_{37}^k$ - index), but can also be used to determine temperature affinities of the present species (Jordan et al. 1996).

Many studies on recent coccolithophores are predominantly taxonomic (Halldal and Markali 1954, Gaarder and Markali 1956, Gaarder and Heimdal 1977, Heimdal and Gaarder 1980, Heimdal and Gaarder 1981, Kleijne 1991, Knappertsbusch 1993), although a number of investigations concerning the dynamics and ecology of calcareous nannoplankton have been published. Individual species are mostly cosmopolitan but with more or less limited latitudinal distributions. Although much information is available on the oceanic-scale distribution of coccolithophores (e.g., McIntyre and Bé 1967, Okada and Honjo 1973, Honjo and Okada 1974, Kleijne 1993) and from smaller areas (e.g., Winter et al. 1979, Reid 1980, Mitchell-Ines and Winter 1987, Samtleben and Schröder 1992, Samtleben et al. 1995, Ziveri et al. 1995), the environmental parameters that control their distribution are still poorly understood. A recent summary of the most important contributions on the distribution of modern coccolithophores is

given by Winter and Siesser (1994). Using the available data, Young (1994) separated three groups generally defined on ecological and morphological criteria. (1) Species characteristic for eutrophic environments. These environments in equatorial waters, high latitudes, as well as in upwelling areas, are dominated by placolith-bearing species. All species within this group are so-called r-strategists, i.e. they respond to nutrient enrichment with enhanced growth rates or productivity. Predominantly bloom-forming coccolithophores (such as *Emiliana huxleyi*, *Gephyrocapsa oceanica*, *G. ericsonii*, *Umbellosphaera sibogae*, *Coccolithus pelagicus*) are included in this group. (2) Upper water communities in subtropical latitudes from all oceans are dominated by the species *Umbellosphaera tenuis*, *U. irregularis*, and *Discosphaera tubifera*. These umbelliform species are so-called K-strategists, which are adapted to low nutrient contents, especially of the oligotrophic mid-ocean gyres. (3) The deep euphotic-zone assemblages (150-200m) in low- to mid-latitude are dominated by a third group of species, such as *Florisphaera profunda* and *Gladiolithus flabellatus*. The absence of these floriform species in surface-waters suggest that they live below the mixed layer where the environment is characterized not only by low light intensity, but also by relatively high nutrient levels. In addition, miscellaneous species do not have an obvious distribution pattern, although some of them occasionally dominate the assemblages.

The described distribution patterns of living communities are generally reflected in bottom sediments (e.g. McIntyre and Bé 1967), although relatively little is known about both the transformation from a living coccolithophore community in the plankton into a coccolith assemblage of the underlying deep-sea sediment and of the coccolithophore (carbonate) fluxes to the surface sediments. It is obvious that coccolith assemblages in sediments are reduced by selective destruction and/or dissolution and form a distorted image of the living communities (e.g. Samtleben and Schröder 1992). Fragile coccolith specimens, especially of the umbelliform assemblages and many species of the miscellaneous groups, are heavily dissolved and, thus, less prevalent in sediment assemblages. Alteration processes during descent through the water column have been studied in sediment traps employed in various water depths (e.g. Andruleit 1997). Also, sediment trap studies have been performed in order to examine the seasonal patterns of coccolithophore communities and to estimate the contribution of coccolithophores to the total carbonate flux (Samtleben and Bickert 1990, Steinmetz 1991, Knappertsbusch and Brummer 1995, Ziveri et al. 1995, Andruleit 1997). However, most of these studies were performed in the Norwegian-Greenland Sea, the North Atlantic, and in the eastern Pacific Ocean, whereas only very scarce information on coccolithophores from sediment traps in the South Atlantic exists (Cepek and Wefer in press).

Recent coccoliths in sediments of the South Atlantic are also only scarcely studied, and most of these studies were limited to the shelf/upper slope region around southern Africa (Fincham and Winter 1989, Giraudeau 1992, Giraudeau and Bailey 1994). This is surprising since both

the equatorial Atlantic and the eastern South Atlantic have been the focus of numerous paleoceanographic studies. Many of the previous reconstructions of Late Quaternary variations of South Atlantic surface circulation using sea-surface temperature proxies have concentrated on these regions (Gardner and Hays 1976, Molino et al. 1982, Mix et al. 1986, McIntyre et al. 1989, Schneider et al. 1996). In addition, the potential of coccolithophores for paleoenvironmental studies in the area off southwest Africa has already been shown by Giraudeau (1992) and Winter and Martin (1990).

The present study deals with coccolithophores and coccoliths from surface-waters, surface sediments, and sediment cores recovered from both areas, the equatorial Atlantic and the eastern South Atlantic off Namibia. Selected examples are presented to document the significance of coccolithophores as indicators of oceanic surface-waters, sea-surface temperatures, and paleoproductivity. The composition and concentration of coccolithophores in the plankton are determined along transects crossing the main water masses and the data are compared with the distribution of coccoliths of the surface sediments. Knowledge of their living occurrences as well as their distribution in surface sediments is still a prerequisite for paleoecological and paleoceanographical studies of coccoliths in Quaternary sediments. These data are used to demonstrate the varying significance of coccoliths for distinct environments. The presence of distinct coccolithophore assemblages associated with equatorial upwelling and the subtropical oligotrophic gyres suggest control by nutrients/trophic level rather than temperature alone. Thus, coccolith assemblages in a sediment core of the equatorial Atlantic will be presented as an example for the significance of coccolith studies in paleoproductivity estimates, whereas variations in sea-surface temperatures derived from coccoliths and alkenones will be presented for the eastern South Atlantic.

## **Hydrography**

In general, surface-waters of the South Atlantic exhibit a complex system of currents. The oceanic upper-layer circulation of the South Atlantic has been summarized by Peterson and Stramma (1991) and only a brief summary will be given here for the equatorial and eastern South Atlantic (see Fig.1).

The surface current system in the South Atlantic is dominated by a subtropical anticyclonic gyre, and is closely coupled to lowered atmospheric wind stress. In the eastern South Atlantic off Southwest Africa, the surface-water circulation is dominated by the northward-directed Benguela Coastal Current (BCC), the coastal tongue of the Benguela Current (BC), and the warmer southward-flowing Angola Current (AC) (Fig 2a). BCC and AC converge between 14° and 16°S building a marked front (Angola-Benguela front) which is well defined in terms of

both temperature and salinity. A horizontal gradient of  $4^{\circ}\text{C}$  per  $1^{\circ}$  of latitude is typically observed on the shelf (Shannon and Nelson 1996). In addition, the prevailing winds in this region in turn drive an offshore surface drift and cause a coastal upwelling of cold, nutrient-rich water especially during austral winter. Upwelling occurs in a number of cells south of about  $18^{\circ}\text{S}$  with a major, semi-permanent cell at  $27^{\circ}\text{S}$  (Fig. 2a, Shannon and Nelson 1996). This upwelling leads to an enhanced biological productivity off Namibia. The typical westward extent of the upwelling is between 150 and 250km off the coast.

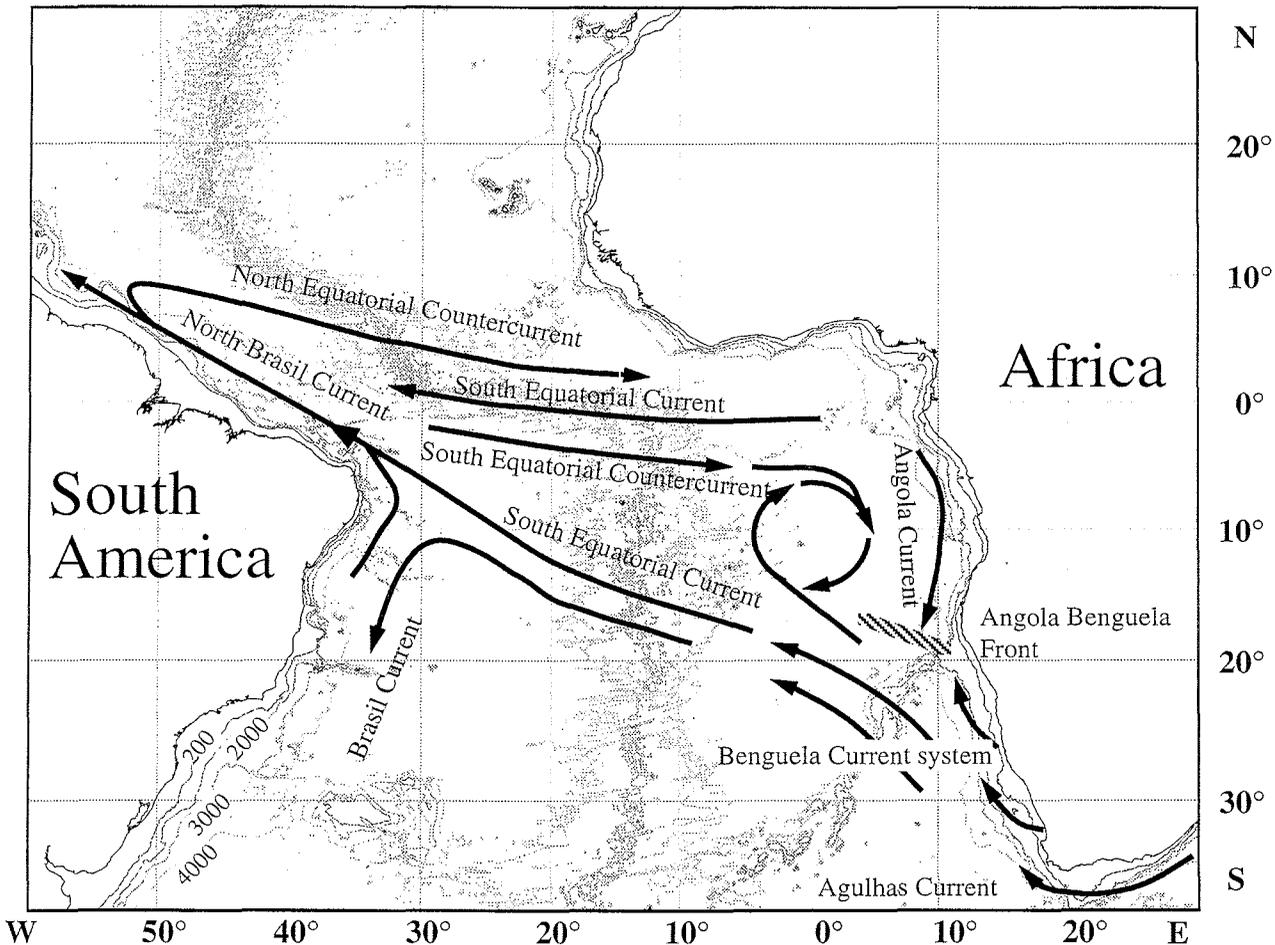


Fig. 1: General surface water circulation patterns in the South Atlantic (after Peterson and Stramma (1991)).

Further offshore the northwestward-flowing Benguela Oceanic Current (BOC), the oceanic portion of the Benguela Current, is characteristic for the upper-layer waters. This flow feeds into a broad, northwestward-flowing South Equatorial Current (SEC), forming the eastern limb of the subtropical gyre (Fig. 1). The SEC consists of two branches, a mainstream flowing south of  $10^{\circ}\text{S}$ , and a smaller, tradewind-forced, faster flowing branch between  $2^{\circ}$  and  $4^{\circ}\text{S}$

(Peterson and Stramma 1991). In the equatorial area, these two branches are separated by the South Equatorial Counter Current (SECC), which moves surface-water eastward. At about 10°S off Brazil the SEC splits into two branches, building the southward-flowing Brazil Current (BC) and the northward-flowing North Brazil Current (NBC) (Stramma and Peterson 1991). The latter contributes to the eastwards flowing North Equator Counter Current (NECC). Its interaction with the northern branch of the SEC lead to a strong convergence of water masses in the mixing area at about 3° to 5°N. This results in downwelling of surface-waters, which supports the eastward flowing Equatorial Undercurrent (EUC). The current occurs at a depth of 50 to 125m (Peterson and Stramma 1991), is present along the entire equator, and feeds surface currents off the African coast. The contact zone of EUC and SEC forms the equatorial divergence where upwelling of colder water from around the thermocline depth occurs (Fig. 2b).

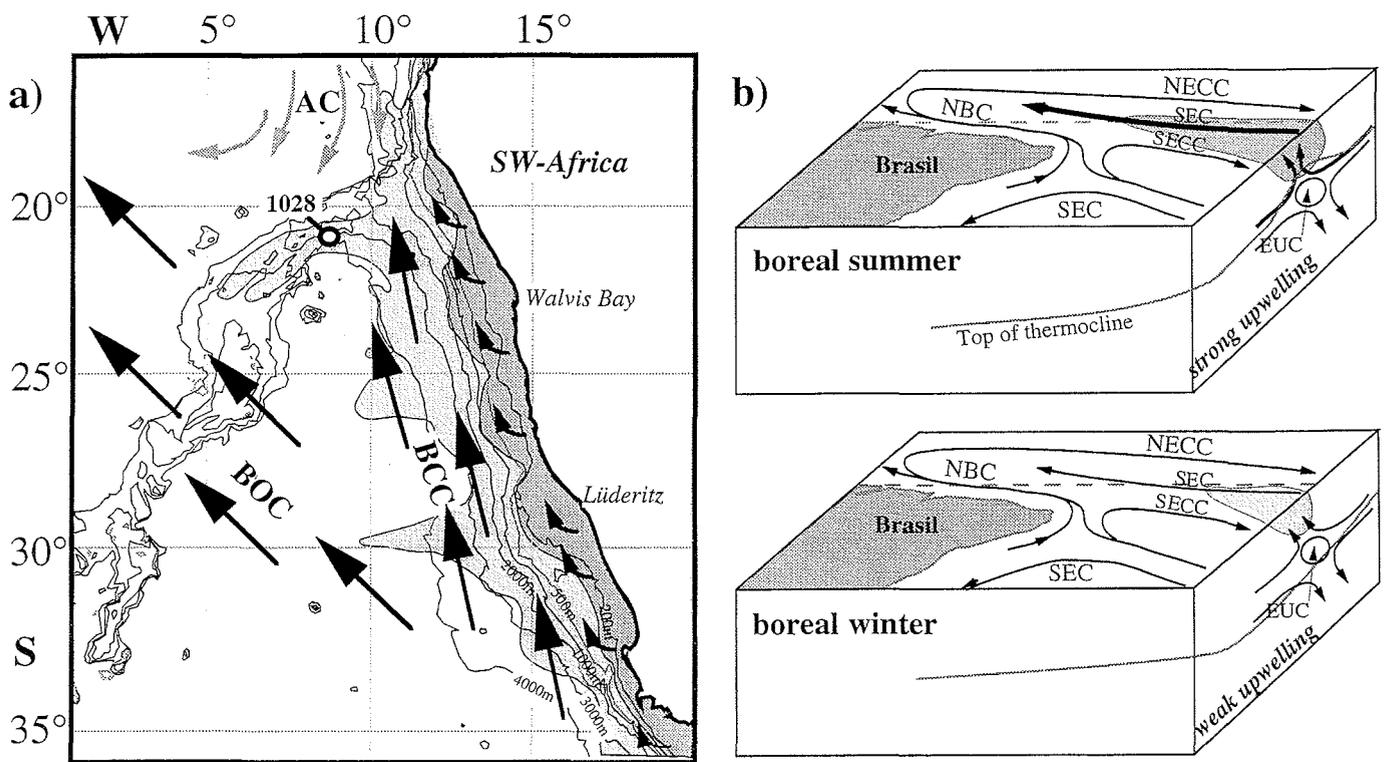


Fig.2: a) Schematic surface current pattern off Southwest Africa. Black arrows indicate relative cool currents of the Benguela Coastal Current (BCC) and the Benguela Oceanic Current (BOC), while grey arrows show the flow pattern of the warm Angola Current (AC). Dark shading indicates Coastal upwelling, whereas light shading shows the extension of upwelling filaments into the mixing zone with oligotrophic open ocean waters. b) Schematic drawing of equatorial Atlantic surface layer structure during boreal summer (June - August) and boreal winter (January - March). During Boreal summer tradewind and South Equatorial Current (SEC) speed reach their maximum and the thermocline is uplifted beneath the equator where nutrient rich water is upwelled into the photic zone causing an increased primary productivity. In boreal winter trade winds cease and SEC current speed is at its minimum. Thermocline is back at equilibrium level and the slowly upwelled waters provide little nutrients to the photic zone, where primary productivity is reduced.

Thus, mean sea surface temperatures (SST) are cooler at, and a little south of, the equator, and warmest north of the equator, especially in the western Atlantic. Strong seasonal variation in the forcing winds, however, produces a fluctuating equatorial system. In boreal summer SST in the eastern equatorial Atlantic is at its minimum, whereas in boreal winter, SST is at its annual maximum and part of the equatorial surface-water flows back as countercurrents. Thus, the SEC and associated features also have different seasonal aspects, such as the thermocline depth which on the mean is deeper in the west and relatively shallow in the east (Fig. 2b). During boreal summer the thermocline sinks in the western equatorial Atlantic due to an increased westward transport of surface-waters which again is a consequence of increased trade winds. Contemporaneously, the thermocline depth slightly shallows towards the east, allowing the thermocline water to mix with warmer surface-waters.

## **Material and Methods**

### Plankton samples

The main proportion of plankton samples was collected in the course of RV "Meteor"-Cruise M 29/3 (Schulz et al. 1995) between August 12th and September 8th in 1994 (Fig. 3). Sampling took place along a transect from 22°S/39°W to about 21°N/21°W, crossing the major surface-water mass boundaries of the equatorial Atlantic. The distribution of coccolithophores in surface-waters of the eastern South Atlantic builds upon samples which were collected on "Meteor"-Cruise M 23/1 along a transect from 29°S/14°E to 37°S/14°W in February 1993 (Fig. 3).

Generally, 5-7 samples of the uppermost 200m of the water column were collected per each station in 5 liter or 10 liter Niskin bottles using a Rosette-sampler. Additional surface-water samples from about 7m water depth were obtained with the ship's seawater pump. For nanoplankton analyses, two to four liters of water was immediately filtered onboard through cellulose nitrate filters (Sartorius™, 47mm or 25mm diameter, 0.45µm pore size) by means of a vacuum pump. Without further washing, rinsing, or chemical conservation the filters were dried at about 40°C. They were stored in plastic Petri dishes and kept in closed boxes using silica gel to assure permanent dryness.

Coccolithophore cell densities were determined with a scanning electron microscope (SEM) usually at 10 KV. For this, a small piece was cut out of the dried filter, mounted on a SEM stub, and sputter-coated with gold/palladium. The number of individuals and the species composition were determined by identifying and counting coccospheres as well as single coccoliths on measured transects (between 1-2mm<sup>2</sup>) at a magnification of 2000x. For species identification, the taxonomy of Jordan and Kleijne (1994) was applied.

### Sediment Samples

The sediment samples used in this study were recovered on the course of several cruises to the eastern South Atlantic (Fig. 3). All surface sediments were obtained with either box corers or multi-corers. Thirty-eight surface sediment samples of the eastern South Atlantic between 19° and 32° S were investigated. Samples mostly originated from the top of the Walvis Ridge as well as from the continental margin off Southwest Africa (Fig. 3).

To obtain late Quaternary records from the equatorial and eastern South Atlantic, two sediment cores with well-established stratigraphies were investigated (Fig. 3). Core GeoB 1117-2 (3°48.9'S 14°53.8'W, water depth 3984 m) is from the Mid-Atlantic-Ridge in the northeasternmost Brasil Basin, whereas core GeoB 1028-5 (20°06.2'S 09°11.1'E, water depth 2209m) comes from the northern crest of the Walvis Ridge. The age models for the cores are based on a graphic correlation of the  $\delta^{18}\text{O}$  records to the SPECMAP standard record (Imbrie et al. 1984). Isotope data are presented elsewhere (Bickert and Wefer 1996, Schneider et al. 1996).

A combined dilution/filtering technique as described by Andruleit (1996) was used for the preparation of sediment samples. A small amount of sediment was weighed and brought into suspension. After treatment with a rotary splitter the suspension was filtered through polycarbonate membrane filters (Schleicher & Schuell<sup>TM</sup>, 50mm diameter, 0.4 $\mu\text{m}$  pore size). A monolayer of all sediment particles was produced and subject to SEM analysis. All coccoliths were recorded in numbers per gram dry sediment.

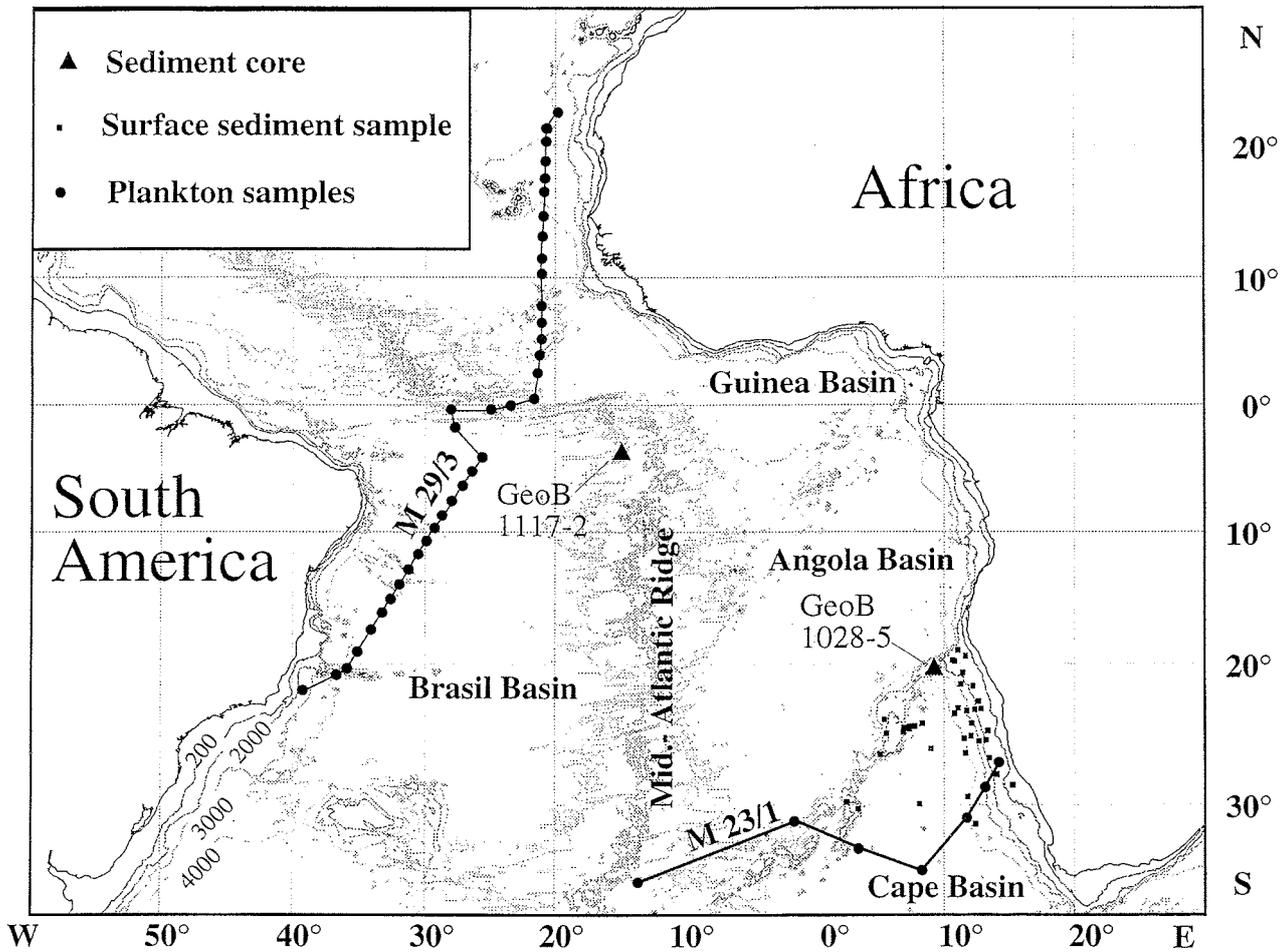


Fig. 3: Location map of the investigated plankton samples, surface sediments, and sediment cores.

## Results

The following chapter mainly contains new and, in part, preliminary results. Additionally, some previously published data which are important in the following discussion will also be reported in brief. The results are presented separately for both investigated regions and the presented information is limited to those species having a geological record.

### Equatorial Atlantic

#### *Plankton*

The spatial distribution patterns of coccolithophore communities in the surface-waters show considerable variation in cell numbers. Maximum values along the M29-3 transect of cell densities up to  $300 \times 10^3$  coccospheres/l were found at 20°S, at the equator, at 10-15°N, and at 20°N (Fig. 4). In between coccolithophore standing crops are less than  $10 \times 10^3$  cells/l.

*Emiliania huxleyi* is the main species causing the variations in cell concentrations, with the exception of the maximum off West-Africa at about 10°N where *Gephyrocapsa oceanica* is dominant.

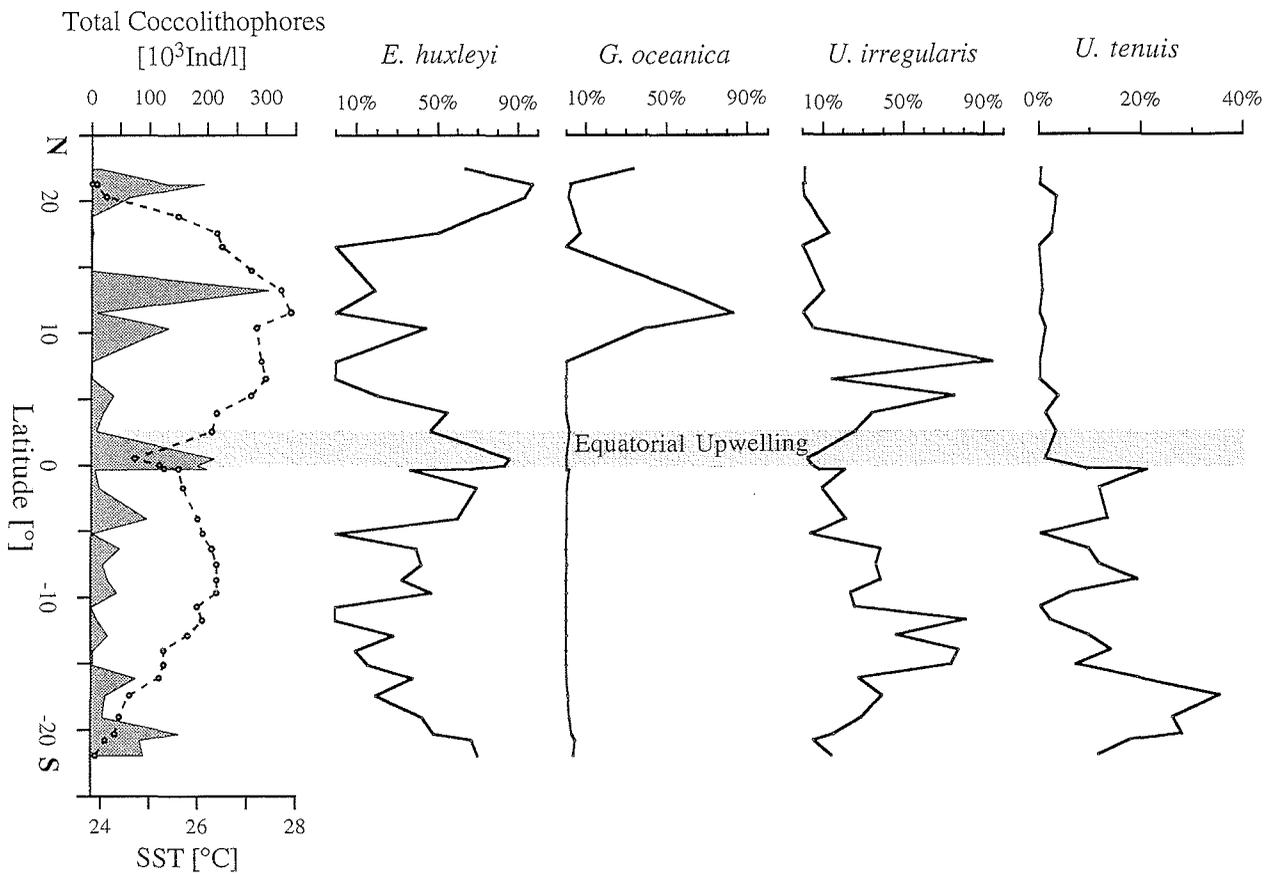


Fig.4: Coccolithophore standing stocks and frequency distributions in surface water samples across the equator collected during Meteor cruises M 29/3 in August/September 1994. Area of main equatorial upwelling is marked with bar.

Samples from the oligotrophic subtropical gyre usually show low concentrations of coccolithophores (always  $<50 \times 10^3$  coccospheres/l) but increased relative abundances of *Umbellosphaera irregularis* and *U. tenuis* (Fig. 4). Other species consistently recorded in the samples are *Calcidiscus leptoporus*, and *Syracosphaera* spp. Together they generally form less than 10% of the flora and never exceed 20% in most samples.

Only few depth transect (0-200m of water depth) have been investigated so far. The highest values were always recorded in the top 20m of the water column and, in addition, the data generally confirm the findings made in the surface-water transects. Therefore, these data will not be presented here.

Sediments

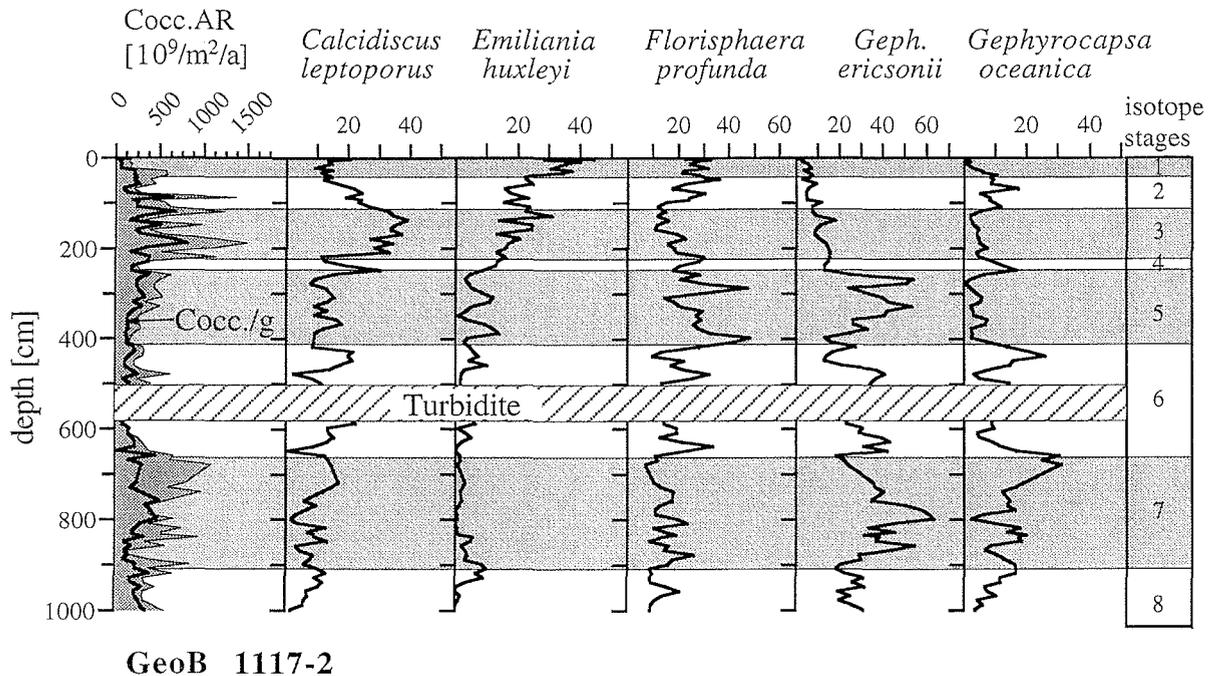


Fig. 5: Total coccolith accumulation rate ( $10^9$  Ind./m<sup>2</sup>/a) and relative frequencies of *C. leptoporus*, *E. huxleyi*, *F. profunda*, *G. ericsonii*, and *G. oceanica*. versus depth in sediment core GeoB 1117. Shaded areas mark interglacial periods. A turbidite sequence that occurs between 4.98 and 5.88 m (with no erosional features so that the stratigraphy remained undisturbed).

The development of the coccolithophore assemblages was investigated in a deep-sea sediment core (GeoB 1117-2) for the past 300.000 years (Fig. 5). Coccolith numbers vary from about  $2.5 \times 10^9$  up to almost  $80 \times 10^9$  coccoliths/g sediment, and accumulation rates vary from  $60 \times 10^9$  up to  $1500 \times 10^9$  coccoliths/m<sup>2</sup>/a. The highest numbers associated with the highest accumulation rates occur in isotope stage 2, 3, and in stage 7. The lowest values are indicative for the Holocene as well as oxygen isotope stages 5 and 6. *Gephyrocapsa* species (*G. ericsonii* and *G. oceanica*) dominate in isotope stages 6 and 7, together making up >50-60% of the assemblage. A first increase in *E. huxleyi* occurs in late stage 6 whereas abundances increase after the stage 5/4 transition. *Gephyrocapsa ericsonii* and *Florisphaera profunda* dominate the assemblage in isotope stage 5. In addition, relative abundances of *F. profunda* show a cyclic variation throughout the record with values ranging from 7 to 48%. A conspicuous increase in *C. leptoporus* can be seen in stage 3, whereas the assemblage is dominated by *F. profunda* and *E. huxleyi* in stages 1-2.

Eastern South Atlantic

Plankton

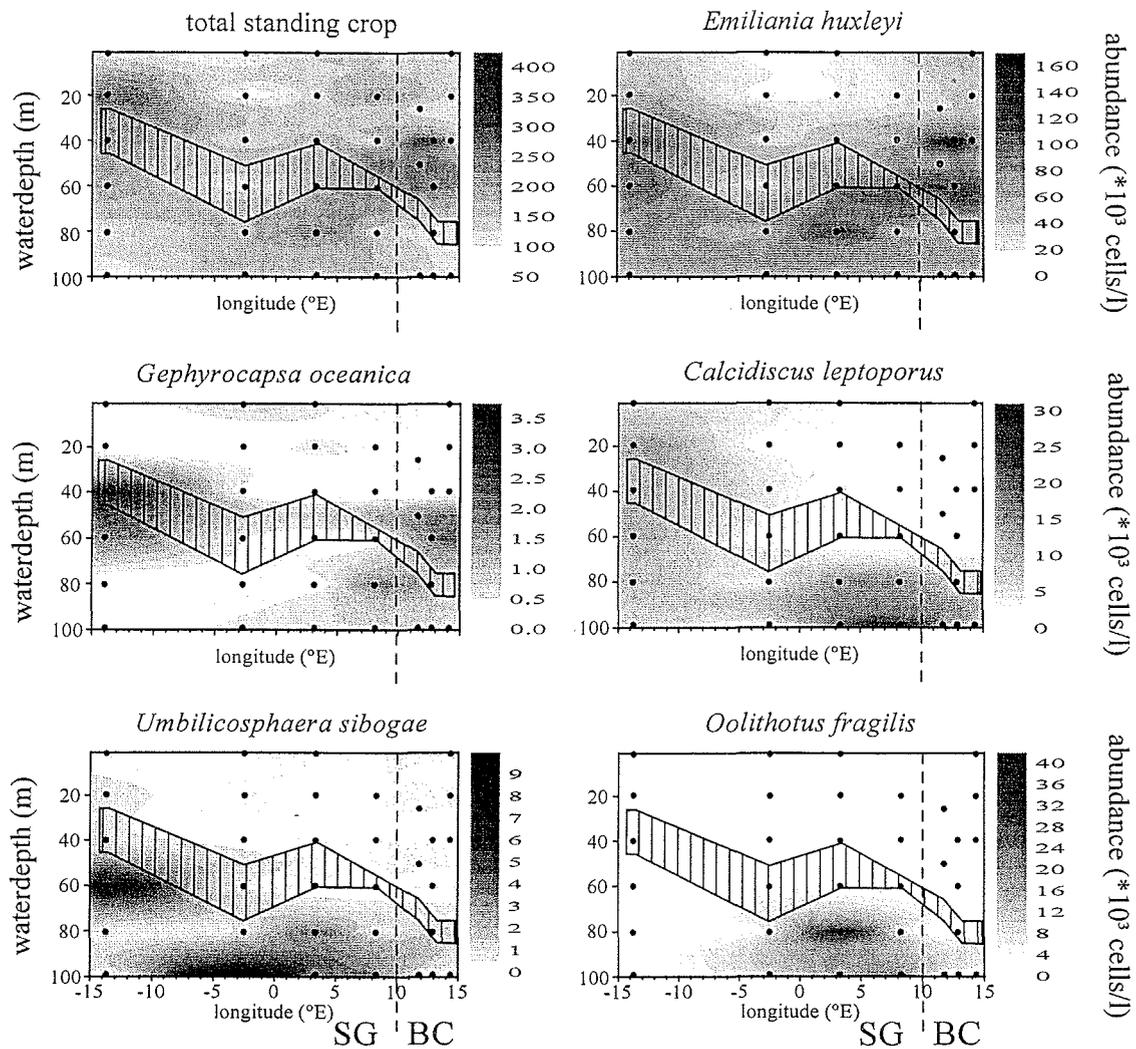


Fig. 6: Lateral distribution and depth stratification of *E. huxleyi*, *G. oceanica*, *C. leptoporus*, *U. sibogae* and *O. fragilis* in plankton samples off Southwest Africa. Dots show the position and depths of the samples. The hatched field marks the thermocline; the dashed line marks the transition from Benguela Current to Subtropical Gyre.

Considerable variation in both cell numbers and species composition are observed. Total cell densities range from less than  $10 \times 10^3$  coccospheres/l to maximum values of more than  $400 \times 10^3$  coccospheres/l. *Emiliana huxleyi* is the dominant species, although *G. ericsonii*, *Umbellosphaera irregularis*, *U. tenuis*, *O. fragilis*, *Syracosphaera* spp., and

holococcolithophores are occasionally prevalent. The lateral and vertical distribution pattern of the geologically important species are shown in Figure 6.

The highest cell numbers of *E. huxleyi* are observed in the Benguela Current above the thermocline at a water depth of 40m ( $199 \times 10^3$  coccospheres/l) and in the subtropical gyre (SG) below the thermocline at 80m ( $129 \times 10^3$  coccospheres/l). Concentrations of *G. oceanica* are generally lower, but its distribution pattern resembles that of *E. huxleyi*. The other species show slightly different distribution and reach highest numbers in the SG below the thermocline (Fig. 6).

Sediments

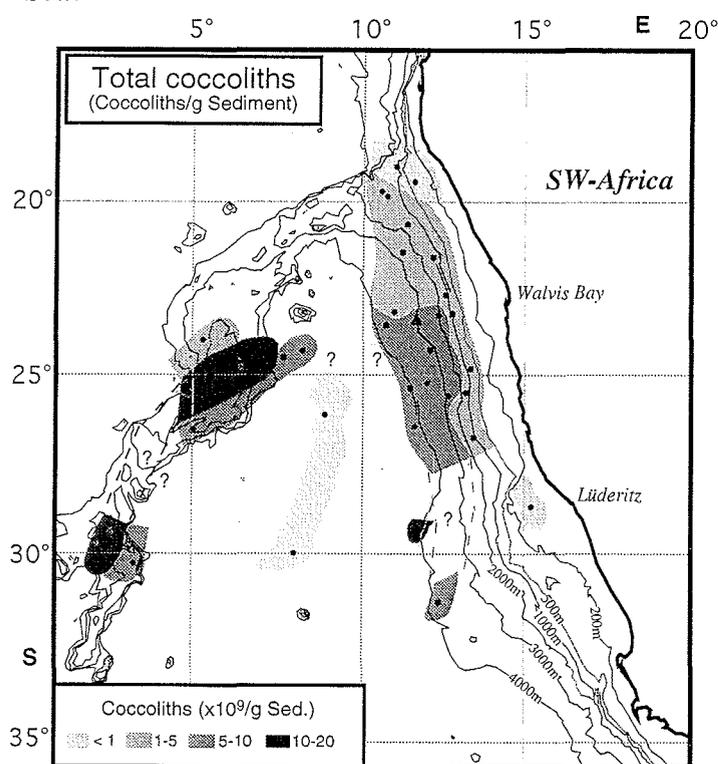


Fig. 7: Distribution of total coccoliths per gram sediment in surface sediments off Southwest Africa.

The highest coccolith numbers in surface sediments of this area were determined in samples derived from the Walvis Ridge ( $>10 \times 10^9$  coccoliths/g sediment), whereas on the upper continental margin off SW-Africa concentrations  $<5 \times 10^9$  coccoliths/g sediment are observed (Fig. 7). The assemblages are dominated by *E. huxleyi*, which usually comprises more than 30-50% in the samples collected from the Walvis Ridge and from the SW African slope and shelf (Fig. 8).

In addition, *C. leptopus* constitutes an important part of the assemblage. Abundances range between 10-30% and rise progressively with increasing water depth. Other species consistently recorded in the samples are *U. sibogae* and *Gephyrocapsa* spp. (*G. oceanica* is shown here as an example), although they never exceed 10% in most of the samples (Fig. 8).

Changes in the relative abundance of the six most abundant species in sediments of the Walvis Ridge are shown for the last 200 kyrs (Fig. 9). Total coccolith numbers vary from about  $4 \times 10^9$  to up to  $22 \times 10^9$  coccoliths/g sediment. *Emiliania huxleyi*, *G. oceanica* and *C. leptopus* are the most abundant species and show prominent downcore changes in relative abundance. Isotope stage 7 is characterized by the dominance of *C. leptopus*, which is also relatively important throughout the last 170 kyrs. Coccolithophores in isotope stage 6 are dominated by *G. oceanica* (up to  $>50\%$ ). Distinct peaks of *E. huxleyi*, *G. ericsonii*, and *U. sibogae* are

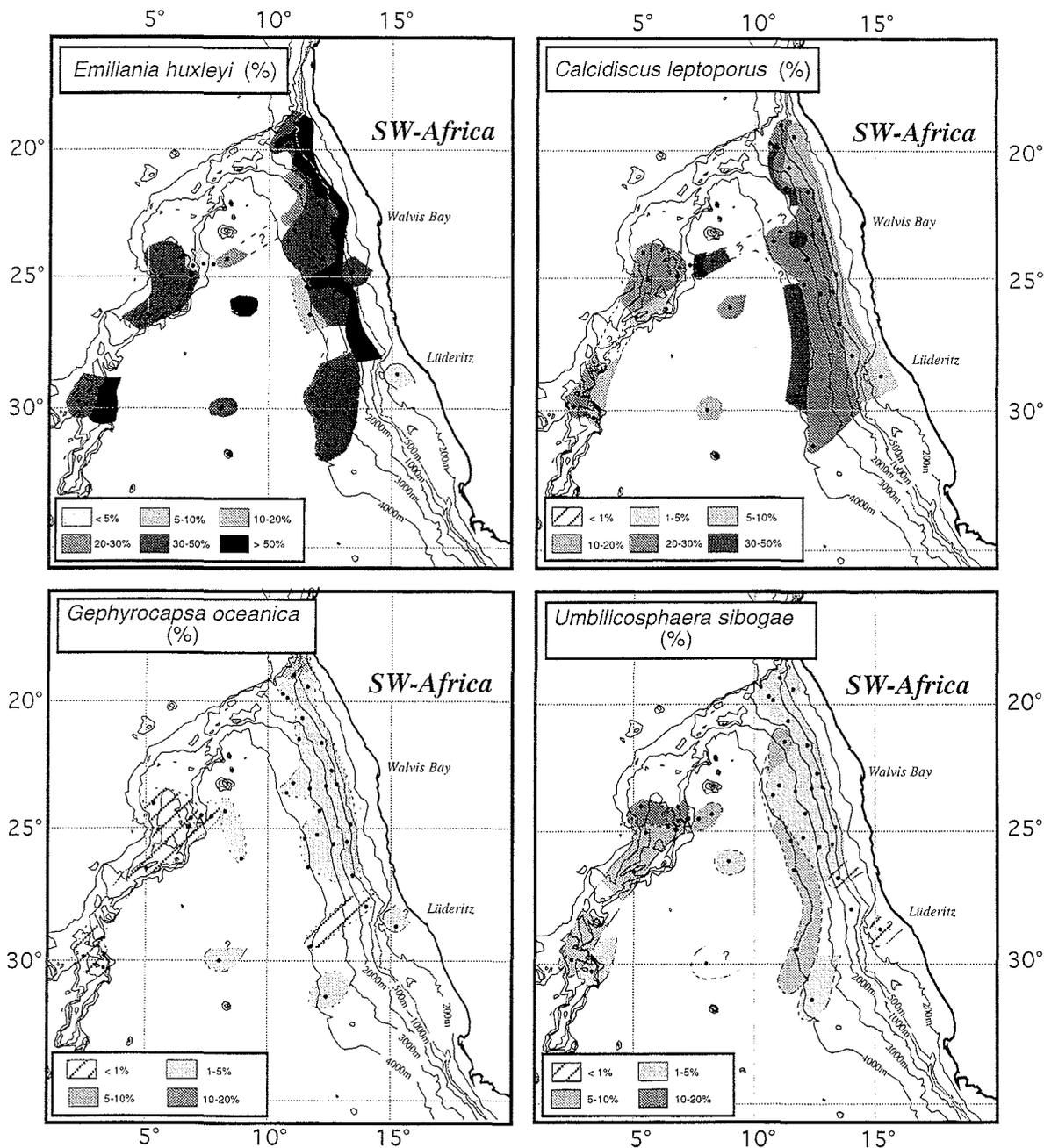


Fig. 8: Distribution of relative frequencies of the most common coccolithophore species in surface sediments from the Walvis-Ridge, the northern Cape Basin and the continental margin off Namibia

observed in isotope stage 5. Above the stage 5/4 transition, abundances of *E. huxleyi* increase progressively, although highest abundances >40% are reached in the Holocene. In addition to *E. huxleyi* and *C. leptoporus*, *G.muellerae* is the main species representing the coccolith assemblages in stages 2-4. However, a conspicuous decrease in *G. muellerae* occurs in early stage 2. Thus, *E. huxleyi* and *C. leptoporus* dominate during most of stages 1-2, whereas *U. sibogae*, *O. fragilis*, and *H. carteri* have a minor but consistent contribution to the assemblages.

GeoB 1028-5

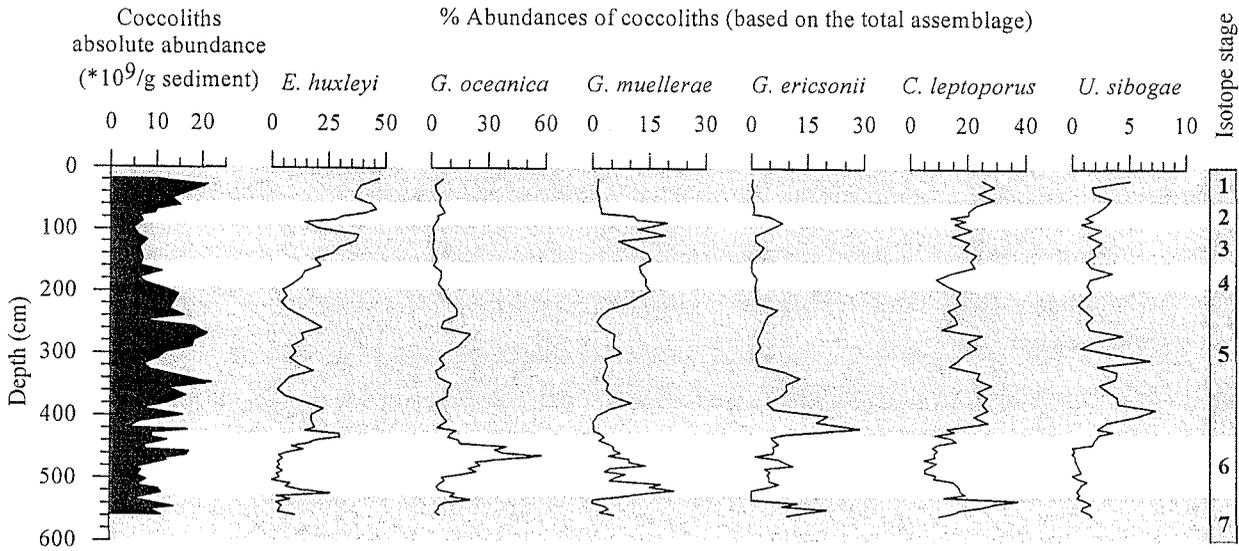


Fig. 9: Total numbers of coccoliths in sedimentcore GeoB 1028 and relative abundances of the most abundant species *E. huxleyi*, *G. oceanica*, *G. muellerae*, *G. ericsonii*, *C. leptoporus*, and *U. sibogae* versus depth. Shaded areas mark interglacial periods.

**Discussion**

In the following, the significance of coccolithophores as a proxy will be discussed for the examples presented. It is intended to show that (1) knowledge of their living occurrences as well as their distribution in surface sediments still provides very useful and necessary information base for studies on coccoliths in sediments. These studies allow to show which hydrographic conditions influence coccolithophore species in the plankton and which sedimentation processes are reflected in the coccolith assemblages of the underlying sediments and, consequently, characterize the fossil record. (2) The presence of distinct coccolithophore assemblages associated with equatorial upwelling and the subtropical oligotrophic gyres suggests control by the nutrients/trophic level rather than temperature alone. Thus, coccolith assemblages in a sediment core of the equatorial Atlantic are presented as an example for the significance of coccolith studies for paleoproductivity estimates. (3) The estimation of surface-water paleotemperatures is one of the necessary inputs for modelling experiments. Exemplary, reconstructions of sea-surface temperatures by means of coccoliths and alkenones will be shown for the eastern South Atlantic.

### Living coccolithophores and their distribution in surface sediments

Understanding the basic coccolithophore ecology is a great need in using their potential as palaeoecological proxies. Thus, investigations of living coccolithophore populations in relation to hydrographic conditions and phytoplankton succession were applied in order to map out the (global) biogeography relative to the large scale oceanographic parameters (especially nutrient distribution, and temperature). The biogeographic distribution patterns of coccoliths in the Holocene are commonly used to infer temperature conditions and circulation patterns (e.g., McIntyre 1967, Roth and Coulbourn 1982, Houghton 1988) because it was shown that coccoliths abundance patterns delineate overlying water masses relatively well. However, the species composition in surface sediments depends on a number of biotic and abiotic processes, such as the environmental conditions in the water zones near the surface, transport by ocean currents, different depth habitats of individual species, lateral transport of species, and dissolution processes in the water column, and the sediment surface in combination with resuspension and transport by bottom currents (e.g., Steinmetz 1994, Samtleben et al. 1995).

The geographic distribution and composition of the living coccolithophore communities in the equatorial Atlantic can be related directly to the environmental conditions of the surface-water at the time and depth of capture. Although plankton data for this area are relatively sparse, an increase both in numbers of total coccolithophore cells as well as in abundance of *E. huxleyi* in samples of the equatorial upwelling which is characterized by lowered temperatures is obvious (see Fig. 4). This finding confirms previous studies in which *E. huxleyi* and/or some other placolith-bearing species predominate in equatorial divergence zones (Okada and Honjo 1973, Nishida 1979). Modern productivity gradients within the equatorial region are, however, relatively small resulting in an estimated doubling of primary productivity in the upwelling domain as compared to the oligotrophic areas (Berger 1989). Except for the equatorial upwelling, the subtropical Atlantic is generally characterized by warm and oligotrophic surface-water masses, where the deep thermocline and nutricline result in a low phytoplankton production. As expected, *Umbellosphaera irregularis* and *U. tenuis* clearly dominate in the surface communities in this area. These species reach abundances of up to 90 % in the warm oligotrophic surface-waters (see Fig. 4), which is in good accordance with previously reported findings from similar latitudes in the Pacific (Nishida 1979, Okada and McIntyre 1979, Kleijne et al. 1989).

In the surface sediments underlying these oligotrophic water masses, *F. profunda* and *G. flabellatus* which are known to live in the lower photic zone (LPZ) are more abundant (e.g. Molino and McIntyre 1990, Hiramatsu and DeDecker 1997, Beaufort et al. 1997, Kinkel et al. in press). Variations in the relative abundance of *F. profunda* were explained with changes of the nutricline depth, with increased relative abundances of LPZ taxa being related to a deep

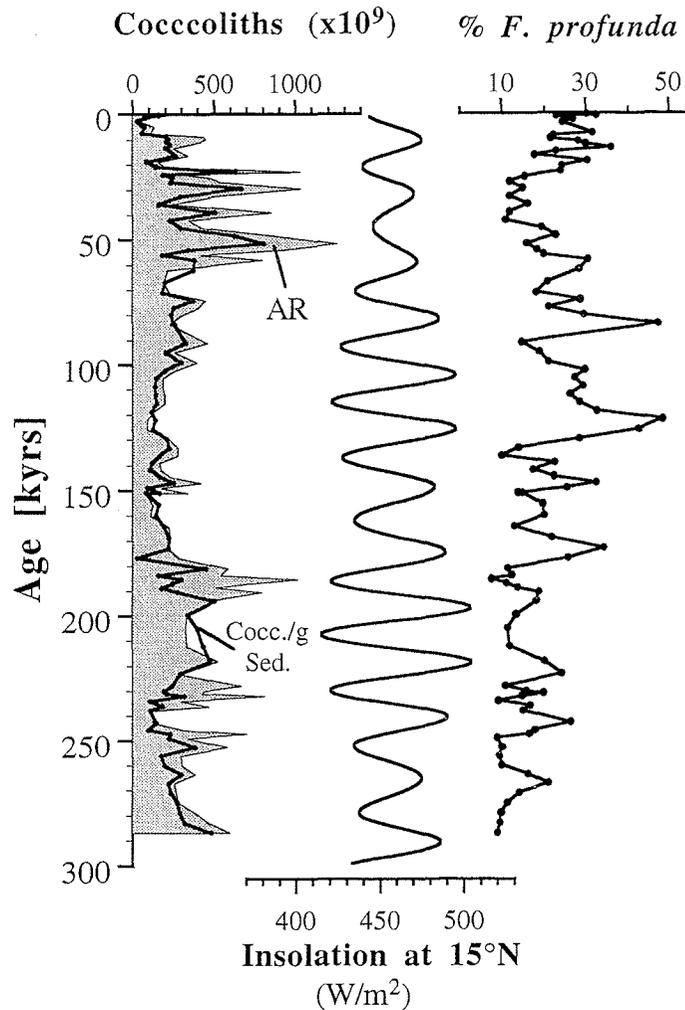


Fig.10: Downcore variation of the relative abundance of *F.profunda*, insolation at 15°N, as well as absolute numbers of coccoliths per gram sediment (black line) together with coccolith accumulation rate (shaded area) in core GeoB 1117.

nutricline and vice versa (Molfino and McIntyre 1990). In general, surface sediment data (Kinkel et al. in press) is consistent with the findings of Molfino and McIntyre (1990). However, this observation mainly demonstrates how severely the living coccolithophore communities are altered as they settle through the water column. Instead, an increase in the abundances of the LPZ is therefore rather caused by the dissolution solubility and lower production of coccolithophores in the upper euphotic zone of oligotrophic areas than by increased production LPZ taxa alone. Nevertheless, the assumption of Molfino and McIntyre (1990) is confirmed as the maximal relative abundance of the LPZ taxa in sediments are indicative of oligotrophic surface-waters with a deep thermocline and nutricline, although the signal is strongly amplified by the dissolution of fragile species. Despite all these difficulties, also in achieving accurate coccolithophore accumulation rates, the present data lead to the conclusion that the pattern in the surface sediments agree well the productivity of the surface-waters.

GeoB 1028-5

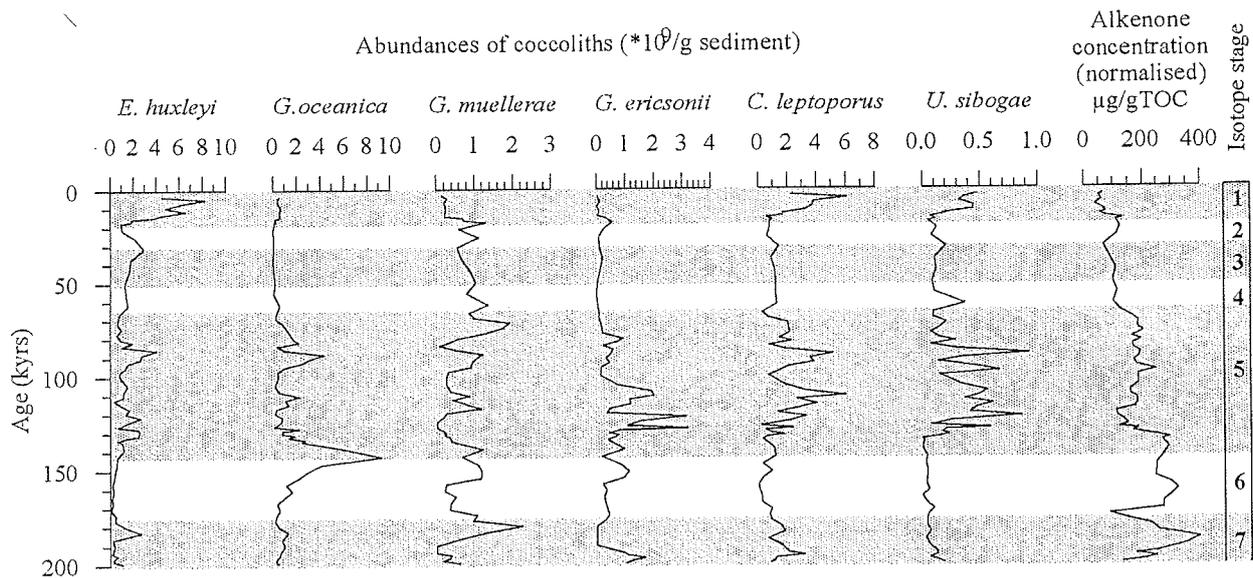


Fig. 11: Total numbers of *E. huxleyi*, *G. oceanica*, *G. muelleriae*, *G. ericsonii*, *C. leptoporus*, and *U. sibogae* together with carbon-normalized alkenone concentration versus age in sediment core GeoB 1028. Shaded areas mark interglacial periods.

Off Namibia, coccolith numbers are high in the surface sediments of the lower slope and of the Walvis Ridge, but they progressively decline towards the shelf (Fig. 8). This pattern can also be continued near-shore to coastal sediments underlying the main areas of upwelling (Giraudeau 1992). This is probably caused by dilution with terrigenous components, and by the spatial variation of phytoplankton productivity in the surface-waters. The diversity was higher in the area where oceanic and upwelled waters mix, whereas upwelling processes probably are responsible for a low diversity population on the shelf. The assemblages found in the latter generally are dominated by *Emiliania huxleyi* and *Calcidiscus leptoporus* (Fig. 8) which, at least in part, is confirmed by their occurrence in the presented plankton data (see Fig. 7). Furthermore, *E. huxleyi* coccoliths make up more than 60% of the assemblage throughout the year in a sediment-trap of the northern Walvis Crest (Cepek and Wefer in press). In fact, this is the only species which was observed in high abundances across the main hydrographical boundaries of this area from the upwelling to the oceanic domain (Fig. 8, Giraudeau and Bailey 1995). Its wide geographical distribution both in the water column and in the surface sediments is probably due to its broad range of ecological tolerance.

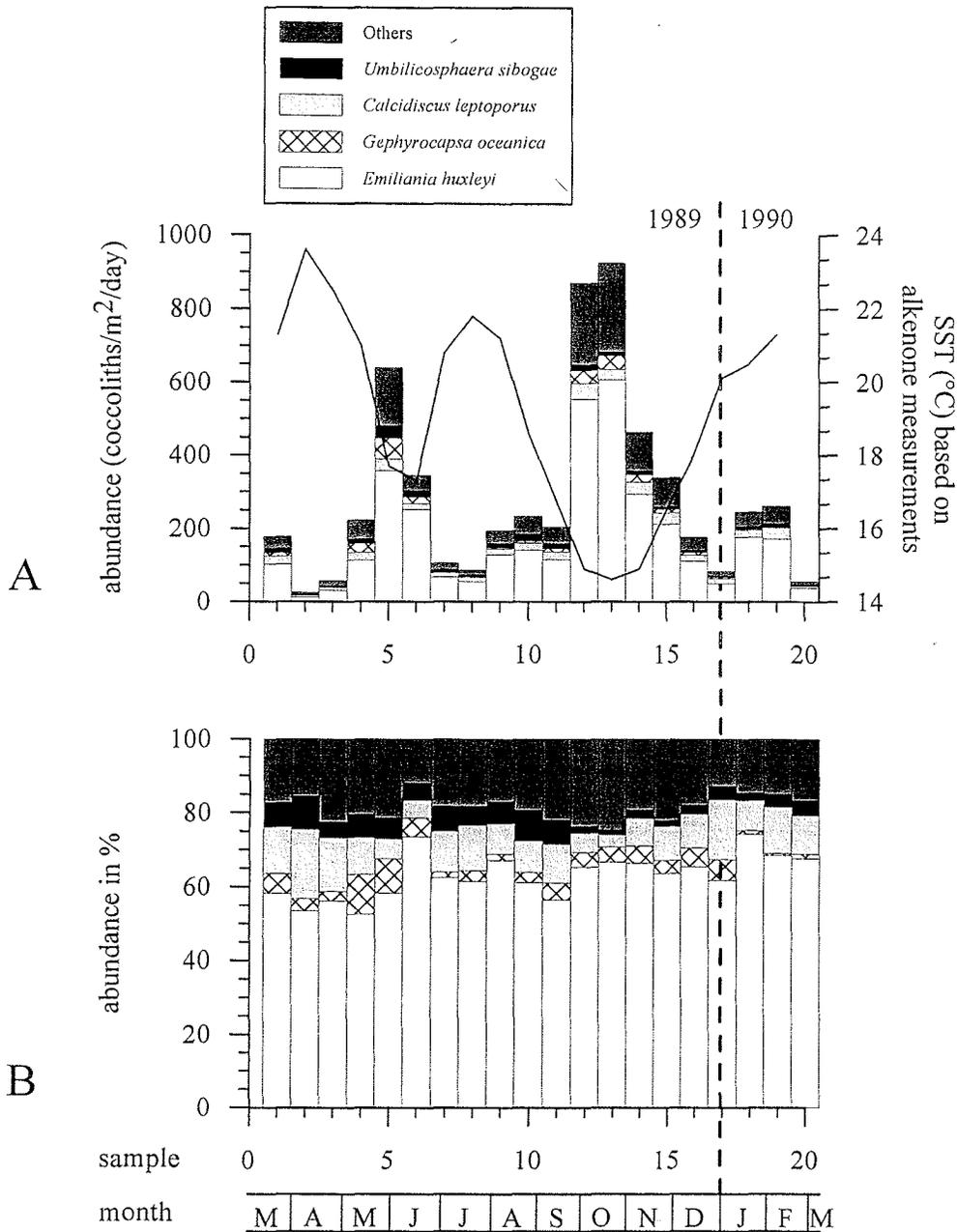


Fig. 12: Data of sediment trap WR 2 deployed in 599m of water depth at the Walvis Ridge off Namibia (from Cepek and Wefer in press). **A**) Absolute numbers (coccoliths/m<sup>2</sup>/day) of the most abundant species together with the alkenone-derived sea-surface temperatures; **B**) Percentage abundances of the most abundant species. The dashed line marks the transition from 1989 to 1990.

The progressive increase in abundance of *C. leptoporus* with increasing water depth may again be due to the resistance of this species against dissolution (see Dittert et al. this issue). Giraudeau (1992) and Giraudeau and Rogers (1994) also suggested that the growth of this species is optimal in oligotrophic conditions west of the main Benguela upwelling. However, this is neither really confirmed by its surface-water distribution pattern nor by its absolute numbers in the surface sediments (Fig. 8, Giraudeau and Bailey 1995). In addition, correlating *C. leptoporus* to oligotrophic conditions, as it is done for the southern Benguela complement

(Giraudeau 1992, Giraudeau and Rogers 1994), is not applicable due to different findings in the equatorial Atlantic (Kinkel et al. in press). The conditions in waters of both equatorial upwelling and off the coast of SW-Africa are possibly more mesotrophic than fully eutrophic or fully oligotrophic and, thus, the areas are comparable. Also, different morphotypes of *C. leptoporus* have been recognized (McIntyre et al. 1970, Knappertsbusch et al. 1997), from which at least one is an eurythermal species, and the other favors warm tropical and subtropical waters. Their occurrences may not only depend on the temperature of the surface-waters, but also on other environmental conditions such as content of nutrients. Differences in morphotype characteristics, such as width and number of elements forming the placolith shield, however, have not been distinguished in the present study.

*Gephyrocapsa oceanica* is found to be less important than described by Giraudeau (1992) from the uppermost slope. This may be due to different counting and preparation techniques, and especially based on the fact that Giraudeau (1992) excluded three dominant taxa (e.g. *E. huxleyi*) from quantitative analysis. *G. oceanica* has been interpreted to prefer waters of high fertility and neritic environments (Mitchell-Innes and Winter 1987, Fincham and Winter 1989), and has been reported to bloom in upwelled waters of low latitudes (Kleijne et al. 1989).

Other species make a minor but consistent contribution to the assemblages in all of the surface sediments, but they constitute less than 5% of all species. Thus, their distribution is more diffuse than the pattern of the prominent species. Nevertheless, the coccolith distribution in the studied area seems to be closely related to the combination of the BC and the upwelling of cold, nutrient-rich subsurface-water off Namibia. In addition, a correlation between the high productivity in the upwelling area and the carbonate production by coccoliths seems to be reasonable, although any dilution with terrigenous material or processes of dissolution may alter this relationship.

#### Primary productivity reconstructions in the equatorial Atlantic

While former studies generally considered coccolith abundances as a proxy for certain oceanographic conditions, the use of quantitative analysis enables a discussion on how the coccolithophore assemblage responds to changing oceanographic conditions in terms of productivity. Until recently only few studies (Backman and Shackleton 1983, Gard 1989, Henrikson 1996, Flores et al. 1997) demonstrated, that quantitative and semi-quantitative analyses of coccolith assemblages can be used for productivity reconstructions in other regions and on different time-scales. Phytoplankton productivity in general is controlled by the availability of nutrients, light and temperature (Winter and Siesser 1994). Since light and temperature are not limiting in the equatorial Atlantic, changes in productivity are triggered by the amount of nutrients available in the euphotic zone. A dilution effect caused by terrigenous

input can be neglected in the equatorial Atlantic. Therefore, fluctuations of the coccolith accumulation rate can be used to monitor coccolithophore production. Using coccolithophores as a productivity proxy provides further information for discussing other existing paleoproductivity estimations (e.g. Müller and Suess 1979, Mix 1989, Brummer and van Eijden 1992, Sarnthein et al. 1992, Struck et al. 1993, Rühlemann et al. 1996), that all have certain inaccuracies. Among all phytoplankton groups coccolithophores may have the best fossil record, as silicate or organic walled microfossils usually are more susceptible to dissolution or oxidation processes than calcareous ones.

The records of the coccolith accumulation rate and the relative abundance of *F. profunda* show contrasting cyclic variations throughout the entire core GeoB 1117-2 (Fig. 10). Based on the surface sediment data (Kinkel et al. in press), this contrast probably results from the variable nutrient supply to the upper euphotic zone where the majority of coccolithophores dwell. The nutrient availability is controlled by the depth location of the nutricline, which can be monitored by the abundance of *F. profunda* (Molfinio and McIntyre 1990). Together with *G. flabellatus* this is the only species that is restricted to the lower euphotic zone (~60 to ~180 m water depth) of the tropical and subtropical oceans (Okada and Honjo 1973), where the availability of light is limited. If the nutricline is shallow, coccolithophore production in the upper euphotic zone is enhanced, and the abundance of *F. profunda* is minimal. This is supported by the presented data from the equatorial upwelling region, where *E. huxleyi* reaches maximum values in the water column as well as in the surface sediments (Kinkel et al. in press). In contrast, a deep nutricline will impede coccolith productivity in the upper euphotic zone and the abundance of *F. profunda* will increase to maximum values. This seems to be the typical situation for the western part of the equatorial Atlantic and outside the equatorial upwelling today, where low concentrations of coccolithophores and high frequencies of fragile species (*U. tenuis* and *U. irregularis*) are found in plankton samples of the surface-waters. As a result, the underlying surface sediments are dominated by *F. profunda* and *G. flabellatus* as shown above.

The cyclic variation in the relative abundance of *F. profunda* is well aligned to the insolation at 15°N (Fig. 10). The insolation is the forcing mechanism that drives the wind systems over the equatorial Atlantic. Cross-spectral analyses of the relative abundances of *F. profunda*, and sea-surface temperatures shown by Molfinio and McIntyre (1990) demonstrated a coherent cyclicity centered on the 23,000 years precessional band. This is in good agreement with other reconstructions based on planktonic foraminiferal assemblages (McIntyre et al. 1989) or records of oxygen isotopes and organic carbon (Schneider et al. 1996, Wefer et al. 1996).

Today, upwelling in the equatorial Atlantic is enhanced in boreal summer and attenuated in the winter. The physical mechanisms that control seasonal nutricline variations and consequently the phytoplankton productivity in the equatorial Atlantic were recently described by Monger et al. (1997). This pattern can be used as a modern analogue for long-term

upwelling fluctuations which can be read in the sedimentary record. If insolation is high, and heating of the African land mass is intense, the air over the continent rises and causes a strengthening of the monsoonal (zonal) wind component. This scenario leads to a weakened upwelling intensity, with a deep thermocline and nutricline and causes the relative abundance of *F. profunda* to increase. The opposite scenario consisting in the reduced heat exposure of the African land mass due to an insolation minimum, will cause an increase of the southeasterly trade wind component, which is the driving factor for intense upwelling. Intensified trade winds cause a shoaling of both nutricline and thermocline. They also increase the upwelling area. The shoaling of the nutricline provides the upper euphotic zone, where most of the coccolithophores dwell, with sufficient nutrients leading to an increased productivity. This can be seen from both the increased coccolith accumulation rates and minimum values of relative abundance of *F. profunda* (Fig. 10). Most significant maxima in coccolith accumulation occur in late stage 8, early stage 7 and at the stage 7/6 boundary. Throughout stages 6 and 5, the accumulation of coccolith remains relatively low demonstrating only smaller fluctuations. At the end of stage 4, the coccolith accumulation rates rise again reaching highest values in stage 3, where fluctuations are extreme. Since the last glacial, the accumulation rates have been dropping to very low values in the Holocene that are comparable to those of stage 5. In general, abundance fluctuations of *F. profunda* show an opposite trend. The majority of species that cause the maximal coccolith accumulation rates (*E. huxleyi*, *Gephyrocapsa* spp. and *C. leptoporus*) have all been reported from areas of upwelling or higher productivity (Kleijne et al. 1989, Giraudeau 1992, Knappertsbusch 1993, Flores et al. 1997). In general, the coccolith accumulation rates show similar trends as paleoproductivity estimates based on carbonate or organic carbon accumulation rates (Bickert 1992, Rühlemann 1996, Schneider, et al. 1996, Wefer, et al. 1996).

The presented results in general confirm those of Molfino and McIntyre (1990). However, it can be concluded that the mechanism that causes a "*F. profunda* signal" differs slightly from their conceptual model. Changes in upper euphotic zone productivity control the occurrence of the surface-water species, whereas the production of *F. profunda* should remain stable, as there are always sufficient nutrients available in its depth habitat. Moreover, alteration of the communities which are characteristic for the oligotrophic surface-water assemblages (such as the decrease in abundance of *U. irregularis* and *U. tenuis*) amplifies the abundance of *F. profunda* with respect to the total coccolithophore flora in the sediments below. The response of *F. profunda* to a changing nutricline depth has been reported from the Northwestern Pacific (Ahagon et al. 1993), the Indian Ocean (Okada and Matsuoka 1996, Beaufort et al. 1997) and the western tropical Atlantic (Bassinot et al. 1997). In all records, *F. profunda* showed cyclicities centered on different frequency bands which control the nutricline depth in those

areas. This gives further evidence that nutricline dynamics rather than other mechanisms that are influenced by precessional forcing cause variations of *F. profunda*.

### Sea-surface temperatures reconstructions

In the following we will discuss two different methods for the use of coccolithophores as proxies in sea-surface temperature reconstructions. These reconstructions are mainly based on the species *E. huxleyi* and those of the genus *Gephyrocapsa*.

The first method deals with the micropaleontological approach considering the evolutionary development and the downcore fluctuations of abundances in correlation with the isotope stages of these taxa. The second method presents a geochemical approach. Here we present and discuss the results of Müller et al. (1997) on the alkenone temperature method as applied to the abundances of coccolithophores.

#### *Micropaleontological approach*

Downcore variations in coccolithophore assemblages can be used to determine relative temperature changes, although the paleoclimatic meaning of some of the coccolithophore taxa, as stated above, remains controversial.

The highest numbers of coccoliths in core GeoB 1028 (Fig. 9) off Namibia are observed in the relatively warm interglacial stages, except in isotope stage 6 where high numbers are recorded. Both concentrations and relative abundances of coccoliths vary between glacials and interglacials in concert with sea-surface temperature variations as recorded by alkenone data (Fig. 13, also Summerhayes et al. 1995, Müller et al. 1997).

At first glance this does not seem to be in good agreement with recent coccolith data provided from a sediment trap located at the northern crest of the Walvis Ridge. As noted by Cepek & Wefer (in press), maximum values of coccolith fluxes occur during austral spring and autumn, when temperatures, recorded by alkenone data, are lowest (Fig. 12). On the other hand this observation corroborates the relatively high numbers of coccoliths, and especially of *G. oceanica* and *E. huxleyi*, during the glacial stage 6. *Emiliana huxleyi* even reached high coccolith numbers during glacial stage 2. In addition, long-term evolutionary trends in coccolithophore development are possibly superimposed on short-term ecological trends, especially if one considers the very rapid evolutionary development in the genus *Gephyrocapsa*, which also include *E. huxleyi* (e.g. Samtleben 1980). Thus, at least the change in dominance from *G. muelleriae* / *G. ericsonii* to *E. huxleyi* may represent a phylogenetic development during which changing abundances may have been caused by variations in ecological conditions.

GeoB 1028-5

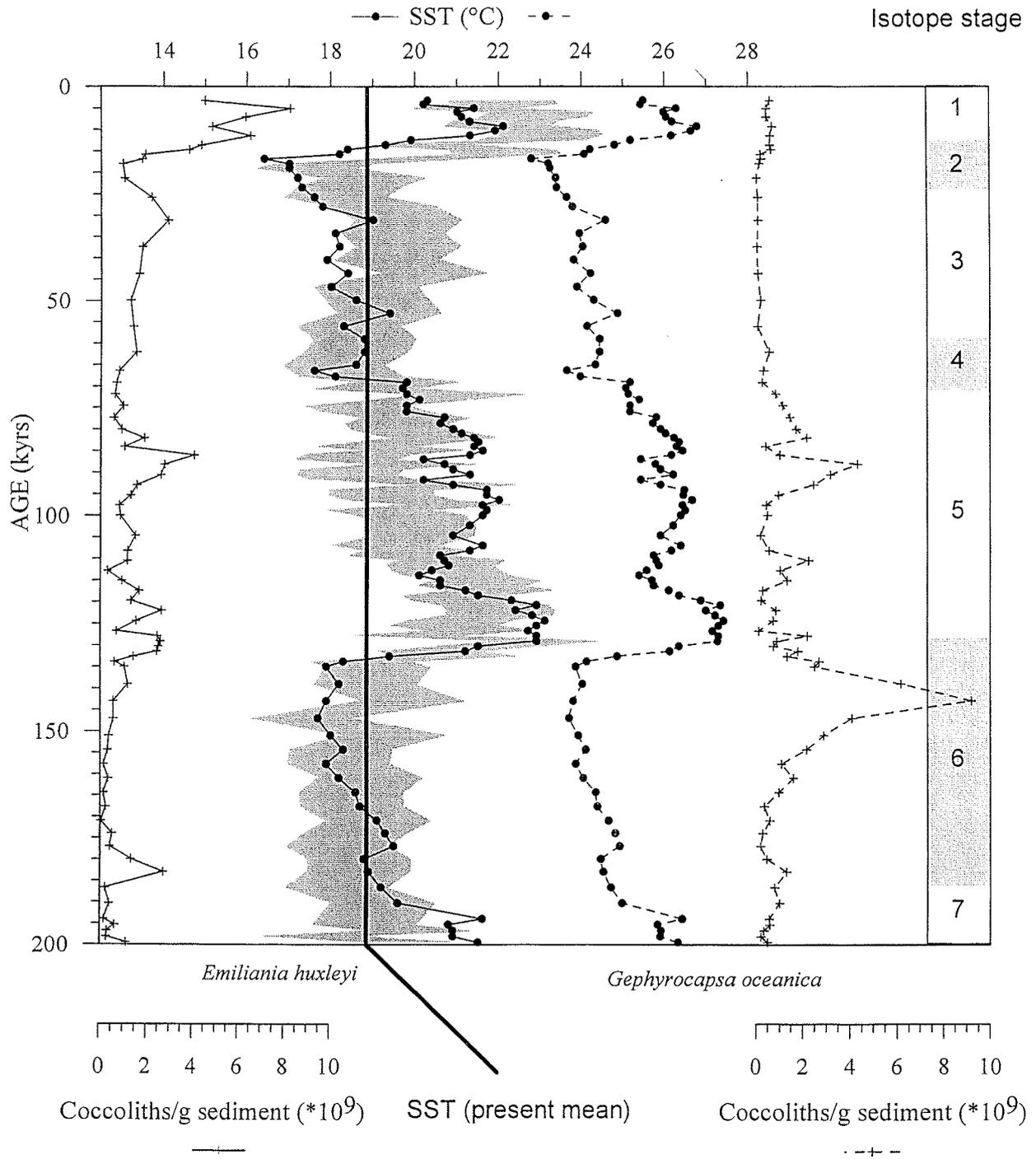


Fig. 13: Oxygen isotope- and alkenone-derived sea surface temperatures (SST) for core GeoB 1028 over the last 200 kyrs (modified from Müller et al. 1997). Isotopic SST was calculated applying the paleotemperature equation of Epstein et al. (1953) using a tolerance in salinity of 1 ‰. SST from the  $U_{37}^{k'}$  were calculated using published relationships for *Emiliana huxleyi* (thick solid curve,  $U_{37}^{k'}=0.034T+0.039$ ; Prahl et al., 1988) and *Gephyrocapsa oceanica* (thin solid curve,  $U_{37}^{k'}=0.049T-0.52$ ; Volkman et al., 1995).

In addition, *E. huxleyi* is a eurythermal species with a worldwide geographic distribution and is not useful in the reconstruction of surface-water temperatures. This species is mainly influenced by the productivity of the surface-water. Counts of *E. huxleyi* often were removed from the quantitative analysis (e.g., Giraudeau 1992, Winter and Martin 1990) in order to resolve difficulties by underestimating abundances of other species. The rapid increase in abundance of *E. huxleyi* after isotope stage 5 (see Fig. 11) is an ubiquitous phenomenon (Thierstein et al. 1977) whereas the dominance of *G. ericsonii* in isotope stage 5e has also been reported from other areas (e.g., Winter 1982, Winter and Martin 1990). The maxima of the latter species during interglacials and especially in substages 5e, 5c, and 5a indicate that *G. ericsonii* may be considered as a relatively warm-water species. This species is progressively replaced by *G. muelleriae* toward higher latitudes in stage 5 (Baumann 1990, Su 1996, Flores et al. 1997). Thus, the ratio of both species probably reflects changes in surface-water conditions with higher values of *G. muelleriae* indicating lower sea-surface temperatures. In addition to the above mentioned species, highest numbers of total coccoliths in GeoB 1028 are also due to few other species, such as *C. leptoporus* and *G. oceanica* (Fig. 11). A change in dominance as an indication for relative temperature changes has also been reported for the ratio of *G. muelleriae* to *G. oceanica* (Weaver and Pujol 1988). However, *G. oceanica* is important only during isotope stage 6 and seems to be more indicative for relatively increased productivity than for higher water temperatures. In contrast, maxima in the abundance of taxa such as *Umbilicosphaera sibogae* and *C. leptoporus* probably indicate higher sea-surface temperatures during most of the interglacial as well as interstadial periods as they are known to prefer relatively warm surface-waters.

#### *Geochemical approach*

In recent years, past SSTs have increasingly been determined on the basis of relative abundances of  $C_{37}$  alkenones ( $U_{37}^{k'}$ -index) in marine sediments (Brassell et al. 1986). Studies by Volkman et al. (1980a,b, 1995) revealed that these lipids are produced by the coccolithophores *E. huxleyi* and *G. oceanica* inter alia. Several culture experiments (e.g., Brassell et al. 1986, Prah1 et al. 1988) have led to the conclusion that the unsaturation ratio  $U_{37}^{k'}$  is closely correlated with water temperature and seems to be relatively unaffected during sedimentation. Since the calibration derived by Prah1 et al. (1988) has yielded reasonable SSTs in various regions of the modern ocean (e.g. McCaffrey et al. 1990, Kennedy and Brassell 1992, Rosell-Melé et al. 1995, Schneider et al. 1995) it has become a standard calibration method for water temperature estimates in paleoceanographic studies (Eglinton et al. 1992, Lyle et al. 1992, Rostek et al. 1993, Zhao et al. 1993, Schneider et al. 1995, 1996). The application of this method to older sediments assumes that *E. huxleyi* is the dominant species within these sediments. However, this is only true for the last 58 kyrs in core GeoB 1028. Prior to the dominance of *E. huxleyi*,

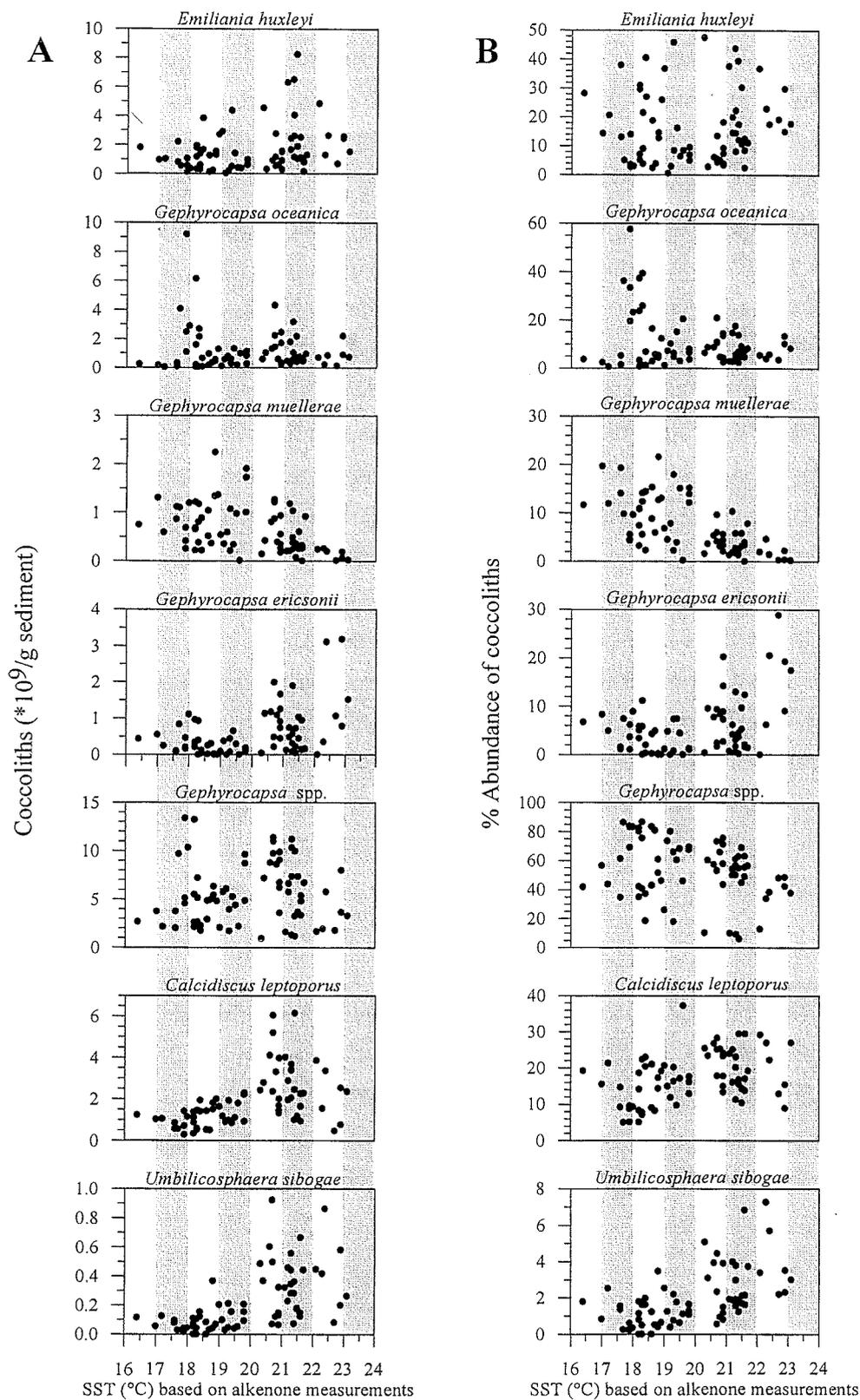


Fig. 14: Plots of normalized alkenone concentrations (K77  $\mu\text{g/g}$  TOC) versus A) absolute numbers ( $\times 10^9$ /g sediment) of most abundant coccoliths and B) relative frequencies (%) of most abundant coccoliths in core GeoB 1028. Black dots indicate samples that are younger than 58 ka before present (the dominance interval of *E. huxleyi*), samples from older sediments are shown by open triangles.

and even before its first appearance 268 kyrs ago (Thierstein et al. 1977), species of the genus *Gephyrocapsa* dominated the assemblages (e.g. Hay 1977, Thierstein et al. 1977, Jordan et al. 1996). Therefore it is questionable whether the equation derived from calibration experiments by Prahl et al. (1988) can be used for SST-estimates in sediments which predate the dominance of *E. huxleyi*. Another calibration derived by Volkman et al. (1995) is based on the unsaturation ratio of alkenones in *G. oceanica*.

Both approximations have already been compared with coccolithophores and the alkenone distribution in core GeoB 1028, to evaluate possible effects of species changes to the  $U_{37}^k$ -index (Müller et al. 1997, Fig. 13). In addition, SST records obtained from the  $U_{37}^k$ -index were also compared with the isotope-derived temperatures. Obviously, in most core sections, SST estimates based on the calibration of Prahl et al. (1988) range within, or close to, the limits of the isotope-derived SST values. A general accordance between isotope-derived temperatures and *E. huxleyi*-based SST estimates persists even in periods that predate the dominance of this species (58 kyr, e.g. during stage 5). Hence, it appears that the equation of Prahl et al. (1988) produces reasonable SST estimates at the Walvis Ridge over the entire 200 kyr record independent of the predominating coccolithophore species. The relationship for *G. oceanica* (Volkman et al. 1995), on the other hand, yields unrealistically high values for the presented core. This led to the suggestion that the equation of Prahl and Wakeham (1987) can be used for paleotemperature reconstruction, regardless whether *E. huxleyi*, *G. oceanica*, or possibly other species dominate the assemblages.

Besides the analytical part, Müller et al. (1997) mainly concentrated on the above mentioned coherence of the different SST records in comparison to relative abundances of *E. huxleyi* and *G. oceanica*. Therefore, we will focus on the correlation between abundances of the six most abundant species and both the normalized alkenone concentration as well as SST estimation, respectively. By simply plotting the alkenone concentrations against the coccolith abundances (both absolute and relative) of the dominant species (Fig. 14), only few trends are apparent in the scatterplots. In general, none of these species correlate well to the alkenone concentrations, neither as to their absolute numbers nor in their relative abundances. Surprisingly, this is also true for *E. huxleyi*, which even is negatively correlated to the alkenone concentration. Numbers and abundances of *G. muelleriae*, *C. leptoporus*, and *U. sibogae* do not correlate to the normalized alkenone concentrations. In contrast, *G. oceanica* and relative abundances of *G. ericsonii* show a slightly positive trend with increasing alkenone concentrations. It has, however, not been demonstrated yet whether all of these species actually do produce alkenones. Alkenones have been identified in lipids of *G. oceanica* (Volkman et al. 1995), as stated above, and therefore it seems reasonable to predict that other species of *Gephyrocapsa* might contain these distinctive biomarkers. The relatively good correlation of *Gephyrocapsa* spp. to the

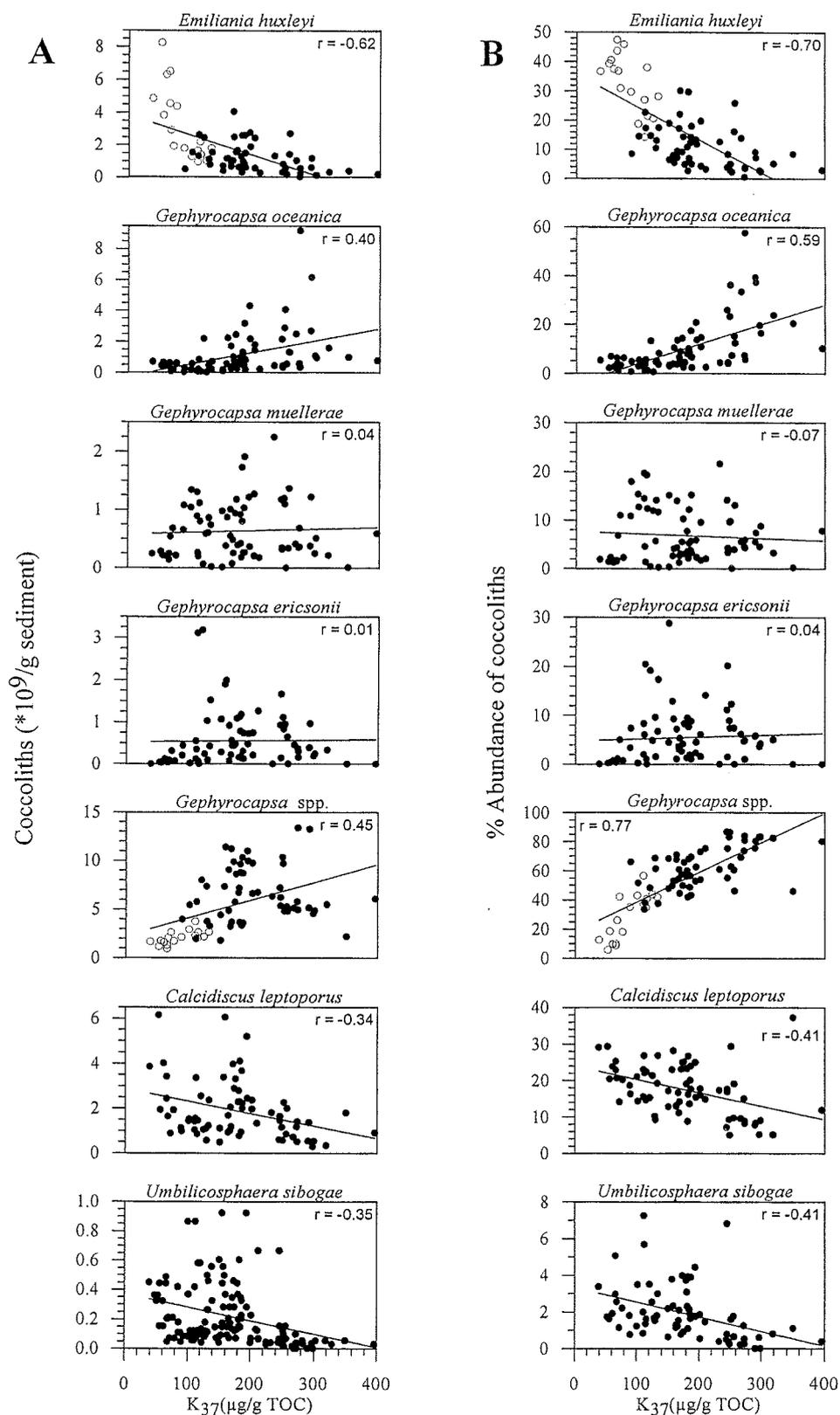


Fig. 15: Plots of SST ( $U_{37}'$ ) versus A) absolute numbers ( $\times 10^9/\text{g sediment}$ ) of most abundant coccoliths and B) relative frequencies (%) of most abundant coccoliths in core GeoB 1028.

alkenone concentrations (Fig. 14) supports the assumption that temperature calculations based on the equation of Volkman et al. (1995) could yield more realistic temperatures than those based on the calibration of Prahl et al. (1988). However, as shown by Müller et al. (1997), this is not the case (Fig. 13), and the reason for this is still an open question.

Using the  $U_{37}^k$ -index as a proxy for SST, a detailed reconstruction of the temperature changes over the last 200ka reveals a cyclic and large scale fluctuation of about 5°C between the maximum interglacial and the minimum glacial temperature estimates (Fig. 13). This confirms earlier findings in the study area made by Summerhayes et al. (1995), although these authors found that minimum temperatures occurred in the interstadial (stage 3). In GeoB 1028, minimum temperatures occurred in glacial stages 6, 4, and 2. The coccolith assemblage generally tends to follow the  $U_{37}^k$  quite closely. Plots of both absolute numbers and relative abundance of the six key species versus SST ( $U_{37}^k$ ) for GeoB1028 demonstrate that only few show a relatively close correlation with paleotemperature estimates (Fig. 15). The abundances of *G. ericsonii*, and *U. sibogae* clearly show a positive correlation with increasing SSTs, whereas those of *G. muellerae*, *G. oceanica*, and *C. leptoporus* are correlated with cooler temperatures. *Emiliania huxleyi* does not show any obvious SST-related trend which may be related to the eurythermal character of this species. Species indicating warmer temperatures can be separated from those indicative of warmer temperatures at about 20°C. These findings independently confirm the above mentioned trends in SST. The relatively cold-water adapted *G. muellerae* clearly predominates exclusively in the cold stages, where SSTs are continuously <19-20°C. In contrast, the warm flora (especially *G. ericsonii* and *U. sibogae*) is much more abundant in interglacials where the temperature is constantl at >20-21°C.

In general, the presented trends are very similar to those found by Jordan et al. (1995) in the upwelling region off Northwest Africa, except for *G. oceanica*. This might rather be related to its affinity to a relatively increased productivity than to higher water temperatures. Also, the connections between the 'warmer' and the 'cooler' species are higher in the upwelling area off Southwestern Africa than observed off Northwest Africa (18°C). The high degree of scattering in all of the plots, however, is not surprising because the distribution of coccolithophores is not necessarily determined by the surface-water temperature alone (see above).

## Conclusions and Perspective

Coccoliths are a major component in the sediments of the South Atlantic, but surprisingly little quantitative information is available from this region. However, as in many other parts of the world's oceans, major oceanographic signals are preserved in coccolith sediment assemblages. Thus, they reflect spatial and temporal changes in the circulation of the surface ocean very well. The following conclusions and perspectives can be drawn from the present study.

1) Distribution and abundances of both coccolithophores in the plankton and coccoliths in the underlying surface sediments of the study areas seem to be related to the combination of surface currents and upwelling. In addition, a correlation between productivity in the upwelling zone and the production of carbonate by coccoliths seems reasonable, although this could be masked by any dilution of terrigenous material and/or dissolution of fragile species.

There is, however, an increasing need to determine present-day biogeographic distribution patterns and to compare them to external controls in terms of biogeography, trophic level and seasonal succession. Thus, more data on the variability of coccolithophores in both species numbers and composition are useful for the identification of environmental tracers as well as to add to the paleoclimatic relevance of some of the coccolithophore taxa. In addition, more information from sediment trap studies is needed for a better understanding of the transformation of a living coccolithophore community into a coccolith assemblage of deep-sea sediments.

2) Analysis of coccoliths from sediment cores of these regions provides useful information on the location of different water masses in the past and consequently on the paleoecology and paleoceanography of these areas. The highest numbers of coccoliths in GeoB 1028 and 1117 are observed during relatively cold periods and are not only due to temperature changes but seem to indicate relatively nutrient-rich waters. In addition, contrasting cyclic variations in coccolith accumulation rate and relative abundance of the deep-dwelling species *F. profunda* are correlated to a varying nutrient supply to the upper euphotic zone. Furthermore, increased occurrences of *G. oceanica* seem to be more indicative of relatively increased productivity than of higher water temperatures.

There are still deficits in understanding the influence effective on the coccolithophores as part of the total phytoplankton primary production, in order to use the record of coccolith production as a primary productivity proxy.

3) Compositional variations in the coccolith assemblage determined in sediment cores already indicate relative temperature changes. Past SSTs can be determined absolutely by alkenones studies ( $U_{37}^k$ -index), which already have become standard technique for temperature estimates in paleoceanographic studies. The  $U_{37}^k$ -based SST record in GeoB 1028 indicates a cyclic and large-scale fluctuation of about 5°C between the maximum interglacial temperatures and the minimum glacial temperatures.

However, determination of the chemotaxonomic significance of variability in these and other potential biomarkers and palaeothermometer calibrations needs to be performed on the species producing alkenones. Also, the relationship between alkenone-derived SST data, alkenone concentrations, and coccolithophore assemblages still is an open question.

## **Acknowledgement**

We are grateful to H. Thierstein (Zürich) and J. Giraudeau (Bordeaux) who made useful suggestions on the manuscript. We would like to express thanks to K. Zonefeld (Bremen), H. Andruleit (Hannover), and G. Fischer (Bremen) for their comments on improving an earlier version of the manuscript. Furthermore, we would like to thank master and crew of the RV 'Meteor' and numerous unnamed colleagues for their help during ship expeditions. C. Wienberg and S. Hüneke is thanked for technical assistance. This research was funded by the Deutsche Forschungsgemeinschaft (Sonderforschungsbereich 261 at Bremen University, Contribution No. xxx).

## References

- Ahagon N, Tanaka Y, Ujiie H (1993) *Florisphaera profunda*, a possible nannoplankton indicator of late Quaternary changes in sea-water turbidity at the northwestern margin of the Pacific. *Mar Micropaleontol* 22: 255-273
- Andruleit H (1996) A filtration technique for quantitative studies of coccoliths. *Micropaleontology* 42: 403-406
- Andruleit H (1997) Coccolithophore fluxes in the Norwegian-Greenland Sea: seasonality and assemblage alterations. *Mar Micropaleontol* 31:45-64
- Backman J, Shackleton NJ (1983) Quantitative Biochronology of Pliocene and Early Pleistocene calcareous nannofossils from the Atlantic, Indian and Pacific Ocean. *Mar Micropaleontol* 8: 141-170
- Bassinot FC, Beaufort I, Vincent E, Labeyrie L (1997) Changes in the Dynamics of western Equatorial Atlantic surface currents and biogenic productivity at the "Mid-Pleistocene Revolution" (930 ka). In Shackleton NJ, Curry WB, Richter C, Bralower TJ (eds) *Proceed. Ocean Drilling Program, Sci. Res. College Station, TX* 154, 269-284.
- Baumann K-H (1990) Veränderlichkeit der Coccolithophoriden-Fauna des Europäischen Nordmeeres im Jungquartär. *Ber SFB 313, Univ Kiel*, 22: 146p.
- Beaufort L, Lancelot Y, Camberlin P, Cayre O, Vincent E, Bassinot F, Labeyrie L (1997) Insolation cycles as a major control of Equatorial Indian Ocean Primary Production. *Science* 278: 21451-1454
- Bickert T (1992) Rekonstruktion der spätquaternären Bodenwasserzirkulation im östlichen Südatlantik über stabile Isotope benthischer Foraminiferen. *Ber FB Geowiss, Univ Bremen*, 27: 205 p
- Bickert T, Wefer G (1996) Late Quaternary deep water circulation in the South Atlantic: reconstruction from carbonate dissolution and benthic stable isotopes. In: Wefer G, Berger WH, Siedler G, Webb D (eds) *The South Atlantic; Present and Past Circulation*. Springer, Berlin, 599-620.
- Boon JJ, van der Meer FW, Schuyl PJW, de Leeuw JW, Schenk PA, Burlingame AL (1978) Organic geochemical analysis of core samples from Site 362, Walvis Ridge, DSDP Leg 40. In: (ed) , *Init. Repts. DSDP, Leg 40, Supplement: 627-637*; U.S. Government Printing Office, Washington, D.C.
- Brassell SC, Eglinton G, Pflaumann U, Sarnthein M (1986) Molecular stratigraphy: a new tool for climatic assesment. *Nature* 320: 129 -133
- Brummer GJA, van Eijden AJM (1992) "Blue-ocean" paleoproductivity estimates from pelagic carbonate mass accumulation rates. *Mar Micropaleontol* 19: 99-117

- Cepek M, Wefer G (in press) Seasonal distribution of recent coccolithophorids in a sediment trap at the Walvis Ridge. *Mar Micropalaeontol*, in press
- Chapman MR, Shackleton NJ, Zhao M, Eglinton G (1996) Faunal and alkenone reconstructions of subtropical North Atlantic surface hydrography and paleotemperature over the last 28 kyr. *Paleoceanography* 11: 343-357
- Crux JA, van Heck SE (1989) Nannofossils and their application - Proceedings of the INA Conference, London 1987. Ellis Horwood Limited, Chichester, 356 p.
- Ditert N, Baumann K-H, Bickert T, Henrich R, Kinkel H, Meggers H.(in press) Carbonate dissolution in the deep sea: Methods, quantification and paleoceanographic application. In: Fischer G, Wefer G (eds) *proxies in Paleoceanography – examples from the south Atlantic*. Springer, Berlin
- Eglinton G, Bradshaw SA, Rosell A, Sarnthein M, Pflaumann U, Tiedemann R (1992) Molecular record of secular sea surface temperature changes on 100-year timescales for glacial terminations I, II and IV. *Nature* 356: 423-426.
- Emeis KC, Anderson DM, Doose H, Kroon D, Schulz-Bull D (1995) Sea-surface temperatures and the history of monsoon upwelling in the Northwest Arabian Sea during the last 500,000 years. *Quat Res* 43: 355-361
- Flores JA, Sierro FJ, Franés G, Vázquez A, Zamarreno I (1997) The last 100,00 years in the western Mediterranean: sea surface-water and frontal dynamics as revealed by coccolithophores. *Mar Micropaleontol* 29: 351-366
- Fincham MJ, Winter A (1989) Paleoceanographic interpretations of coccoliths and oxygen-isotopes from the sediment surface of the Southwest Indian Ocean. *Mar Micropaleontol* 13: 325-351
- Gaarder KR, Heimdal BR (1977) A revision of the genus *Syracosphaera* Lohmann (Coccolithineae). "Meteor" *Forsch-Ergebn D* 24: 54 -71
- Gaarder KR, Markali J (1956) On the coccolithophorid *Crystallolithus hyalinus* n. gen., n. sp. *Nytt Mag Bot* 5: 1-5
- Gardner JV, Hays JD (1976) Response of sea surface temperature and circulation to global climatic change during the past 200,000 years in the eastern equatorial Atlantic Ocean. *Mem Geol Soc Am* 145: 221-246
- Gard G (1989) Variations in coccolith assemblages during the last glacial cycle in high and mid - latitude Atlantic and Indian oceans. In: Crux JA and Van Heck SE (eds) *Nannofossils and their applications*. Ellis Horwood Limited, Chichester, 1-24.
- Geitzenauer KR, Roche MB, McIntyre A (1977) Coccolith Biogeography from North Atlantic and Pacific Surface Sediments. In: Ramsay ATS (eds) *Oceanic Micropaleontology*. Academic Press, London, 973-1008.

- Giraudeau J (1992) Distribution of Recent nannofossil beneath the Benguela system: southwest African continental margin. *Mar Geol* 108: 219 - 237.
- Giraudeau J, Bailey GW (1995) Spatial dynamics of coccolithophore communities during an upwelling event in the Southern Benguela system. *Cont Shelf Res* 15: 1825-1852.
- Giraudeau J, Monteiro PMS, Nikodemus K (1993) Distribution and malformation of living coccolithophores in the northern Benguela upwelling system off Namibia. *Mar Micropalaeontol* 22: 93 - 110.
- Giraudeau J and Rogers J (1994) Phytoplankton biomass and sea-surface temperature estimates from sea-bed distribution of nannofossils and planktonic foraminifera in the Benguela upwelling system. *Micropaleontology*, 40 (3): 1825 - 1852.
- Halldal P, Markali J (1954) Observations on coccoliths of *Syracosphaera mediterranea* Lohman and *S. molischii* Schiller in the electron microscope. *J Cons perm Internat Expl Mer* 19: 329-336.
- Hay WW (1977) Calcareous Nannofossils. In: Ramsay ATS (ed) *Calcareous Nannofossils*. Academic Press, London, 1055-1200.
- Heimdal BR, Gaarder KR (1980) Coccolithophorids of the eastern part of the central Atlantic.I. "Meteor" *Forsch-Ergebn D* 32: 1-14
- Heimdal BR, Gaarder KR (1981) Coccolithophorids of the eastern part of the central Atlantic.II. "Meteor" *Forsch-Ergebn D* 33: 37 - 69
- Henrikson AS (1996) Calcareous nannoplankton productivity and succession across the Cretaceous-Tertiary boundary in the Pacific (DSDP site 465) and Atlantic (DSDP site 527) oceans. *Cretaceous Res* 17: 451-478
- Hiramatsu C, DeDecker, P (1997) The calcareous nannoplankton assemblages of surface sediments in the Tasman and coral Seas. *Paleogeogr Paleoclimatol Paleoecol* 131: 257-285
- Honjo S, Okada H (1974) Community structure of coccolithophores in the photic layer of the mid-Pacific. *Micropaleontology* 20: 209-230
- Houghton SD (1988) Thermocline control on coccolith diversity and abundance in recent sediments from the Celtic Sea and English Channel. *Mar Geol* 83: 313-319
- Hulburt EM (1976) Limitation of phytoplankton species in the ocean off western Africa. *Limnol Oceanogr* 21: 193-211
- Hulburt EM, Corwin N (1969) Influence of the Amazon River Outflow on the Ecology of the Western Tropical Atlantic. III. The Planktonic Flora between the Amazon River Outflow and the Winward Islands. *J Mar Res* 27: 55 -73
- Imbrie J, Hays JD, Martinson DG, McIntyre A, Mix AC, Morley JJ, Pisias NG, Prell WL, Shackleton NJ (1984) The orbital theory of Pleistocene climate: support from revised chronology of the marine  $\delta^{18}\text{O}$  record. In: Berger A, Imbrie J, Hays JD, Kukla G, Saltzman B (eds) *Milankovitch and Climate, Part I*. D. Reidel, Dordrecht, 269-305.

- Jordan RW, Kleijne A (1994) A classification system for living coccolithophores. In: Winter A, Siesser W.G. (eds) *Coccolithophores*. Cambridge University Press, Cambridge, 83-106.
- Jordan RW, Zhao M, Eglington G, Weaver PPE (1996) Coccolith and alkenone stratigraphy at an upwelling site off NW Africa (ODP 658C) during the last 130,00 years. In: Mognilevsky A, Whatley R (eds) *Microfossils and Oceanic Environments*. Aberystwyth Press, Aberystwyth, 111-130.
- Kennedy JA, Brassell SC (1992) Molecular records of the Santa Barbara basin: comparison with historical records of annual climate change. *Org Geochem* 19: 235-244.
- Kinkel H, Baumann K-H, Cepek M (in press) Coccolithophores in the equatorial Atlantic Ocean: response to seasonal and Late Quaternary surface-water variability. *Mar Micropaleontol*, in press.
- Kleijne A (1991) Holococcolithophorids from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. *Mar Micropaleontol* 17: 1-76.
- Kleijne A (1993) Morphology, taxonomy and distribution of extant coccolithophorids (calcareous nannoplankton). Proefschr. Vrije Univ. Amsterdam, 321p.
- Kleijne A, Kroon D, Zevenboom W (1989) Phytoplankton and foraminiferal frequencies in northern Indian Ocean and Red Sea surface-waters. *Netherlands J Sea Res* 24: 531-539.
- Knappertsbusch M (1993) Geographic distribution of living and Holocene coccolithophores in the Mediterranean sea. *Mar Micropaleontol* 21: 219-247.
- Knappertsbusch M, Brummer GJA (1995) A sediment trap investigation of sinking coccolithophorids in the North Atlantic. *Deep-Sea Res* 42: 1083-1109.
- Longhurst A (1993) Seasonal cooling and blooming in tropical oceans. *Deep-Sea Res* 40: 2145-2177.
- Lyle MW, Prah FG, Sparrow MA (1992) Upwelling and productivity changes inferred from a temperature record in the central equatorial Pacific. *Nature* 355: 812-815.
- McCaffrey MA, Farrington JW, Repeta DJ (1990) The organic geochemistry of Peru margin surface sediments: I. A comparison of the C<sub>37</sub> alkenone and historical El Niño records. *Geochim Cosmochim Acta* 54: 1671-1682.
- McIntyre A (1967) Coccoliths as paleoclimatic indicators of Pleistocene glaciation. *Science* 158: 1314-1317.
- McIntyre A, Bé A (1967) Modern Coccolithophoridae in the Atlantic Ocean. I. Placoliths and cryoliths. *Deep-Sea Res* 14: 561-597.
- McIntyre A, Ruddiman WF, Karlin K, Mix AC (1989) Surface water response of the equatorial Atlantic ocean to orbital forcing. *Paleoceanography* 4: 19 - 55.
- Mitchell-Ines BA, Winter A (1987) Coccolithophores: A major phytoplankton component in mature upwelled waters off the Cape Peninsula, South Africa in March 1983. *Mar Biol* 95: 25-30.

- Mix AC (1989) Pleistocene Paleoproductivity: Evidence from organic carbon and foraminiferal species. In: Berger WH, Smetacek VS, Wefer G (eds) Productivity of the Oceans: Present and Past. Dahlem Workshop, Wiley, New York, 313-340.
- Mix AC, Ruddiman WF, McIntyre A (1986) Late Quaternary Paleoceanography of the tropical Atlantic, I: Spatial variability of annual mean Sea - Surface Temperatures, 0 - 20,000 years B.P. *Paleoceanography* 1: 43-66.
- Molfino B, Kipp NG, Morley JJ (1982) Comparison of Foraminiferal, Coccolithophorid and Radiolarian Paleotemperature Equations: Assemblage Coherency and Estimate Concordancy. *Quat Res* 17: 279 -313.
- Molfino B, McIntyre A (1990) Precessional Forcing of Nutricline Dynamics in the Equatorial Atlantic. *Science* 249: 766-769.
- Monger B, McClain C, Murtugudde R (1997) Seasonal phytoplankton dynamics in the eastern tropical Atlantic. *J Geophys Res* 102: 12,389-12,411.
- Müller PJ, Cepek M, Schneider R, Ruhland G (1997) Alkenone and coccolithophorid changes in Late Quaternary sediments from the Walvis Ridge: Implications for the alkenone paleotemperature method. *Paleogeogr Paleoclimatol Paleoecol* 135: 71-96.
- Müller PJ, Suess E (1979) Productivity, sedimentation rate, and sedimentary organic matter in the oceans. I. Organic carbon preservation. *Deep-Sea Res* 26A: 1347-1362.
- Nishida S (1979) Atlas of Pacific nanoplankton. *NOM Spec Paper* 3: 1-23.
- Okada H, Honjo S (1973) The distribution of oceanic coccolithophorids in the Pacific. *Deep-Sea Res* 20: 355-374.
- Okada H, Matsuoka M (1996) Lower-photic nanoflora as an indicator of the late Quaternary monsoonal paleo-record in the tropical Indian Ocean. In: Mokuilevsky A, Whatley R (eds) *Microfossils and Oceanic Environments*. Aberystwyth Press, Aberystwyth, 231-240.
- Peterson RG, Stramma L (1991) Upper-level circulation in the South Atlantic Ocean. *Progr Oceanogr* 26: 1-73.
- Prahl FG, De Lange GJ, Lyle M, Sparrow MA (1988) Post-depositional stability of long-chain alkenones under contrasting redox conditions. *Nature* 341: 434-437.
- Prahl FG, Wakeham SG (1987) Calibration of unsaturation patterns in long-chain ketone compositions for paleotemperature assessment. *Nature* 330: 367-369.
- Reid FMH (1980) Coccolithophorids from the North Pacific central gyre with notes on their vertical and seasonal distribution. *Micropaleontology* 26: 151-176.
- Rosell-Melé A, Eglinton G, Pflaumann U, Sarthein M (1995) Atlantic core-top calibration of the  $U^{K}_{37}$  index as a sea-surface palaeotemperature indicator. *Geochim Cosmochim Acta* 59: 3099-3107.

- Rostek F, Ruhland G, Bassinot FC, Müller PJ, Labeyrie LD, Lancelot Y, Bard E (1993) Reconstructing Indian Ocean sea surface temperatures and salinity using  $\delta^{18}\text{O}$  and alkenone records. *Nature* 364: 319-321.
- Roth PH, Coulbourn WT (1982) Floral and solution patterns of coccoliths in surface sediments of the North Pacific. *Mar Micropaleontol* 7: 1-52.
- Rühlemann C (1996) Akkumulation von Carbonat und organischem Kohlenstoff im tropischen Atlantik: Spätquartäre Produktivitätsvariationen und ihre Steuerungsmechanismen. *Ber FB Geowiss, Univ Bremen*, 84: 139p.
- Rühlemann C, Frank M, Hale W, Mangini A, Mulitza S, Müller PJ, Wefer G (1996) Late Quaternary productivity changes in the western equatorial Atlantic: Evidence from  $^{230}\text{Th}$ -normalized carbonate and organic carbon accumulation rates. *Mar Geol* 135: 127-152.
- Samtleben C, Bickert T (1990) Coccoliths in Sediment Traps from the Norwegian Sea. *Mar Micropal* 16: 39 - 64.
- Samtleben C (1980) Die Evolution der Coccolithophoriden-Gattung *Gephyrocapsa* nach Befunden im Atlantik. *Paläont Z* 54: 91-127.
- Samtleben C, Schaefer P, Andrleit H, Baumann A, Baumann K-H, Kohly A, Matthiessen J, Schroeder-Ritzrau A (1995) Plankton in the Norwegian-Greenland Sea: From Living communities to Sediment Assemblages - an actualistic approach. *Geol Rundsch* 84: 108-136.
- Samtleben C, Schröder A (1992) Coccolithophore communities in the Norwegian-Greenland Sea and their record in sediments. *Mar Micropaleontol* 19: 333-354.
- Sarnthein M, Pflaumann U, Ross R, Tiedemann R, Winn K (1992) Transfer functions to reconstruct ocean paleoproductivity, a comparison. In: Summerhayes CP, Prell WL, Emeis KC (eds) *Upwelling systems: Evolution since the early Miocene*. *Geol Soc Spec Publ* 64: 411-427.
- Schneider R, Müller PJ, Ruhland G (1995) Late Quaternary surface circulation in the east equatorial South Atlantic: evidence from alkenone sea surface temperatures. *Paleoceanography* 10: 197-219.
- Schneider RR, Müller PJ, Ruhland G, Meinecke G, Schmidt H, Wefer G (1996) Late Quaternary surface temperatures and productivity in the east-equatorial South Atlantic: response to changes in Trade / Monsoon wind forcing and surface-water advection. In: Wefer G, Berger, W.H., Siedler, G., Webb, D. (eds) *The South Atlantic; Present and past Circulation*. Springer, Berlin, 527-551.
- Schulz H, Bleil U, Henrich R, Segel M (1995) *Geo Bremen SOUTH ATLANTIC 1994, Cruise No. 29, 17 June-5 September 1994*. *Meteor Ber Univ Hamburg* 95-2: 323 p.

- Shannon LV, Nelson G (1996) The Benguela: Large scale features and processes and system variability. In: Wefer G, Berger, W.H., Siedler, G., Webb, D. (eds) *The South Atlantic; Present and past Circulation*. Springer, Berlin, 163-210.
- Steinmetz JC (1991) Calcareous Plankton Biocoenosis: Sediment Trap Studies in the Equatorial Atlantic, Central Pacific, and Panama Basin. In: S. Honjo (ed) *Ocean Biocoenosis Series 1*, Woods Hole Oceanogr. Inst. Press, 85 p.
- Steinmetz JC (1994) Sedimentation of coccolithophores. In: Winter A, Siesser WG (eds) *Coccolithophores*. Cambridge University Press, Cambridge, 179-197.
- Struck U, Sarnthein M, Westerhausen L, Barnola JM, Raynaud D (1993) Ocean-atmosphere carbon exchange: impact of the "biological pump" in the Atlantic equatorial upwelling belt over the last 330,000 years. *Paleogeogr Palaeoclimatol Palaeoecol* 103: 41-56
- Su X (1996) Development of Late Tertiary and Quaternary coccolith assemblages in the Northeast Atlantic. *Geomar Repts*, 48: 119p.
- Summerhayes CP, Kroon D, Rosell-Melé A, Jordan RW, Schrader H-J, Hearn R, Villanueva J, Grimalt JO, Eglinton G (1995) Variability in the Benguela Current upwelling system over the past 70,000 years. *Progr Oceanogr* 35: 207-251.
- Thierstein HR, Geitzenauer KR, Molfino B, Shackleton NJ (1977) Global synchronicity of late Quaternary coccolith datum levels: Validation by oxygen isotops. *Geology* 5: 400-404.
- Volkman JK, Barrett SM, Blackburn SI, Sikes EL (1995) Alkenones in *Gephyrocapsa oceanica*: Implications for studies of paleoclimate. *Geochim Cosmochim Acta* 59: 513-520.
- Volkman JK, Eglinton G, Corner EDS, Forsberg TEV (1980a) Long-chain alkenes and alkenones in the marine coccolithophorid *Emiliania huxleyi*. *Phytochem* 19: 2619-2622.
- Volkman JK, Eglinton G, Corner EDS, Sargent JR (1980b) Novel unsaturated straight-chain C<sub>37</sub>-C<sub>39</sub> methyl and ethyl ketones in marine sediments and a coccolithophore *Emiliania huxleyi*. In: Douglas AG, Maxwell JR (eds) *Advances in Organic Geochemistry 1979*. Pergamon, Oxford, 219-227.
- Weaver PPE, Pujol C (1988) History of the last deglaciation in the Alboran Sea (western Mediterranean) and adjacent North Atlantic as revealed by coccolith floras. *Palaeogeogr Palaeoclimatol Palaeoecol*, 64: 35-42.
- Wefer G, Berger WH, Bickert T, Donner B, Fischer G, Kemle-von-Mücke S, Meinecke G, Müller PJ, Mulitza S, Niebler H-S, Pätzold J, Schmidt H, Schneider RR, Segl M (1996) Late Quaternary surface circulation of the South Atlantic: The stable isotope record and Implications for Heat Transport and Productivity. In: Wefer G, Berger WH, Siedler G, Webb D (eds) *The South Atlantic; Present and past Circulation*. Springer, Berlin, 461-502.
- Wefer G, Bleil U, Schulz H, Fischer G (1997) *Geo Bremen South Atlantic 1996 (Volume II)*, Cruise No. 34, 21 February-15 April 1996. *Meteor Ber Univ Hamburg* 97-2: 268p.

- Westbroek P, Brown CW, van Bleijswijk J, Brownlee C, Brummer GJ, Conte M, Egge J, Fernández E, Jordan R, Knappertsbusch M, Stefels J, Veldhuis M, van der Waal P, Young JR (1993) A model system approach to biological climate forcing. The example of *Emiliana huxleyi*. *Glob Planet Change* 8: 27-46.
- Winter A (1982) Paleoenvironmental interpretation of Quaternary coccolith assemblages from the Gulf of Aqaba (Elat), Red Sea. *Rev Espan Micropal*, 14: 291-314.
- Winter A, Martin K (1990) Late Quaternary history of the Agulhas Current. *Paleoceanography* 5: 479-486.
- Winter A, Reiss Z, Luz B (1979) Distribution of living coccolithophore assemblages in the Gulf of Elat (Aqaba). *Mar Micropaleontol* 4: 197-223
- Winter A, Siesser W (1994) *Coccolithophores*. Cambridge University Press, Cambridge, 242 pp.
- Young JR (1994) Functions of coccoliths. In: Winter A and Siesser WG (ed) *Functions of coccoliths*. Cambridge Academic Press, Cambridge, 63-82.
- Young JR, Bown PR, and Burnett JA (1994) Palaeontological perspectives on Haptophyte biology. In: Green J.C. and Leadbeater B.S.C. (eds.), *The Haptophyte Algae, System. Assoc. Spec. Vol.*, 51, Oxford University Press, 379-392.
- Zhao M, Rosell A, Eglinton G (1993) Comparison of two  $U^{K}_{37}$ -sea surface temperature records for the last climatic cycle at ODP Site 658 from the sub-tropical Northeast Atlantic. *Palaeogeogr Palaeoclimatol Palaeoecol*. 103: 57-65.
- Ziveri P, Thunell RC, Rio D (1995) Seasonal changes in coccolithophore densities in the Southern Californian Bight during 1991-1992. *Deep- Sea Res* 42: 1881-1903.

---

---

## **Coccolithophores in the equatorial Atlantic Ocean: response to seasonal and Late Quaternary surface water variability**

Hanno Kinkel\*, Karl-Heinz Baumann, Martin Cepek

*FB Geowissenschaften, Univ. Bremen, Postfach 330440, D-28334 Bremen, Germany*

### **Abstract**

The present study was initiated to ascertain the significance of coccolithophores as a proxy for paleoceanographic and paleoproductivity studies in the equatorial Atlantic. Data from a range of different samples, from the plankton, surface sediments as well as sediment cores are shown and compared with each other.

In general, the living coccolithophores in the surface and subsurface waters show considerable variation in cell numbers and distribution patterns. Cell densities reached a maximum of up to  $300 \times 10^3$  coccospheres/l in the upwelling area of the equatorial Atlantic. Here, *Emiliania huxleyi* is the dominant species with relatively high cell numbers, whereas *Umbellosphaera irregularis* and *U. tenuis* are characteristic for oligotrophic surface waters. Although they are observed in high relative abundances, these species only occur in low absolute numbers. The lower photic zone is dominated by high abundances and considerable cell numbers of *Florisphaera profunda*.

The geographical distribution pattern of coccoliths in surface sediments reflects the conditions of the overlying surface water masses. However, abundances of the oligotrophic species *U. irregularis* and *U. tenuis* are strongly diminished, causing an increase in relative abundance of the lower photic zone taxa *F. profunda* and *Gladiolithus flabellatus*.

During the past 140.000 years the surface water circulation of the equatorial Atlantic has changed drastically, as can be seen from changes in the coccolithophore species composition, absolute coccolith numbers, as well as coccolith accumulation rates. Significant increases in coccolith numbers and accumulation rates is observed in the southern equatorial Atlantic during the last glacial interval (oxygen isotope stages 2-4), which we attribute to enhanced upwelling intensities and advection of cool nutrient rich waters at this site. In the western equatorial Atlantic we observe an opposite trend with decreasing numbers of coccoliths during glacial periods, which probably is caused by a deepening of the thermocline.

## 1. Introduction

Coccolithophores form a major component of the oceanic micro- and nanoplankton and are one of the main open ocean primary producers. Hence, they may provide a good index of open ocean primary productivity (Brummer and van Eijden, 1992). They play a significant role in the CO<sub>2</sub>-O<sub>2</sub>-exchange between the ocean and atmosphere and are exceptional because of their effect on both the biological and the carbonate pumps (Sikes et al., 1994). Because of their optical and biochemical effects they probably produce an additional feedback to climate change (Westbroek et al., 1993). Their cell surfaces are covered by coccoliths, which constitute the single most important component of deep-sea sediments and provide floral, and biomarker signals for interpreting global change in the geological record. Therefore, they are extensively used in paleoecological and paleoceanographical studies (e.g. McIntyre and Bé, 1967; Geitzenauer et al., 1977; Roth and Coulbourn, 1982).

Most coccolithophore species are cosmopolitan but with more or less limited latitudinal distributions. Knowledge of their living occurrences as well as their distribution in surface sediments are prerequisites for paleoecological and paleoceanographical studies using coccoliths as proxies in Quaternary sediments. However, although much information is available on the large oceanic scale distribution of coccolithophores (McIntyre and Bé, 1967; Okada and Honjo, 1973; Honjo and Okada, 1974; Kleijne, 1993) as well as of small regional areas (e.g., Winter et al., 1979; Mitchell-Innes and Winter, 1987; Samtleben and Schröder, 1992; Samtleben et al., 1995; Ziveri et al., 1995), the environmental parameters that control their distribution are still poorly understood. In addition, there have been hardly any studies that have provided information on the distribution and occurrence of coccolithophores in surface waters of the equatorial Atlantic, except for the surface distribution of a few abundant and widespread species off central Africa (Hulburt, 1976).

Nevertheless, biogeographic distribution patterns of coccoliths in surface sediments are commonly used to infer temperature conditions and circulation patterns (e.g., McIntyre, 1967; Roth and Coulbourn, 1982; Houghton, 1988), as well as productivity gradients (Molfino and McIntyre, 1990a; Beaufort et al., 1997). In surface sediments underlying the oligotrophic water masses of the equatorial Atlantic, deep-dwelling species such as *F. profunda* and *G. flabellatus* (Lower Photic Zone = LPZ flora) are most abundant and changes in their occurrence are correlated with changes in nutricline depth (Molfino and McIntyre, 1990 a). According to their model, high abundances of the LPZ flora are associated with a deep nutricline and deep thermocline, while low abundances are characteristic of a shallow nutricline and thermocline. In addition, relative abundances of *F. profunda* have been used as an excellent indicator for reconstructing past changes in the thermocline dynamics especially of the equatorial Atlantic (Molfino and McIntyre, 1990 a, b; McIntyre and Molfino, 1996; Bassinot et al., 1997), but

also for the northwestern Pacific (Ahagon et al., 1993) and the Indian Ocean (Okada and Matsuoka, 1996; Beaufort et al., 1997).

Quantitative coccolith data enables one to discuss the response of the assemblage to changing oceanographic conditions in terms of productivity (e.g., Backman and Shackleton, 1983; Gard, 1989; Henrikson, 1996; Flores et al., 1997). Phytoplankton productivity is generally controlled by the availability of nutrients, light, and temperature (Brand, 1994; Nanninga and Tyrrell, 1996). Since light and temperature are not limiting factors in the equatorial Atlantic, changes in productivity are most likely to be triggered by the amount of nutrients available in the euphotic zone. Using coccolithophores as a productivity proxy provides further information for discussing existing paleoproductivity estimations (e.g., Müller and Suess, 1979; Mix, 1989; Sarnthein et al., 1992; Rühlemann et al., 1996; Beaufort et al., 1997). However, the final accumulation of coccolithophores in surface sediments depends on a number of biotic and abiotic processes, such as the environmental conditions of the near surface waters, transport by ocean currents, different depth habitats of individual species, lateral advection of species, and dissolution processes in the water column as well as at the sediment surface (e.g. Steinmetz, 1994; Samtleben et al., 1995).

Consequently, in the present study observations from a range of different samples - from surface waters, surface sediments, and sediment cores from the equatorial Atlantic - are combined and can be cross-checked. Studied samples document the significance of coccolithophores as indicators of ocean surface water masses, sea-surface temperatures, and paleoproductivity. The presence of coccolithophores associated with equatorial upwelling and the subtropical oligotrophic gyres suggests, that control is at the nutrient/trophic level rather than temperature alone. Thus, coccolith assemblages in the sediment cores of the equatorial Atlantic are presented as an example of the significance of coccolith studies for paleoproductivity estimates.

## 2. Hydrography

In general, today's surface current system in the South Atlantic is characterized by a northward transport of warm ( $>24^{\circ}\text{C}$ ) surface water across the equator, which feeds the Gulf Stream and North Atlantic Drift and, thus, is crucial for the global thermohaline circulation and, especially, for the heat transfer to the Northern Atlantic (Macdonald and Wunsch, 1996).

Surface currents of the study area are dominated by a subtropical anticyclonic gyre, and are closely coupled to lower atmospheric wind stress. Surface waters (upper 50-100m) of the northwestward flowing South Equatorial Current (SEC) form the eastern limb of the subtropical gyre (Fig. 1). The SEC itself consists of two branches, a mainstream flowing south of  $10^{\circ}\text{S}$ , and a trade wind-forced smaller, faster flowing branch between  $2^{\circ}$  and  $4^{\circ}\text{S}$  (Peterson

and Stramma, 1991). In the equatorial area, these two branches are separated by the South Equatorial Counter Current (SECC), which moves surface water eastward and, at about 10°S off Brazil, splits into two branches, the southward flowing Brazil Current (BC) and the northward flowing North Brazil Current (NBC) (Peterson and Stramma, 1991). The latter contributes to the eastward flowing North Equator Counter Current (NECC). Its interaction with the northern branch of the SEC leads to a strong convergence of water masses in a mixing area at about 3° to 5°N. This results in downwelling of surface waters, which supports the eastward flowing Equatorial Undercurrent (EUC). The current extends to a depth of 50 to 125m (Peterson and Stramma, 1991) and is present along the entire equator and feeds surface currents off the African coast. The contact zone of EUC and SEC forms the equatorial divergence where colder water is upwelled from the thermocline (Fig. 1). The source of the upwelled water is essential, as it determines the nutrient concentrations in the upper photic zone, where most of the phytoplankton productivity takes place. If, for example, water becomes upwelled from the EUC, which is a nutrient depleted "recycled" water mass, no significant increase in nutrients and associated phytoplankton production, is observed in the surface waters (Monger et al., 1997).

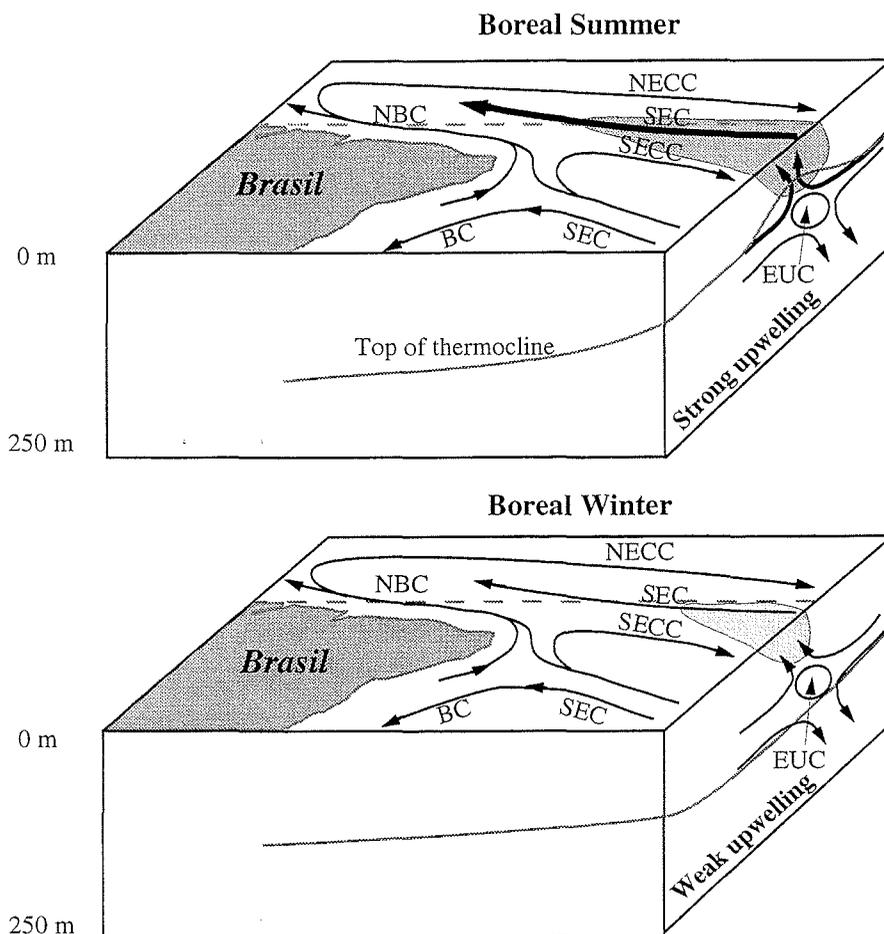


figure caption see opposite page

**Fig. 1.** Schematic drawing of the surface water circulation in the equatorial Atlantic and its seasonal variation (a: Boreal summer, b: Boreal winter) in upwelling intensity. NECC: North Equatorial Counter Current, SECC: South Equatorial Countercurrent, SEC: South Equatorial Current, NBC: North Brazil Current, BC: Brazil Current., EUC: Equatorial Undercurrent.

Mean sea surface temperatures (SST) are cooler at and a little south of the equator, and warmest north of the equator, especially in the western Atlantic. Strong seasonal variation in the forcing winds, however, produces a fluctuating equatorial system. In boreal summer SST in the eastern equatorial Atlantic is at its minimum, whereas in boreal winter, SST is at its annual maximum and part of the equatorial surface water flows back as countercurrents. Thus, the SEC and associated features also have different seasonal aspects, such as the thermocline depth, which on average is deeper in the west and relatively shallow in the east (Fig. 1). During boreal summer the depth of the thermocline deepens in the western equatorial Atlantic due to increased westward transport of surface waters which again is a consequence of increased trade winds. Contemporaneously, the thermocline depth slightly shallows towards the east, allowing thermocline water to mix with warmer surface waters.

### 3. Material and Methods

#### 3.1. Plankton samples

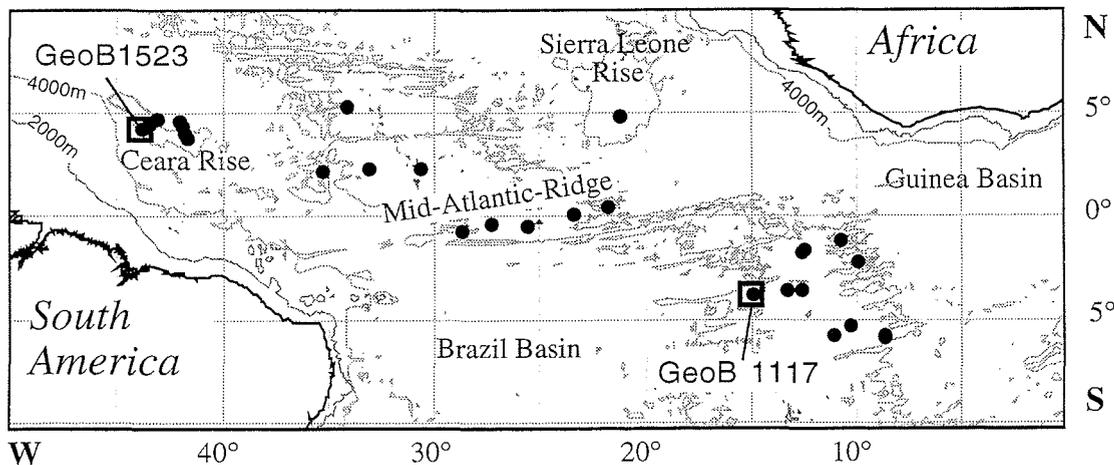
Plankton samples were collected during RV "Meteor"-Cruises M 29/3 between August 12th and September 8th 1994 (Schulz et al., 1995), M 34/4 between March 19th and April 15th 1996 (Fischer et al., 1996), and M 38/1 between January 25th and March 1st 1997 (Fischer et al. in prep.)(for location see Fig. 4, Tab. 1 and 2).

Generally, 5-7 samples of the uppermost 200m of the water column were taken in 5 liter or 10 liter Niskin bottles with a Rosette-sampler. Additional surface water samples from about 5m water depth were obtained with the ship's seawater pump. For coccolithophore analyses, two to four liters of each water sample were immediately filtered onboard through cellulose nitrate filters (Sartorius<sup>TM</sup>, 47mm or 25mm diameter, 0.45 $\mu$ m pore size) using a vacuum pump. Without further washing, rinsing or chemical conservation the filters were dried at about 40°C. They were stored in plastic Petri dishes and kept permanently dry in closed boxes using silica gel.

Coccolithophore cell densities were determined with a scanning electron microscope (SEM) usually at 10 KV. For that purpose, a small piece was cut out of the dried filter, fixed on a SEM stub, and sputtered with gold/palladium. The number of individuals and the species composition were determined by identifying and counting coccospheres as well as single coccoliths on measured transects (between 1-2mm<sup>2</sup>) at a magnification of 3000x. Generally, the taxonomy of Jordan and Kleijne (1994) was applied.

### 3.2. Sediment Samples

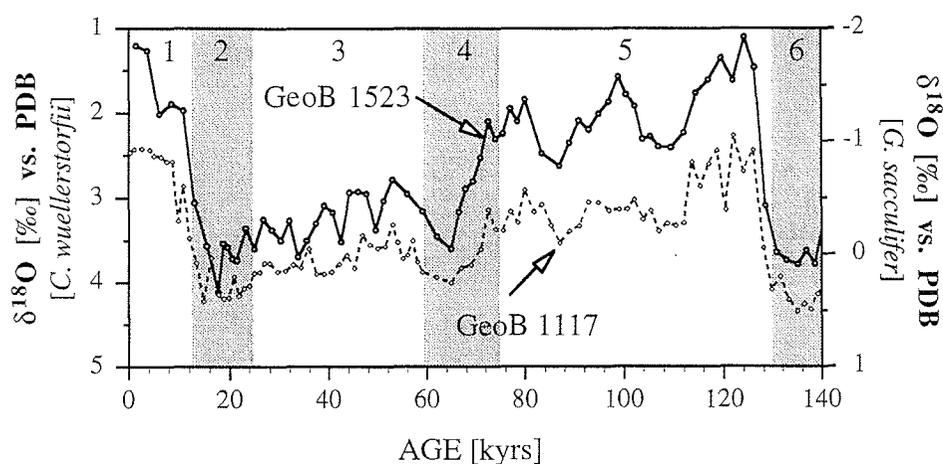
The sediment samples of this study were recovered during several cruises to the equatorial Atlantic. All surface sediments were obtained with either box corers or multi-corers. Twenty-seven surface sediment samples of the study area between 15°S and 12°N were investigated (Fig. 2, Tab. 3).



**Fig. 2.** Location of surface sediment samples (dots) and position of sediment cores GeoB 1117-2 and GeoB 1523-1 (open squares). Positions are given in Tab. 3.

To obtain late Quaternary records from the equatorial Atlantic, two sediment cores with well-established stratigraphies were investigated; Core GeoB 1117-2 (3°48.9'S 14°53.8'W, water depth 3984 m) from the eastern flank of the Mid-Atlantic Ridge and core GeoB 1523-1 (03°49.9'N 41°37.3'W, water depth 3292m) from the top of the eastern Ceará Rise (Fig. 2). Age models for the cores are based on graphic correlation of the  $\delta^{18}\text{O}$  records to the SPECMAP standard record (Imbrie et al., 1984). Isotope data and applied age models have been published elsewhere (Bickert and Wefer, 1996; Rühlemann et al., 1996) (Fig. 3).

For preparation of sediment samples a filtration technique described by Andruleit (1996) was used. A small amount of sediment was weighed and brought into suspension. After dilution with a rotary splitter the suspension was filtered through polycarbonate membrane filters (Schleicher & Schuell™, 50mm diameter, 0.4 $\mu\text{m}$  pore size). A monolayer of all sediment particles was produced which was successively studied by SEM. All coccoliths were recorded in numbers per gram dry sediment.



**Fig. 3.** Stable oxygen isotope records of the investigated cores (solid line *G. sacculifer* GeoB 1523-1 from Rühlemann et al., 1996; dashed line *C. wuellerstorffii* GeoB 1117-2 from Bickert and Wefer, 1996). Numbers on the top mark isotope stages. Grey areas indicate glacial intervals.

Interpretation of coccolith numbers / g sediment may be biased by dilution. Therefore we calculated accumulation rates of coccoliths, which were expressed in coccoliths  $m^{-2} a^{-1}$ . Accumulation rates enable comparison to coccolith(ophore) fluxes from sediment studies and other particle flux reconstructions ( e.g. paleoproductivity estimations).

For core GeoB 1117-2 we used the method of van Andel et al. (1975), which includes linear sedimentation rates and dry bulk densities, whereas  $^{230}Th_{ex}$  - corrected accumulation rates were applied for core GeoB 1523-1 (Rühlemann et al., 1996).

## 4. Results

### 4.1 Plankton sampling results

During plankton sampling the concentrations of coccolithophores varied in regard to the different transects. We differentiated between results of the uppermost surface water at a depth of 5m (Fig.4) and those of the profiles down to a maximal water depth of 200m (Fig. 5). The most abundant species were *E. huxleyi* and *F. profunda*, followed by *U. irregularis*, *U. tenuis* and different species of the genus *Gephyrocapsa*.

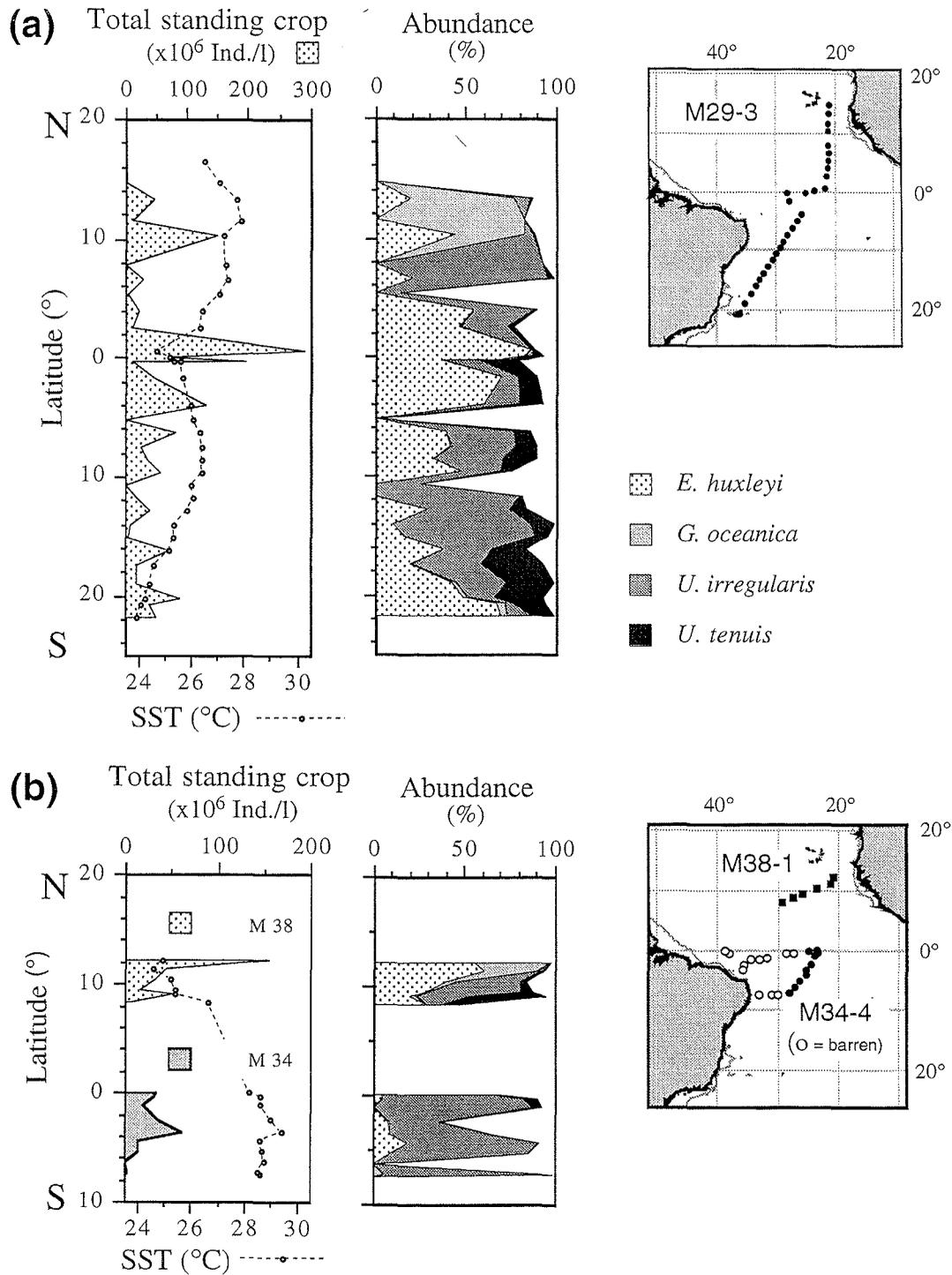


Fig. 4. Total standing crop of coccolithophores, relative abundance of the most common species and sea surface temperatures (dashed line), sampled at three different cruises (see small maps (a) M29/3, (b) M34/4 and M38/1) and seasons in the equatorial Atlantic.

### Upper surface sampling

Results of the upper surface sampling from a water depth of 5 m during the transects of Meteor cruises M29/3, 38/1 and Meteor 34/4 are shown in Fig. 4.

During M29/3 large variations in concentrations of the total coccolithophore standing crop were observed (Fig. 4a). In the Brazil Basin concentrations did not exceed values higher than  $57 \times 10^3$  Ind./l. Concentrations remained consistently low and rose rapidly in the equatorial area, where numbers of up to  $291 \times 10^3$  Ind./l were reached. Between the equatorial upwelling and the north equatorial divergence zone a decrease in the coccolithophore concentration was observed followed by a further rise up to values of  $150 \times 10^3$  Ind./l. The dominating species in the surface waters are *E. huxleyi* all along the transect and *U. irregularis* especially in the Brazil Basin.

Great differences appear regarding the transects of M34/4 and M38/1 (Fig 4b). Cell concentrations are relatively low compared to that of M29/3. Especially in the samples of the Brazil Basin and in the area between the equatorial upwelling and the northequatorial divergence zone coccolithophores are rare to absent. In the equatorial upwelling zone concentrations of coccolithophores showed highest number reaching  $68 \times 10^3$  Ind./l. As already observed during transect M29/3 *E. huxleyi* and *U. irregularis* dominated the assemblage with *U. tenuis* contributing considerably to the community especially in the Brazil Basin. The samples that are labeled barren in figure 4 have extremely low coccolithophore concentrations.

### Plankton depth profiles

Coccolithophore concentrations from three different transects of profile sampling were examined for this study. We took 6 depth profiles during M29/3, 3 profiles during M34/4, and 4 profiles during M38/1 from the studied area (Fig. 5).

In figure 5 the seasonal variation in the distribution of the total coccolithophore standing crop in the upper 200m of the water column is shown. Highest concentrations were observed above 30m (up to  $100 \times 10^3$  Ind./l) during M 29/3. In contrast, highest cell numbers during M34/4 and 38/1 were identified at a depth of 100 m ( $67 \times 10^3$  and  $38 \times 10^3$  Ind./l respectively) and 50m ( $68 \times 10^3$  Ind./l, M38/1 only).

Highest concentrations of coccolithophores seem to be fixed to the upwelling areas of the Equator and the northequatorial divergence zone during M29/3 and especially during M38/1, whereas the cell concentrations during M34/4 appeared to be highest in the Brazil Basin.

Highest concentrations of *E. huxleyi* were generally observed in the equatorial upwelling and the northequatorial divergence zone (Fig. 5). Since this species dominated the assemblages of the upper 30m its main abundance compares well with highest standing crop.



*Florisphaera profunda* is known as a deep-living species, which was confirmed by samples from all three transects of the present study (Fig. 5). Highest concentrations were observed at a depth of 100m in the lower photic zone. In addition, the occurrence of this species correlated with the upwelling in the equatorial area, reaching abundances of up to 74% (M29/3), 38% (M34/4), and 91% (M38/1).

*Umbellosphaera irregularis* was observed in highest concentrations at water depths above 50 m, except the maximum at 100m in the Brazil Basin during M29/3 (Fig. 5). Even though the maxima during M29/3 and M34/4 appeared to be forced by the upwelling at the Equator, this species occurred in remarkable abundances of up to 86% in the Brazil Basin. *U. tenuis* is the only species examined, which constantly showed highest concentrations in the Brazil Basin during all transects (Fig. 5). The appearance of this species in the two upwelling areas of the study area is scarce to absent. Water depth of maximal abundances varied from 100m (M34/4) to the upper 50m (M29/3 and M38/1).

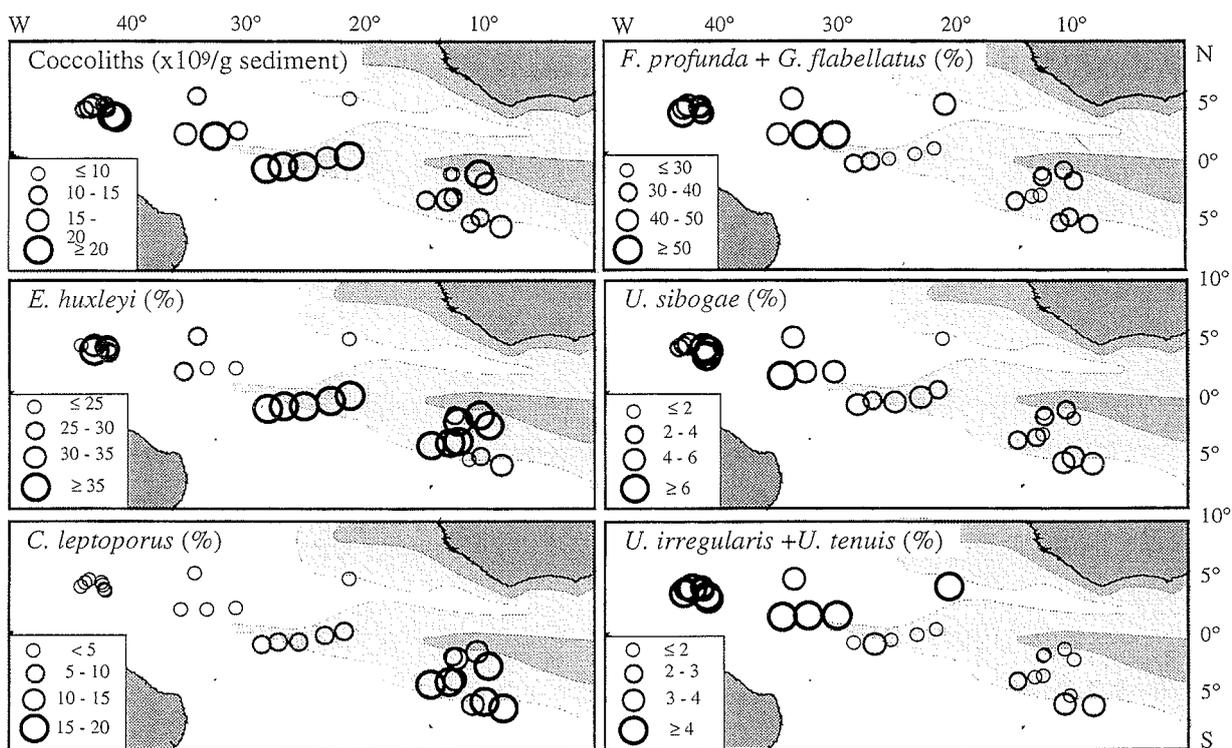
#### 4.2 Sediment samples

##### Surface sediments:

Twenty-seven surface sediment samples from the equatorial Atlantic between 6° S and 6° N were investigated (see Fig. 2, Table 3). All samples are from sites above the modern lysocline (~ 4000m water depth) to avoid influence of carbonate dissolution. As deep basins cover the largest parts of the equatorial Atlantic, the distribution of samples cannot be homogeneous, but is following the structure of the Mid-Ocean Ridge or elevations, such as the Ceara Rise or Sierra Leone Rise.

For interpretation of the surface sediment samples both relative frequencies of the most common species and absolute numbers of total coccoliths were considered. The total number of coccoliths/g. sediment varies between  $6 \times 10^9$  and  $35 \times 10^9$  (Fig. 6). Highest numbers were observed in the central equatorial Atlantic (20 - 30°W) and lowest numbers are found at the Sierra Leone Rise.

The sediments beneath the equatorial upwelling are characterized by relatively high abundances of *E. huxleyi*, which reached values of more than 35 % (Fig. 6). Outside the equatorial upwelling and in the western part of the investigated area relative abundances of this species are lower (20-35 %), with lowest values beneath the NECC and the SECC. A rather similar pattern can be noticed for the distribution of *C. leptoporus* (Fig. 6), which is furthermore characterized by a significant east-west gradient, with less than 5% in sediments from the western equatorial Atlantic and up to 20 % in the eastern equatorial Atlantic. In contrast to the distribution pattern of *E. huxleyi*, abundances of *C. leptoporus* remain constantly high south of the upwelling area.



**Fig 6.** Distribution of total coccoliths/g. sediment and relative abundance of the most common species in surface sediments from the equatorial Atlantic. The grey shadings indicate higher phytoplankton pigment concentrations (> 0.4 mg/m<sup>3</sup>) recorded by the Coastal Zone Color Scanner (CZCS) from 1979-1986.

Opposite results, in comparison to the above mentioned species, are recorded for the deep living coccolithophore species *F. profunda* and *G. flabellatus* (Fig.6). It is obvious that these species reach higher relative abundances of more than 40% in the western equatorial Atlantic and outside the upwelling zone. The same is true for *U. irregularis*, *U. tenuis* and *U. sibogae* (Fig. 6), although abundances of these species are always very low (<5%).

### Sediment cores

We investigated coccolith numbers and assemblage compositions in two sediment cores from the southern (core GeoB 1117-2) and western equatorial Atlantic (core GeoB 1523-1).

Coccolith numbers in core GeoB 1117-2 vary from about  $2.5 \times 10^9$  up to  $80 \times 10^9$  coccoliths/g. sediment, while accumulation rates vary from  $60 \times 10^9$  up to  $1500 \times 10^9$  coccoliths m<sup>-2</sup> a<sup>-1</sup> (Fig. 7). In general, variability in numbers of coccoliths resembles coccolith accumulation rates, with slight disagreement in isotope stage 4. Highest numbers and highest accumulation rates occur during isotope stages 2 and 3, while lowest concentrations are indicative for the Holocene as well as for oxygen isotope stages 5. *G. ericsonii* and *F. profunda* dominate the assemblage during isotope stage 5 (Fig. 8). At this point *G. ericsonii* reaches abundances of up to 54%, while it shows subordinate abundance in Holocene sediments. A sharp drop in the abundance of this species is observed at the oxygen isotope stage boundary

4/5. Contemporaneously, relative abundances of *E. huxleyi* began to rise and reached their maximum of 44% in the Holocene. In addition, abundances of *F. profunda* show a cyclic variation throughout the record with values varying between 10 and 48%. Highest abundances with two significant peaks appeared in isotope stage 5. In general, lower abundances of *F. profunda* are observed in the glacial intervals. *Calcidiscus leptoporus* reached almost 40% in isotope stage 3, and additional maxima occur in glacial stages 4 and 6. A similar pattern can be seen in the abundance of *G. oceanica*, which reveals significant maxima up to 26% in glacial stages 2, 4 and 6, and subordinate abundances in the rest of the record.

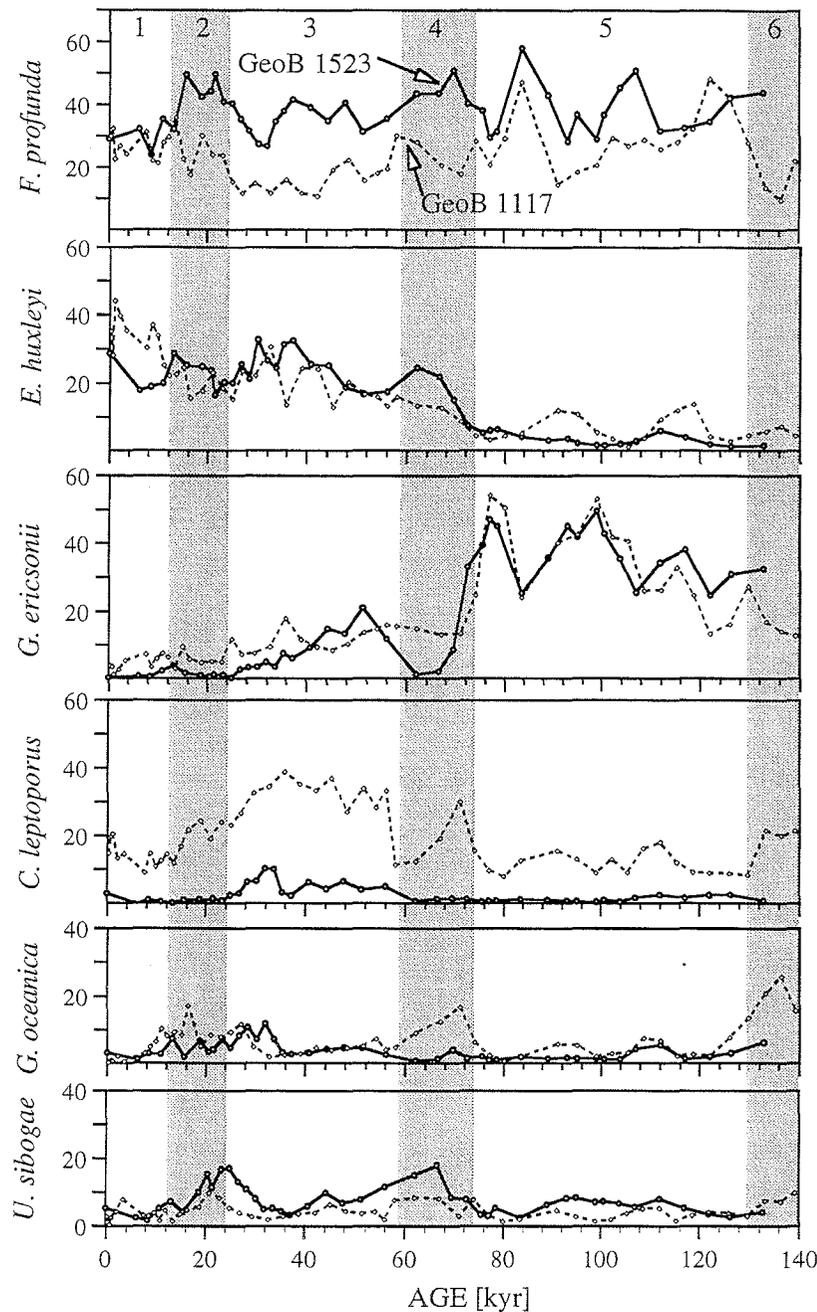


Fig. 7. Relative abundance of the most common coccoliths in core GeoB 1523-1 (solid line) and GeoB 1117-2 (dashed line). Numbers on the top indicate oxygen isotope stages, glacial stages are marked by grey bars.

Less clear is the distribution of *U. sibogae*, which never exceeds values of 10% and has no preferential distribution pattern. Coccolith numbers in core GeoB 1523-1 vary between  $10 \times 10^9$  and  $40 \times 10^9$  coccoliths/g. sediment, and accumulation rates range from  $85 \times 10^9$  to  $450 \times 10^9$  coccoliths  $m^{-2} a^{-1}$ . Highest numbers are observed during the Holocene and in isotope stage 5. During the last glacial interval (isotope stages 2-4) the numbers are slightly lower with minima occurring in stage 2 and 4 (Fig. 8).

In general, *F. profunda* is the most abundant species, making up 24 - 58% of the assemblages. Distinctive maxima are observed in glacial isotope stages 2 and 4, and two further significant peaks in isotope stage 5 (Fig. 8).

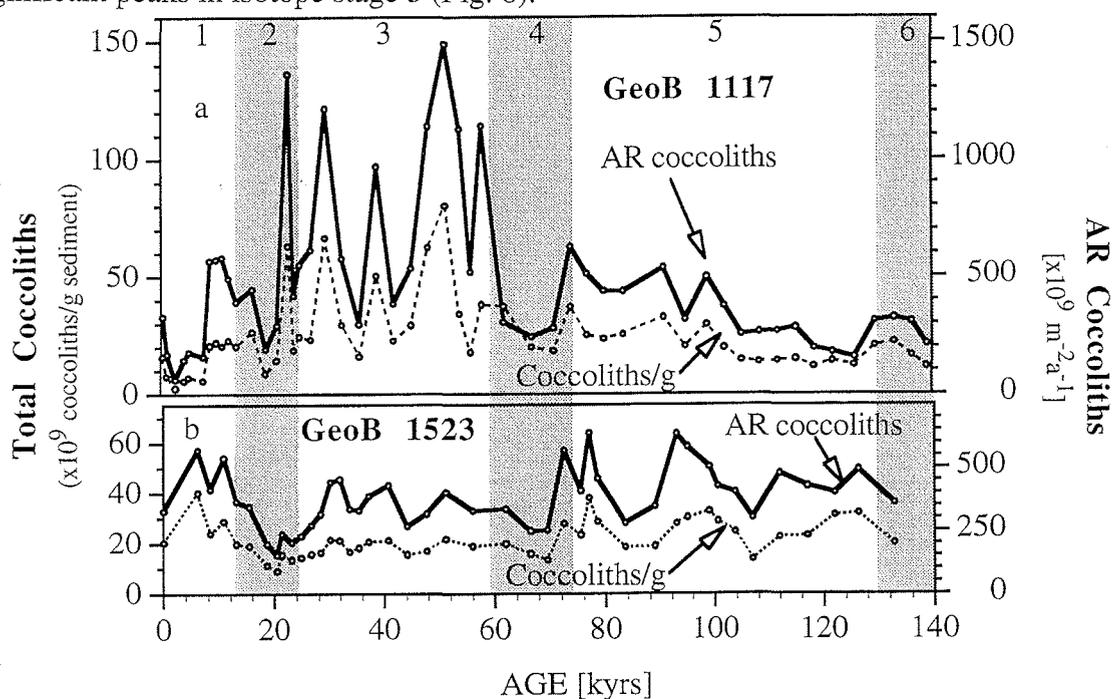


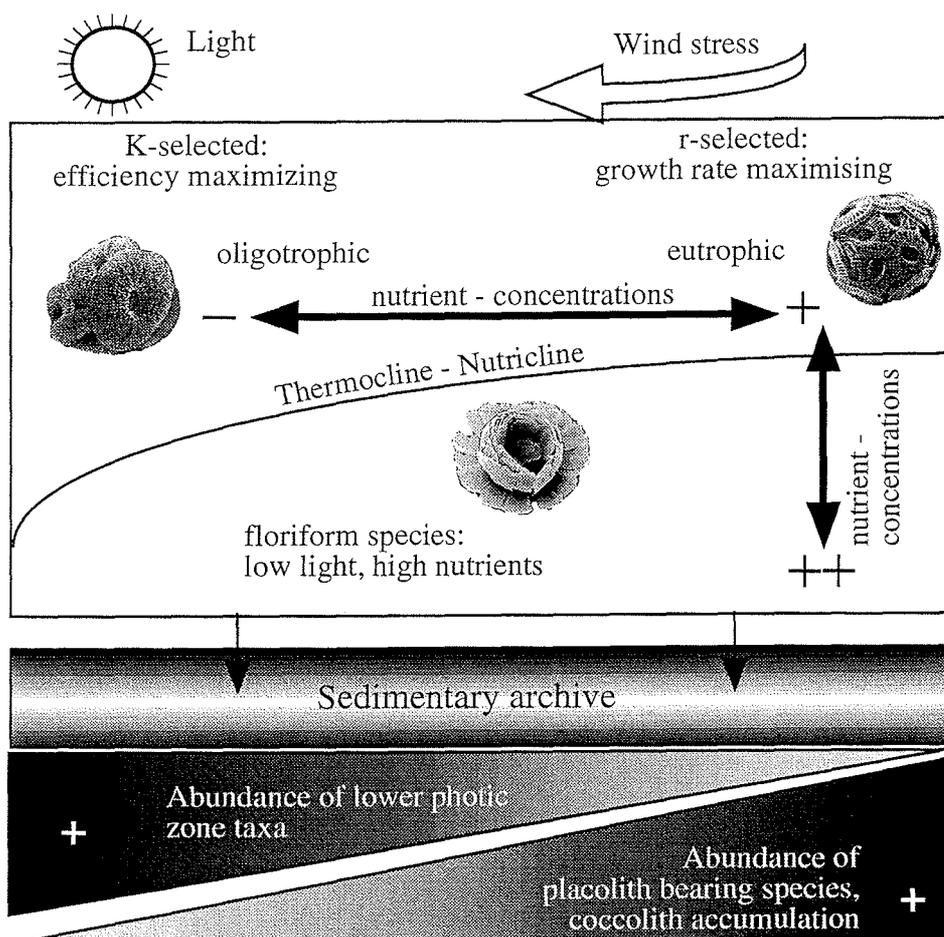
Fig. 8. Numbers of  $10^9$  coccoliths / g sediment (dashed line) and coccolith accumulation rates (solid line) in core GeoB 1117-2 (upper panel) and GeoB 1523-1 (lower panel).

*Emiliana huxleyi* became the second most abundant species in sediments younger than 70 kyrs (after isotope stage 4), with values reaching up to 33 % in isotope stage 3. The increase in *E. huxleyi* in early stage 4 started after a sharp drop in the abundance record of *G. ericsonii*. The latter species reached values of up to 50% of the assemblages during isotope stage 5, where it is clearly anticorrelated to *F. profunda*.

*Calcidiscus leptoporus* only occurred in subordinate abundances throughout the core, with slightly increased values of about 10% during isotope stage 3. *Gephyrocapsa oceanica* is also represented by low values, showing a small increase (about 10%) in late isotope stage 3 and isotope stage 2. In contrast slightly higher values are characteristic for *U. sibogae*, which increases to maxima of 19 % in isotope stage 4 and at the isotope stage 2/3 boundary.

## 5. Discussion

There are various modelistic approaches which combine changes in coccolithophores with environmental parameters, on actual and geological time scales (Westbroek et al., 1993; Brand, 1994; Young, 1994; Jordan et al., 1996). We present here one such approach, which combines all of our studied samples to give an overview of the impacts, changing surface water conditions in the equatorial Atlantic will have on coccolithophores in the surface waters and in the geological archive (Fig. 9).



**Fig. 9.** Model of the coccolithophore response to changing surface water circulation in the equatorial Atlantic and its sedimentary proliferation.

### 5.1. Spatial and temporal variability of the plankton communities

The geographic distribution and composition of the living coccolithophore communities in the equatorial Atlantic can be related to the environmental conditions of the surface waters. In addition, the data fits well to annually averaged daily primary production estimates, which reveal a drastic decline in the primary production away from the upwelling region in the eastern equatorial Atlantic (Longhurst, 1993; Monger et al., 1997). Despite the still relatively sparse

surface plankton data for the study area, an increase both in numbers of total coccolithophore cells as well as in abundance of *E. huxleyi* in samples of the equatorial upwelling is obvious (Figs. 4 and 5). This finding is also in good agreement with other studies in which *E. huxleyi* and/or some other placolith-bearing species predominate in equatorial divergence zones (e.g., Okada and Honjo, 1973; Nishida, 1979; Holligan et al., 1993). However, numbers are by far lower compared to other productive areas in the world's oceans, where coccolithophores can occur in large blooms with cell concentrations exceeding  $10^6$  cells/l (e.g., Berge, 1962; Holligan et al., 1993; Samtleben et al., 1995). Subpolar latitudes, especially the subarctic North Atlantic, account for the most extensive blooms (Brown and Yoder, 1994), while only small blooms are apparent in nearshore equatorial and subtropical regions of the western Atlantic (Okada and McIntyre, 1979). Modern productivity gradients within the equatorial region, therefore, are relatively small, resulting in an estimated doubled productivity in the upwelling compared to the oligotrophic areas (Berger, 1989; Mix, 1989). Nevertheless, Longhurst (1993) pointed out the significance of phytoplankton productivity in tropical areas, as it takes place throughout the year and covers much larger areas, than the impressive seasonal blooms in higher latitudes. He calculated that the tropical Atlantic between 10°S and 10°N contribute about one third (2.5 Gt) of the Atlantic's annual carbon production (7.7 Gt) by phytoplankton, while even higher estimations of 2.3 Gt for the area 5°N-10°S, 25°W-10°E were given by Monger et al. (1997).

Although it can be assumed, that coccolithophore production takes place throughout the year, there are distinct seasonal variations, which are a result of varying nutrient supply to the upper euphotic zone where the majority of coccolithophores reside. The nutrient availability is controlled by the depth of the nutricline, which can be monitored by the abundance of *F. profunda* (Fig. 5). This is the most prominent species, which, together with *G. flabellatus* and a number of less common species (Jordan and Chamberlain, 1997), is restricted to the lower euphotic zone (~60 to ~180 m water depth) of the tropical and subtropical oceans (Okada and Honjo, 1973), where light becomes limited. If the nutricline is shallow, coccolithophore production in the upper euphotic zone is enhanced, and the abundance of *F. profunda* is minimal (Fig. 9). This is supported by the present data, where *E. huxleyi* reaches maximum values in the water column in the upwelling area at the equator. In contrast, a deep nutricline will hamper the coccolith productivity in the upper euphotic zone and the abundance of *F. profunda* will increase to maximum abundances. Except for the equatorial upwelling, the tropical Atlantic is mainly characterized by warm oligotrophic surface water masses, where both the thermocline and nutricline are deep, resulting in low phytoplankton production. In these areas, *Umbellosphaera irregularis* and *U. tenuis* clearly dominate surface communities (see Figs. 4 and 5), which is in good accordance with previously reported findings from similar latitudes in the Pacific (Nishida, 1979; Okada and McIntyre, 1979; Kleijne et al., 1989).

### 5.2 Distribution patterns of coccolithophores in surface sediments of the equatorial Atlantic

The coccolithophore assemblages in surface sediments of the equatorial Atlantic clearly reflect the oceanographic features of the circulation pattern in the mixed layer above, as they compare well to the distribution and composition of the living coccolithophore communities within those water masses. However, settling assemblages are significantly affected by dissolution and fragmentation (Samtleben et al., 1995), which can clearly be seen by the diminishing *U. irregularis* and *U. tenuis* abundances from over 70% in the plankton samples, to less than 10% in the surface sediments. Nevertheless, the general features of the communities in surface waters still remain visible in the underlying sediments.

In the tropical Atlantic seasonally increased meridional wind stress causes an uplift of the thermocline as well as the nutricline leading to an enhanced phytoplankton productivity (Longhurst, 1993; Monger et al., 1997). This corresponds well to the higher frequencies of *E. huxleyi* and slightly higher numbers of coccoliths within this area. Modern productivity gradients within the equatorial region are relatively small, with an estimated doubled productivity in the upwelling compared to the oligotrophic areas (Berger, 1989; Mix, 1989). With all the difficulties in achieving accurate coccolithophore accumulation rates, we conclude, that the pattern in the surface sediments fairly matches the above productivity. It seems obvious from our downcore results (see below) that the accumulation patterns are much clearer when the productivity increased drastically as in the last glacial.

The higher abundances of *C. leptoporus* in the eastern and southern equatorial Atlantic may indicate a combination of both, higher nutrients and cooler temperatures, due to an advection of water masses via the eastern boundary currents. This species shows significantly higher abundances in surface sediments from the southeastern Atlantic, where cooler and nutrient rich waters influence coccolithophore assemblages (Shokati et al., in press). It was suggested, that an increase of *C. leptoporus* abundances in surface sediments from the western equatorial Pacific may be due to increased nutrients, but is also well correlated to decreased sea surface temperatures (Hiramatsu and De Decker, 1997).

In contrast to the equatorial upwelling area, the rest of the tropical Atlantic is characterized by warm oligotrophic surface water masses, where both the thermocline and nutricline are deep, which causes low phytoplankton production. This is well reflected by the distribution of *U. irregularis* and *U. tenuis*, although these species become extremely diminished in their abundance in surface sediments compared to the plankton record, and variations in the study area are almost negligible.

The deep-dwelling coccolithophore species *F. profunda* and *G. flabellatus* indicate a significant correlation between higher relative abundances of these species in surface sediments

and more oligotrophic water masses. Variations of the relative abundance of *F. profunda* are related to changes in nutricline depth (Molfino and McIntyre, 1990 a), leading to an increase in the LPZ flora over all other coccolithophores when the nutricline is deep and vice versa, when it is shallow (Fig. 9). Similar distribution patterns were observed in surface sediments from the Indian Ocean (Beaufort et al., 1997), the Tasman and Coral Sea (Hiramatsu and De Decker, 1997) and around Japan (Ahagon et al., 1993), although the latter authors correlated the distribution pattern of *F. profunda* with surface water transparency.

### 5.3 *Coccolithophore productivity and assemblage variations in the last 140 kyrs*

If we compare the two sediment cores from the southern and western equatorial Atlantic (GeoB 1117-2 and GeoB 1523-1 respectively), we observe similar patterns for the coccolith accumulation rates during interglacial stages 1 and 5, but significantly enhanced accumulation rates at the southern equatorial site from late stage 4 until early stage 2 (Fig. 8). The up to 5 times higher coccolith numbers and accumulation rates at this site during this interval are most likely explained by the strengthening and lateral extension of the equatorial upwelling zone by increased zonal wind stress and enhanced advection of cool and nutrient rich waters from the eastern boundary currents. For the same time interval we found the largest differences in abundance of *F. profunda* between the two sites. This is a further indication for a steeper thermocline and nutricline gradient between the western and southern equatorial Atlantic. Additional support for enhanced productivity can be seen in the abundance increase of *C. leptoporus* during most of stages 2-4. The increase of *C. leptoporus* in the eastern part of the equatorial Atlantic may indicate both, increased productivity and advection of cooler waters from the south. It was suggested before, that increased abundances of *C. leptoporus* may indicate higher productivity (Knappertsbusch, 1993; Flores et al., 1997), which is in agreement with our own downcore data. The fact that there is also an increase in *C. leptoporus* in the western equatorial Atlantic may be due to cooler sea surface temperatures, as already indicated by their occurrence in the surface sediments.

The increase in coccolith numbers and accumulation rates in the southern equatorial Atlantic is basically in accordance with other paleoproductivity reconstructions for this region (Struck et al., 1993; Verardo and McIntyre, 1994; Schneider et al., 1996; Wefer et al., 1996), although a maximum of organic carbon contents indicate that highest productivity occurred in isotope stage 2. However, the relative abundance of *G. oceanica* corroborates the organic carbon contents with maxima in isotope stages 2, 4 and 6 (Fig. 10). Our own plankton data show a maximum in *G. oceanica* abundances and numbers at 10° N, which correlated to the influence of the Northwest African upwelling system (Fig. 4). Higher abundances of *G. oceanica* in plankton and surface sediment samples from upwelling areas were previously reported from the Indian

Ocean and the Benguela upwelling area (Mitchell-Innes and Winter, 1987; Kleijne et al., 1989; Giraudeau, 1992). There are various possibilities to explain this discrepancy between the organic carbon and coccolith accumulation record. It is possible that highest organic carbon contents are related to an increase in productivity of other phytoplankton (e.g. diatoms), which are able to outcompete coccolithophores at high nutrient levels. This is supported by our surface sediment data, where we can see the highest numbers of coccoliths at the western rim of the equatorial upwelling area, rather than in the more productive eastern part (see Fig. 6).

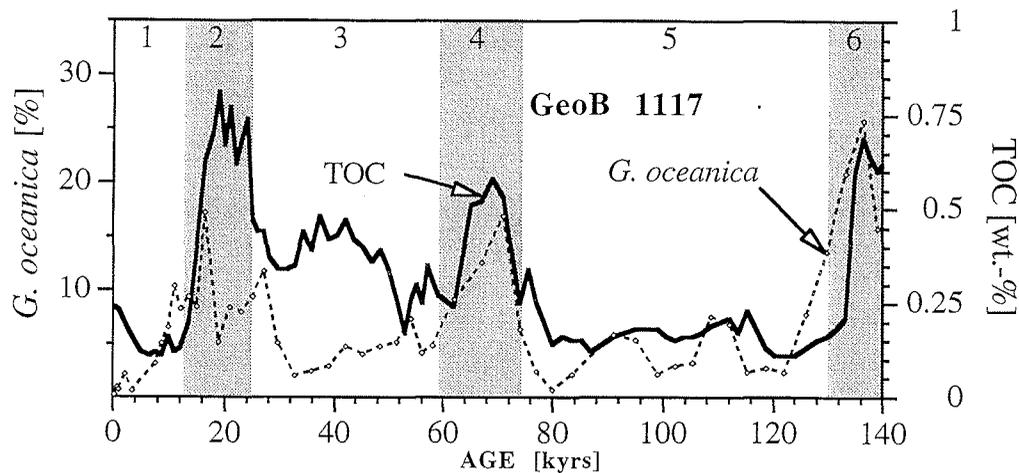
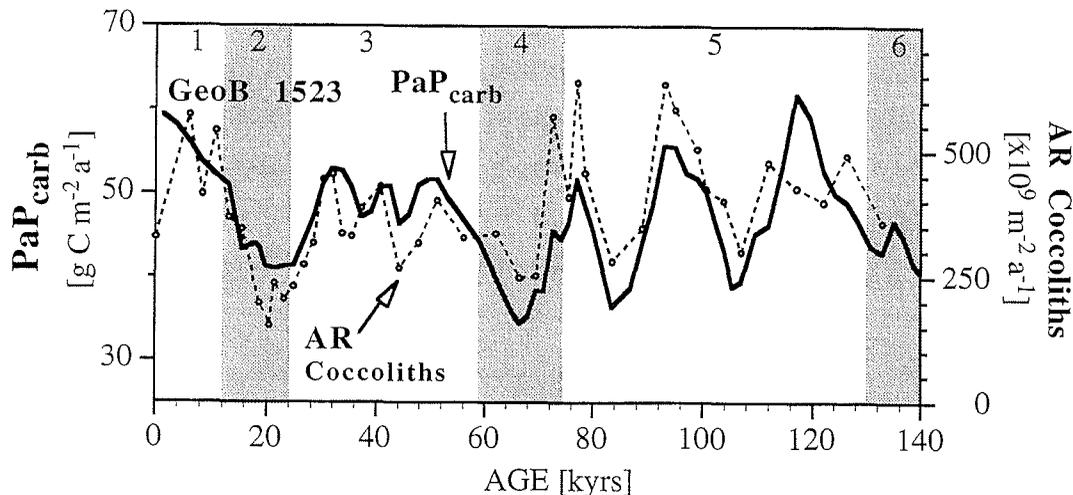


Fig. 10.F Comparison of total organic carbon contents (TOC) and the relative abundance of *G. oceanica* in Core GeoB 1117-2

Moreover, there is the possibility of an overestimation in organic carbon records due to an increased input of terrestrial organic matter (Verardo and Ruddiman, 1996). However, we have to take into account, that carbonate dissolution may have influenced the record at the southern equatorial site especially during isotope stages 2 and 4 (Verardo and McIntyre, 1994; Bickert and Wefer, 1996), due to a rise of the lysocline above the depth of the coring site (3984 m). The complex interaction between productivity and dissolution signals at the southern equatorial Atlantic (GeoB 1117-2) are discussed elsewhere (Kinkel et al., *subm.*)

Coccolith numbers and accumulation rates in the western equatorial Atlantic (GeoB 1523) show variations of about a factor of two, with lower values during glacial isotope stages 2 and 4 (Fig. 8) This is in agreement to paleoproductivity estimations based on carbonate accumulation rates reported for this site by Rühlemann et al. (1996) (Fig. 11). This gives further support to the idea, that the seasonal cycle (Fig. 2) of a tilting thermocline, which leads to an opposite behavior in terms of productivity between the western and eastern equatorial Atlantic, can be used as an equivalent to long term productivity variability (Fig. 8, 10, and 11). The better correlation of paleoproductivity estimates at core GeoB 1523-1 compared to the southern equatorial Atlantic (GeoB 1117-2), may be explained by the fact that coccolithophores may form the most important contribution to the biogenic sedimentation in the more oligotrophic western equatorial Atlantic.



**Fig. 11.** Comparison between the Paleoproductivity estimations (from Rühlemann et al., 1996) (solid line) and coccolith accumulation rates (dashed line) in core GeoB 1523-1

Further indication for increased surface water productivity is given by the low abundance of *F. profunda*, as proposed in several recent studies (Molfino and McIntyre, 1990 a; Okada and Matsuoka, 1996; Beaufort et al., 1997). There is an obvious difference in the *F. profunda* records of both cores, with generally higher values in the western equatorial Atlantic (GeoB 1523-1). Differences in the *F. profunda* record are most pronounced during the last glacial interval, coeval with the strong increase of coccolith accumulation rates in core 1117-2 (see Figs. 7 and 8). We do not discuss the orbital forcing, that drives the wind stress and thus the surface water circulation in the equatorial Atlantic, which can be deciphered by the coccolith record (Molfino and McIntyre, 1990 a; McIntyre and Molfino, 1996; Beaufort et al., 1997), as the temporal resolution of our present records is not sufficient for spectral analysis. However paleoceanographic interpretations for core GeoB 1117 of the last 300 kyrs show a significant 23-kyr periodicity for *F. profunda* and *G. oceanica* (Kinkel et al., subm.).

During stage 5 the relative abundance of *F. profunda* in both cores is rather similar again, as is the coccolith accumulation rate (Figs. 7, 8). Although we have large fluctuations in the *F. profunda* record during this interval, the accumulation rates remain relatively low, compared to the glacial interval. This points out that one has to be cautious when interpreting *F. profunda* records especially if they are used for paleoproductivity estimations (e.g. Beaufort et al., 1997). It has to be considered, that upwelling does not necessarily trigger higher productivity, as the nutrient levels of the upwelled waters can vary seasonally (Monger et al., 1997) and over geological time scales (Hay, 1995), mainly depending on the source of the upwelled waters. Thus, a slight increase in nutrient supply can be large enough to alter the relative abundance values, but do not necessarily need to induce a strong rise in overall productivity. Moreover, absolute numbers of *F. profunda* increase parallel to the increase in numbers of all other

coccoliths. This is in good agreement with recent sediment trap results (Broerse et al., in press; Sprengel et al., subm.), where the flux of *F. profunda* is well aligned with the total coccolith flux. Additionally, the *F. profunda* signal is easily amplified, as this species has much more coccoliths per sphere than most other coccolithophores, i.e. a small change in the abundance between living cells will be much larger in the sediments, where only coccoliths are taken into account.

## 6. Conclusions

The principal response of coccolithophores to changing surface water circulation in the equatorial Atlantic is summarized in a schematic drawing (Fig. 9). In addition, concluding remarks on the composition of coccolithophores in plankton, surface sediments and in the sedimentary archive are as follows:

(1) The response of living coccolithophores to seasonal changing surface water circulation in the equatorial Atlantic was demonstrated by the plankton samples taken from three cruises and different months. We have shown, that equatorial upwelling causes an increase in coccolithophore standing stock, due to an increase in numbers and abundances of *E. huxleyi*. Oligotrophic areas and seasons are both characterized by lower standing stocks and a significant increase in the abundance of *U. irregularis* and *U. tenuis*. The lower photic zone is dominated by *F. profunda* and *G. flabellatus*.

(2) The surface sediments clearly reflect the situation in the surface water masses, although a significant degradation in the relative abundance of *U. tenuis* and *U. irregularis* is observed, which leads to an increase in the relative abundance of *F. profunda* and *G. flabellatus* in sediments underlying oligotrophic water masses. Additionally, higher numbers of coccoliths as well as higher abundances of *E. huxleyi* are found under the area influenced by equatorial upwelling activity.

(3) The variations of coccolith assemblages, expressed in numbers of coccoliths/g. sediment as well as coccolith accumulation rates from two sediment cores reveal drastic variations during the last 140 kyrs. Most spectacular is the increase in coccolith numbers and accumulation rates in core GeoB 1117-2 from the southern equatorial Atlantic, which we attribute to a lateral extension of the equatorial upwelling area and increased advection of cool and nutrient rich water masses from the southeastern Atlantic via the eastern boundary currents. This is supported by the floral composition of the coccolithophore assemblages. In contrast to the southern equatorial Atlantic, the fluctuations in the coccolith numbers and accumulation rates in the western equatorial Atlantic remain low, but the variations are still detectable and fit well to previously reported paleoceanographic reconstructions of this area.

**Tab.1.** Location of surface water samples, surface-water temperature, total standing stock and abundance of the most common species.

Latitude	Longitude	Surface-water Temperature (°C)	Total standing crop (x103Ind./l)	<i>E. huxleyi</i> (%)	<i>G. oceanica</i> (%)	<i>U. irregularis</i> (%)	<i>U. tenuis</i> (%)
<i>M29-3 (August - September)</i>							
21.92 S	39.23 W	23,9	50,4	70,17	3,67	13,58	11,17
20.77 S	36.67 W	24,1	38,51	67,23	4,58	4,67	17,66
20.31 S	35.90 W	24,3	89,88	48,27	2,86	14,76	27,52
19.07 S	35.12 W	24,4	18,07	42,73	1,84	28,41	25,83
17.44 S	34.11 W	24,6	17,17	19,41	0,83	38,44	34,94
16.11 S	33.29 W	25,2	70,43	37,55	0,13	26,88	18,84
15.09 S	32.66 W	25,3	3,85	15,87	0	72,73	6,94
14.00 S	32.00 W	25,3	9,26	9,6	0	76,32	13,68
12.85 S	31.29 W	25,8	39,31	28,13	0,24	45,79	9,33
11.70 S	30.57 W	26,1	17,55	0	0	80,15	1,9
10.69 S	29.95 W	26,0	1,33	0	0	25,04	0
9.64 S	29.31 W	26,4	57,67	46,92	0,25	23,01	5,9
8.67 S	28.72 W	26,4	37,31	32,61	0	38,06	18,94
7.51 S	28.02 W	26,4	27,12	41,99	0,53	35,89	11,55
6.32 S	27.19 W	26,3	81,76	39,41	0	37,92	9,46
5.17 S	26.40 W	26,1	2,07	0	0	3,24	0
4.05 S	25.66 W	26,0	130,89	59,8	0,15	20,58	13,09
1.73 S	27.73 W	25,7	47,15	69,34	0,3	9,05	11,59
0.32 S	28.06 W	25,6	11,58	36,46	1,64	20,15	20,87
0.29 S	24.98 W	25,3	195,54	66,76	0,22	7,47	9,21
0.02 N	23.45 W	25,2	69,86	83,23	0,07	4,29	6,25
0.50 N	21.63 W	24,7	291,26	85,85	0,05	1,9	1,09
2.57 N	21.36 W	26,3	11,18	46,22	1,7	25,26	3,13
3.97 N	21.17 W	26,4	22,42	54,76	0	34,2	1,12
5.25 N	21.05 W	27,1	3,5	0	0	14,29	0
6.52 N	21.01 W	27,4	30,02	20,54	0	74,67	3,66
7.85 N	21.02 W	27,3	0,06	0	0	93,33	0
10.35 N	21.05 W	27,2	150,88	43,78	39,04	4,71	1,16
11.5 N	21.05 W	27,9	11,38	0	82,43	0	0
13.20 N	20.99 W	27,7	46,42	19,03	57,45	10,17	0,54
14.70 N	20.93 W	27,1	0	0	0	0	0
16.52 N	20.86 W	26,5	0,18	0	0	0	0
<i>M34-4 (March - April)</i>							
7.85 S	32.89 W	28,6	0	0	0	0	0
7.70 S	30.97 W	28,8	0	0	0	0	0
7.60 S	29.97 W	28,4	0	0	0	0	0
7.48 S	28.43 W	28,4	0	0	0	0	0
7.42 S	28.13 W	28,5	2,52	0	6,35	92,86	0
6.50 S	27.44 W	28,8	0	0	0	0	0
5.58 S	26.78 W	28,7	14,36	9,61	0	76,11	0
4.50 S	25.83 W	28,6	14,62	19,36	0	72,23	0
3.92 S	25.69 W	29,4	61,28	9,92	0	55,47	0,34
2.73 S	24.97 W	29,0	36	8,67	0,56	27,33	1,06
1.22 S	24.14 W	28,6	19,65	0,71	0	88,19	4,22
0.67 S	23.83 W	28,6	30,28	5,05	0,17	78,5	6,77
0.08 S	23.44 W	28,2	33,57	4,5	0	62,35	3,96
0.28 S	23.92 W	28,2	0	0	0	0	0
0.67 S	25.06 W	28,6	0	0	0	0	0
0.88 S	27.21 W	28,6	0	0	0	0	0
1.48 S	31.73 W	28,3	0	0	0	0	0
1.72 S	32.97 W	28,6	0	0	0	0	0
1.92 S	34.05 W	28,6	0	0	0	0	0
2.88 S	35.23 W	28,8	0	0	0	0	0
3.40 S	35.65 W	29,0	0	0	0	0	0
0.80 S	37.99 W	29,0	0	0	0	0	0
0.01 S	38.26 W	28,7	0	0	0	0	0
<i>M38-1 (January - February)</i>							
12.12 N	20.98 W	24,9	155,9	56,09	41,09	0,19	0
11.48 N	21.02 W	24,6	43,79	61,89	28,66	2,72	0,55
10.62 N	23.62 W	25,2	32,74	40,62	5,53	34,91	3,63
9.91 N	26.02 W	25,4	15,82	28,63	0,51	52,47	6,32
9.21 N	27.85 W	25,4	52,65	20,51	2,85	30,22	41,48
8.54 N	29.88 W	26,6	4,72	29,45	0	8,9	8,9

**Tab. 2.** Location of depth profile samples, sampling depth, total standing stock and abundance of the most common species.

Station	Latitude	Longitude	Waterdepth (m)	Total standing crop $\times 10^3$ Ind./l	<i>E. huxleyi</i> (%)	<i>F. profunda</i> (%)	<i>U. irregularis</i> (%)	<i>U. tenuis</i> (%)
<b>M 29/3 (August - September)</b>								
GeoB 2902	14.00 S	32.00 W	5	3,38	9,60	0,00	76,32	13,68
"	"	"	20	37,67	19,50	0,00	53,07	9,46
"	"	"	100	9,40	0,59	0,00	68,95	2,50
"	"	"	200	0,01	0,00	75,00	0,00	0,00
GeoB 2903	7.51 S	28.02 W	5	20,29	41,99	0,00	35,89	11,55
"	"	"	20	3,37	0,00	0,00	54,55	22,73
"	"	"	50	1,03	0,00	0,00	6,24	0,00
"	"	"	90	4,06	0,00	0,00	34,24	35,58
"	"	"	110	27,67	39,30	11,01	16,64	12,70
"	"	"	200	0,00	0,00	0,00	0,00	0,00
GeoB 2904	4.05 S	25.66 W	5	95,19	59,80	0,00	20,58	13,09
"	"	"	20	35,00	46,76	0,00	38,03	10,97
"	"	"	100	32,40	66,86	0,01	6,66	2,83
GeoB 2909	0.29 N	21.37 W	5	211,82	85,85	0,00	1,90	1,09
"	"	"	30	100,25	75,11	0,00	3,30	2,42
"	"	"	70	78,53	83,19	0,00	5,88	1,32
"	"	"	100	20,79	14,24	56,35	10,34	3,66
"	"	"	130	0,01	0,00	50,00	0,00	0,00
GeoB 2910	4.50 N	21.03 W	5	39,30	20,54	0,00	74,67	3,66
"	"	"	20	24,72	4,41	0,00	37,07	5,00
"	"	"	50	0,29	0,00	0,00	99,19	0,00
"	"	"	100	0,00	0,00	0,00	0,00	0,00
"	"	"	130	0,00	0,00	0,00	0,00	0,00
"	"	"	200	0,00	0,00	0,00	0,00	0,00
GeoB 2911	11.50 N	21.05 W	5	8,28	0,00	0,00	0,00	0,00
"	"	"	20	5,48	0,00	0,00	0,00	0,00
"	"	"	50	0,00	0,00	0,00	0,00	0,00
"	"	"	100	0,00	0,00	0,00	0,00	0,00
<b>M 34/4 (March - April)</b>								
GeoB 3906	7.42 S	28.01 W	5	2,52	0,00	0,00	2,34	0,00
"	"	"	20	21,47	1,26	0,00	1,75	0,00
"	"	"	40	32,22	1,88	0,00	2,45	0,83
"	"	"	50	24,69	0,56	0,00	0,00	0,17
"	"	"	100	67,07	4,39	0,00	11,78	34,90
GeoB 3907	3.92 S	25.68 W	5	61,22	6,08	0,00	33,99	0,21
"	"	"	20	60,21	5,35	0,00	26,35	0,14
"	"	"	50	48,79	7,00	0,00	25,74	2,09
GeoB 3908	0,00	23.39 W	5	22,79	1,06	0,00	11,40	1,33
"	"	"	20	24,29	6,93	0,00	2,72	10,49
"	"	"	50	28,77	10,95	0,00	3,23	7,09
"	"	"	100	42,48	8,88	16,49	0,47	0,53
"	"	"	200	11,58	5,19	1,43	1,53	0,27
<b>M 38/1 (January - February)</b>								
GeoB 4316	4.20 N	31.00 W	20	20,54	12,57	0,00	3,43	1,11
"	"	"	50	68,40	38,67	0,11	1,49	4,32
"	"	"	100	8,61	0,21	5,75	0,26	0,04
"	"	"	150	3,50	0,03	2,85	0,18	0,00
"	"	"	200	1,69	0,00	1,37	0,24	0,00
GeoB 4318	0.02 N	23.45 W	20	11,45	10,36	0,01	0,79	0,07
"	"	"	50	15,39	11,47	0,33	0,44	0,00
"	"	"	100	38,01	13,55	9,79	1,16	0,04

Station	Latitude	Longitude	Waterdepth (m)	Total standing crop $\times 10^3$ Ind./l	<i>E. huxleyi</i> (%)	<i>F. profunda</i> (%)	<i>U. irregularis</i> (%)	<i>U. tenuis</i> (%)
"	"	"	150	36,68	1,40	25,54	0,52	0,09
"	"	"	200	0,00	0,00	0,00	0,00	0,00
GeoB 4319	3.86 S	25.66 W	20	5,79	3,24	0,01	0,66	1,23
"	"	"	50	25,50	5,38	0,00	2,64	1,40
"	"	"	100	10,53	4,28	2,67	0,45	0,00
"	"	"	150	10,22	2,75	0,92	2,31	2,64
"	"	"	200	18,58	0,00	17,09	0,23	0,18
GeoB 4320	7.50 S	28.18 W	20	5,99	0,06	3,04	2,64	0,17
"	"	"	50	6,41	0,31	0,61	5,03	0,37
"	"	"	100	2,68	0,00	0,03	2,10	0,46
"	"	"	150	5,68	0,00	3,91	1,19	0,15
"	"	"	200	5,92	0,00	1,45	2,29	0,17

**Tab.3.** Location of surface sediment samples, total number of coccoliths/g. sediment and abundance of the most common species.

Latitude	Longitude	GeoB-Nr.	Water depth (m)	Total coccoliths ( $\times 10^9$ /g sediment)	<i>C. leptoporus</i>	<i>E. huxleyi</i>	<i>G. flabellatus</i>	<i>F. profunda</i>	<i>Gephyrocapsa spp.</i>	<i>U. irregularis</i>	<i>U. tenuis</i>
1.16 S	10.71 W	1104-5	3724	21,42	11,2	37,5	0,0	34,3	2,5	1,1	0,0
1.67 S	12.43 W	1105-3	3232	9,77	14,3	40,4	1,4	26,5	2,8	1,1	0,0
1.76 S	12.55 W	1106-5	2471	9,25	7,0	28,4	1,1	37,9	5,3	0,3	0,3
2.17 S	9.87 W	1108-3	3875	19,09	17,9	40,3	0,3	30,2	0,6	0,3	0,3
5.84 S	8.65 W	1111-5	3757	19,90	15,6	30,3	4,4	27,5	3,3	3,9	0,0
5.75 S	11.04 W	1113-7	2473	10,60	14,0	24,2	6,7	27,2	3,0	3,0	0,3
5.28 S	10.20 W	1114-3	3422	12,80	19,4	28,4	2,0	30,9	3,1	1,7	0,0
3.56 S	12.58 W	1115-4	2921	13,54	13,4	41,3	0,0	27,4	3,2	0,5	0,5
3.62 S	13.19 W	1116-1	3471	16,53	18,6	37,7	0,0	25,9	2,4	0,8	0,3
3.82 S	14.90 W	1117-3	3977	14,64	15,5	36,1	0,0	31,8	3,3	1,8	0,3
2.31 N	30.65 W	1503-2	2298	12,71	1,2	22,3	30,4	22,8	0,6	3,8	0,3
2.27 N	33.01 W	1505-4	3703	24,68	2,4	23,3	3,5	48,1	1,6	3,7	1,3
2.21 N	35.18 W	1506-1	4267	16,82	2,0	29,3	0,6	44,2	2,6	3,7	0,9
5.33 N	34.03 W	1508-1	3685	12,11	1,2	26,5	2,0	45,1	4,3	3,1	0,8
4.24 N	43.67 W	1515-2	3125	12,30	1,4	24,3	25,1	25,7	2,5	4,5	0,3
4.50 N	43.34 W	1516-1	3592	18,00	1,7	35,1	8,4	32,9	2,2	2,8	0,3
4.74 N	43.05 W	1517-2	4006	15,34	0,3	31,0	2,3	41,1	4,0	2,9	1,2
4.59 N	41.94 W	1520-1	3911	11,62	2,1	30,1	3,0	39,2	4,9	2,7	0,3
4.31 N	41.83 W	1521-2	3725	11,87	1,6	31,6	6,7	30,8	2,4	2,7	0,5
4.03 N	41.68 W	1522-1	3478	20,29	0,5	25,5	11,3	35,0	2,9	3,2	1,1
3.82 N	41.62 W	1523-2	3291	20,42	2,9	28,8	9,3	29,1	4,4	3,2	1,2
0.66 S	28.64 W	2905-1	4166	21,83	6,3	36,1	0,0	35,5	3,0	1,2	0,3
0.41 S	27.25 W	2906-3	3870	20,79	6,2	40,5	0,0	32,7	1,3	2,2	0,9
0.43 S	25.51 W	2907-1	3675	34,98	6,8	38,7	0,3	28,2	3,7	0,6	0,9
0.10 N	23.32 W	2908-8	3815	19,73	8,2	39,6	0,0	29,3	0,3	1,2	0,0
0.50 N	21.63 W	2909-1	4383	21,23	8,5	37,7	0,0	29,3	1,3	0,6	1,3
4.85 N	21.05 W	2910-2	2701	6,58	1,8	22,6	0,4	47,0	2,2	3,6	1,4

Tab. 4. Total number of coccoliths/g. sediment, coccolith accumulation rates and abundance of most common species from cores Geob 1117-2 and Geob 1523-1.

Depth (cm)	Age (kyrs)	Total coccoliths ( $\times 10^9$ /g sediment)	AR coccoliths ( $\times 10^9$ m <sup>-2</sup> a <sup>-1</sup> )	C. leptopus	E. huxleyi	F. profunda	G. ericsonii	G. oceanica	U. sibogae
<i>Geob 1117-2 (03°S 14° 54'W, 3977m water depth)</i>									
0	0.3	15.91	329.6	14.9	35.3	30.1	3.9	0.3	3.0
4	1.0	7.45	168.5	19.9	28.3	32.5	3.6	1.0	0.5
3	2.6	2.51	61.6	20.5	44.2	22.8	1.3	0.8	2.6
8	4.2	5.63	144.5	13.4	39.8	26.9	2.7	2.2	4.5
13	5.0	7.04	178.2	14.7	35.5	24.4	5.4	0.7	8.0
23	7.6	5.61	159.1	9.2	30.4	31.5	7.3	3.2	3.4
28	8.7	20.68	567.6	14.8	37.1	22.2	3.5	5.1	3.2
33	9.8	21.96	573.2	11.0	34.1	21.5	6.0	6.6	4.1
38	10.9	20.51	581.5	12.7	25.3	28.1	7.6	10.4	1.8
43	12.0	23.02	492.2	14.6	22.2	29.9	6.4	8.3	4.8
48	13.5	20.34	392.8	12.0	22.6	36.0	3.0	9.4	1.6
58	16.4	26.38	445.7	16.8	24.7	22.8	9.5	8.5	3.7
68	18.8	8.51	191.9	21.8	15.7	17.7	5.8	17.2	5.0
78	20.9	14.21	292.5	24.4	17.8	30.3	4.8	5.2	5.9
88	22.9	63.12	1361.3	19.2	23.1	24.2	5.2	8.4	10.0
93	23.9	18.58	419.0	24.1	18.6	23.9	5.1	8.0	8.5
98	24.9	24.42	550.7	23.2	15.4	15.4	11.8	9.4	5.6
108	27.0	23.23	614.9	26.8	23.6	11.8	7.3	11.8	4.2
118	29.6	66.57	1214.7	32.7	22.3	14.9	7.6	5.1	3.0
128	32.7	29.48	575.7	34.5	30.8	11.8	9.5	2.1	2.1
138	35.8	15.98	296.6	38.9	13.7	16.1	17.9	2.5	2.9
148	38.9	50.38	967.7	35.3	24.5	11.8	11.7	3.0	3.9
158	42.1	22.59	383.2	33.4	24.2	10.8	9.5	4.8	4.1
168	45.2	29.34	535.4	37.0	13.0	19.3	8.5	4.1	6.6
178	48.3	62.41	1138.7	27.1	20.4	22.6	10.4	4.8	4.6
188	51.4	80.04	1486.1	34.0	16.9	15.8	13.8	5.2	3.9
198	54.0	34.12	1126.0	28.4	16.0	18.2	14.8	7.4	4.4
208	56.0	17.62	519.8	33.3	13.3	19.7	16.0	4.2	2.1
218	58.0	37.98	1139.4	11.5	16.1	30.3	15.7	4.9	7.9
228	62.0	37.27	304.4	12.5	13.5	28.2	15.0	9.2	8.6
238	67.0	19.87	243.4	19.4	12.9	20.7	13.2	12.6	8.4
248	71.0	18.29	280.5	30.2	8.8	18.1	13.5	16.9	3.3
258	74.0	36.96	628.3	15.6	4.6	28.5	24.9	6.4	8.0
268	77.0	25.17	511.9	9.8	3.4	21.0	54.2	2.5	3.4
278	80.0	23.57	437.7	8.0	4.5	29.4	50.6	0.8	1.5
288	83.5	25.46	436.4	12.7	5.3	47.2	24.2	2.2	2.2
308	91.0	32.53	536.8	15.6	12.1	14.5	40.2	5.9	4.9
318	95.0	20.18	317.9	13.1	10.9	18.6	42.6	5.4	2.9
328	99.0	29.42	496.4	9.1	5.5	20.8	53.2	2.2	1.6
338	102.2	19.52	372.1	13.1	3.6	29.5	41.9	3.0	2.1
348	105.4	14.29	254.5	9.2	1.3	27.0	40.7	3.3	4.0
358	108.7	13.48	263.0	16.3	3.9	29.0	26.2	7.6	5.4
368	112.0	13.95	267.8	18.1	9.4	26.0	26.4	6.9	5.5
378	115.3	14.71	282.3	12.2	12.2	28.3	33.0	2.4	1.8
388	118.7	11.58	194.6	9.3	13.9	32.5	24.8	2.8	3.4
398	122.0	13.86	176.7	9.1	4.3	48.3	13.4	2.4	4.3
408	126.0	12.12	154.6	8.9	2.9	42.3	16.2	7.8	4.0
418	129.8	20.55	311.3	8.5	4.7	28.1	27.4	13.6	3.2
428	133.3	22.14	322.6	21.6	5.9	13.6	17.0	20.9	7.7
438	136.4	16.23	306.9	20.0	7.4	9.7	14.2	25.8	7.4
448	139.1	11.42	211.7	21.5	4.5	22.2	12.9	15.8	10.0

Depth (cm)	Age (kyrs)	Total coccoliths ( $\times 10^9$ /g sediment)	AR coccoliths ( $\times 10^9$ m <sup>-2</sup> a <sup>-1</sup> )	C. leptopus	E. huxleyi	F. profunda	G. ericsonii	G. oceanica	U. sibogae
<i>Geob 1523-1 (03°50'N 41° 37'W, 3292m water depth)</i>									
0	0	20.42	233.1	2.91	28.78	29.07	0.29	3.2	5.52
13	6.1	40.05	387.1	0.00	17.87	32.27	0.8	1.33	2.67
18	8.4	23.90	314.2	1.10	19.03	24.12	0.66	3.1	2.21
23	10.8	28.73	348.9	0.57	20	35.43	2.29	2.86	5.72
28	13.1	19.76	248.6	0.28	28.73	32.32	3.87	7.46	7.74
33	15.5	19.03	174.1	1.01	25.25	49.49	1.68	2.02	4.38
43	18.7	11.26	113.5	1.31	24.92	42.62	0.98	6.89	10.49
53	20.5	8.95	85.3	0.64	23.79	44.37	0.64	3.54	15.75
58	21.4	15.44	119.2	1.53	16.56	49.69	1.23	4.29	11.66
63	23.2	13.48	121.0	0.84	20.34	40.96	1.13	7.34	16.95
68	24.9	14.36	137.2	2.51	20.06	40.44	0.31	4.7	17.24
73	26.7	15.72	176.3	3.18	25.72	35.55	2.89	8.38	13.29
78	28.4	16.40	216.3	6.30	21.32	31.83	3.3	10.81	11.71
83	30.2	21.44	320.9	6.68	32.89	27.54	3.48	7.22	9.09
88	31.9	21.25	332.1	10.38	26.65	26.89	4.95	12.03	6.13
93	33.7	16.61	219.1	10.19	24.52	34.71	3.5	7.32	5.41
98	35.4	18.23	204.8	3.29	31.44	38.02	7.49	3.29	4.49
103	37.2	20.73	225.5	2.39	32.63	41.64	6.1	2.92	3.45
113	40.7	21.15	260.6	6.39	25.58	39.24	9.3	3.2	6.1
123	44.2	15.52	173.5	4.38	25.25	35.02	14.81	4.38	10.1
133	47.7	16.95	188.2	6.73	18.91	40.71	13.46	4.81	7.05
143	51.2	21.63	275.3	4.17	16.96	31.55	21.13	4.76	8.04
153	56	18.76	210.9	5.05	17.51	35.69	11.78	2.69	11.78
163	62	19.83	189.3	0.80	24.6	43.58	1.34	0.8	16.58
173	66.5	15.71	140.2	1.41	21.99	43.62	2.13	1.42	18.8
183	69.5	13.30	123.8	1.51	15.09	50.94	8.68	4.15	9.06
193	72.5	27.75	338.4	1.39	7.64	40.51	33.1	1.62	8.1
203	75.5	23.34	252.8	0.54	5.45	38.15	39.51	2.18	4.63
208	77	37.85	448.4	0.84	6.16	29.69	47.06	1.12	3.08
213	78.5	28.50	312.4	0.92	6.45	31.57	45.16	1.15	5.53
223	83.5	18.38	117.7	1.32	4.29	58.09	25.41	1.98	2.64
233	89	18.77	197.3	1.05	3.15	43.04	35.7	1.57	6.82
243	93	27.84	453.4	0.94	3.76	28.47	45.18	1.88	8.47
248	95	30.17	368.3	0.66	2.41	36.84	41.89	1.54	8.55
258	99	32.67	357.8	0.50	1.75	29.07	49.62	1.5	7.27
263	100.6	28.70	268.1	1.11	1.66	36.84	42.94	1.39	8.03
273	103.8	24.53	219.5	0.52	2.1	45.41	35.43	1.31	7.34
283	107	13.58	147.6	1.76	2.94	50.88	25.59	4.41	6.17
293	112	22.52	325.5	2.62	6.12	31.78	34.4	5.54	8.45
303	117	22.94	286.8	1.71	3.99	32.76	38.18	1.42	6.26
313	122	31.01	260.2	2.56	1.99	34.76	24.79	1.99	3.98
323	126.3	31.92	283.3	2.60	1.3	42.45	30.99	3.13	2.86
338	132.8	20.00	200.7	0.86	1.73	44.09	32.56	6.34	4.9

## Acknowledgements

We would like to thank the master and crew of the RV 'Meteor' and numerous unnamed colleagues for their help during ship expeditions. C. Wienberg and S. Hüneke are thanked for technical assistance. Finally we thank Elisabetta Erba, Ric Jordan and Amos Winter for their critical review and the valuable comments, that helped to improve this manuscript. This research was funded by the Deutsche Forschungsgemeinschaft (Sonderforschungsbereich 261 at Bremen University, Contribution No. 248).

## References

- Ahagon, N., Tanaka, Y. and Ujiie, H., 1993. *Florisphara profunda*, a possible nannoplankton indicator of late Quaternary changes in sea-water turbidity at the northwestern margin of the Pacific. *Mar. Micropaleontol.* 22, 255-273.
- Andrulleit, H., 1996. A filtration technique for quantitative studies of coccoliths. *Micropaleontology* 42, 403-406.
- Backman, J. and Shackleton, N. J., 1983. Quantitative Biochronology of Pliocene and Early Pleistocene calcareous nannofossils from the Atlantic, Indian and Pacific Ocean. *Mar. Micropaleontol.* 8, 141-170.
- Bassinot, F. C., Beaufort, L., Vincent, E. and Labeyrie, L., 1997. Changes in the Dynamics of Western Equatorial Atlantic surface currents and biogenic productivity at the "Mid - Pleistocene Revolution" (930 ka) In: N. J. Shackleton, W. B. Curry, C. Richter and T. J. Bralower (Eds), *Proceedings of the Ocean Drilling Program, Scientific Results. 154.* College Station, TX (Ocean Drilling Program), pp 269 - 284.
- Beaufort, L., Lancelot, Y., Camberlin, P., Cayre, O., Vincent, E., Bassinot, F. and Labeyrie, L., 1997. Insolation cycles as a major control of Equatorial Indian Ocean Primary Production. *Science* 278, 1451-1454.
- Berge, G., 1962. Discoloration of the sea due to *Coccolithus huxleyi* "bloom". *Sarsia* 6, 27-40.
- Berger, W. H., 1989. Global Maps of Ocean Productivity In: W. H. Berger, V. S. Smetacek and G. Wefer (Eds), *Productivity of the Ocean: Present and Past.* John Wiley & Sons, Chichester, pp 429-455.
- Bickert, T. and Wefer, G., 1996. Late Quaternary deep water circulation in the South Atlantic: reconstruction from carbonate dissolution and benthic stable isotopes. In: G. Wefer, W. H. Berger, G. Siedler and D. Webb (Eds), *The South Atlantic: Present and Past Circulation.* Springer - Verlag., Berlin, pp 599-620.
- Brand, L. E., 1994. Physiological ecology of marine coccolithophores In: A. Winter and W. Siesser (Eds), *Coccolithophores.* Cambridge University Press, Cambridge, pp 39-49.

- Broerse, A. T. C., Ziveri, P., van Hinte, J. E. and Honjo, S., in press. Coccolithophore export production, seasonal species composition and coccolith CaCO<sub>3</sub> fluxes in the NE Atlantic (34°N 21°W and 48°N 21°W). *Deep-Sea-Res.*
- Brown, C. W. and Yoder, J. A., 1994. Coccolithophorid blooms in the global ocean. *J. Geophys. Res.* 99, 7467-7482.
- Brummer, G. J. A. and van Eijden, A. J. M., 1992. "Blue-ocean" paleoproductivity estimates from pelagic carbonate mass accumulation rates. *Mar. Micropaleontol.* 19, 99-117.
- Fischer, G. and Fahrteilnehmer, 1996. Report and preliminary results of Meteor-Cruise M 34/4, Recife-Bridgetown, 19.3.-15.4. 1996. *Berichte , Fachbereich Geowissenschaften, Universität Bremen* 80, 105.
- Flores, J. A., Sierro, F. J., Franés, G., Vázquez, A. and Zamarreno, I., 1997. The last 100,000 years in the western Mediterranean: sea surface water and frontal dynamics as revealed by coccolithophores. *Mar. Micropaleontol.* 29, 351-366.
- Gard, G., 1989. Variations in coccolith assemblages during the last glacial cycle in high and mid - latitude Atlantic and Indian oceans. In: J. A. Crux and S. E. van Heck (Eds), *Nannofossils and their application*. Ellis Horwood Limited, Chichester, pp 1-24.
- Geitzenauer, K. R., Roche, M. B. and McIntyre, A., 1977. Coccolith Biogeography from North Atlantic and Pacific Surface Sediments In: A. T. S. Ramsay (Eds), *Oceanic Micropalaeontology*. Academic Press, London, pp 973-1008.
- Giraudeau, J., 1992. Distribution of Recent nannofossil beneath the Benguela system: southwest African continental margin. *Mar. Geol.* 108, 219 - 237.
- Hay, W. H., 1995. Paleooceanography of marine organic-carbon-rich sediments In: A.-Y. Huc (Eds), *Paleogeography, Paleoclimate, and Source Rocks*. Nr.40. American Association of Petroleum Geologists, Tulsa, Oklahoma, pp 21-59.
- Henrikson, A. S., 1996. Calcareous nannoplankton productivity and succession across the Cretaceous-Tertiary boundary in the Pacific (DSDP site 465) and Atlantic (DSDP site 527) oceans. *Cretaceous research* 17, 451-478.
- Hiramatsu, C. and De Decker, P., 1997. The calcareous nannoplankton assemblages of surface sediments in the Tasman and Coral Seas. *Paleogeogr., Paleoclimatol., Paleoecol.* 131, 257-285.
- Holligan, P. M., Fernández, E., Aiken, J., Balch, W. M., Boyd, P., Burkill, P. H., Finch, M., Groom, S. B., Malin, G., Muller, K., Purdie, D. A., Robinson, C., Trees, C. C., Turner, S. M. and van der Waal, P., 1993. A biogeochemical study of the coccolithophore *Emiliana huxleyi*, in the North Atlantic. *Global Biogeochem. Cycles* 7, 879 - 900.
- Honjo, S. and Okada, H., 1974. Community structure of coccolithophores in the photic layer of the mid-Pacific. *Micropaleontology* 20, 209-230.
- Houghton, S. D., 1988. Thermocline control on coccolith diversity and abundance in recent sediments from the Celtic Sea and English Channel. *Mar. Geol.* 83, 313-319.

- Hulburt, E. M., 1976. Limitation of phytoplankton species in the ocean off western Africa. *Limnol. and Oceanog.* 21, 193-211.
- Imbrie, J., Hays, J. D., Martinson, D. G., McIntyre, A., Mix, A. C., Morley, J. J., Pisias, N. G., Prell, W. L. and Shackleton, N. J., 1984. The orbital theory of Pleistocene climate: support from revised chronology of the marine  $\delta^{18}O$  record. In: A. Berger, J. Imbrie, J. D. Hays, G. Kukla and B. Saltzman (Eds), *Milankovitch and Climate. Part 1.D.* Reidel, Dordrecht, pp 269-305.
- Jordan, R. W. and Chamberlain, A. H. L., 1997. Biodiversity among haptophyte algae. *Biodiv. Conserv.* 6, 131-152.
- Jordan, R. W. and Kleijne, A., 1994. A classification system for living coccolithophores In: A. a. S. Winter W.G. (Eds), *Coccolithophores.* Cambridge University Press, Cambridge, pp 83-106.
- Jordan, R. W., Zhao, M., Eglinton, G. and Weaver, P. P. E., 1996. Coccolith and alkenone stratigraphy at an upwelling site off NW Africa (ODP 658C) during the last 130,00 years In: A. Mokuilevsky and R. Whatley (Eds), *Microfossils and Oceanic Environments.* Aberystwyth Press, Aberystwyth, pp 111-130.
- Kinkel, H., Dittert, N. and Henrich, R., submitted. Calcareous plankton record in the Equatorial Atlantic: A 300 kyrs record of climate feedback, productivity and dissolution.
- Kleijne, A., 1993. Morphology, Taxonomy and distribution of extant Coccolithophorids (Calcareous Nannoplankton).
- Kleijne, A., Kroon, D. and Zevenboom, W., 1989. Phytoplankton and foraminiferal frequencies in Northern Indian Ocean and Red Sea surface waters. *Neth.J. Sea Res.* 24, 531 - 539.
- Knappertsbusch, M., 1993. Geographic distribution of living and Holocene coccolithophores in the Mediterranean sea. *Mar. Micropaleontol.* 21, 219-247.
- Longhurst, A., 1993. Seasonal cooling and blooming in tropical oceans. *Deep-Sea Research* 40, 2145-2177.
- Macdonald, A. M. and Wunsch, C., 1996. An estimate of global ocean circulation and heat fluxes. *Nature* 382, 436-439.
- McIntyre, A., 1967. Coccoliths as paleoclimatic indicators of Pleistocene glaciation. *Science* 158, 1314-1317.
- McIntyre, A. and Bé, A., 1967. Modern Coccolithophoridae in the Atlantic Ocean. I. Placoliths and cyrtholiths. *Deep-Sea-Res.* 14, 561-597.
- McIntyre, A. and Molfino, B., 1996. Forcing of Atlantic Equatorial and Subpolar Millennial Cycles by Precession. *Science* 274, 1867-1870.
- Mitchell-Innes, B. A. and Winter, A., 1987. Coccolithophores: A major phytoplankton component in mature upwelled waters off the Cape Peninsula, South Africa in March 1983. *Mar. Biol.* 95, 25-30.
- Mix, A. C., 1989. Influence of productivity variations on long - term atmospheric  $CO_2$ . *Nature* 337, 541 - 544.
-

- Molfinio, B. and McIntyre, A., 1990 a. Precessional Forcing of Nutricline Dynamics in the Equatorial Atlantic. *Science* 249, 766-769.
- Molfinio, B. and McIntyre, A., 1990 b. Nutricline Variation in the equatorial Atlantic coincident with the Younger Dryas. *Paleoceanography* 5, 997 - 1008.
- Monger, B., McClain, C. and Murtugudde, R., 1997. Seasonal phytoplankton dynamics in the eastern tropical Atlantic. *J. Geophys. Res.* 102, 12,389-12,411.
- Müller, P. J. and Suess, E., 1979. Productivity, sedimentation rate, and sedimentary organic matter in the oceans-I. Organic carbon preservation. *Deep-Sea Res.* 26A, 1347-1362.
- Nanninga, H. J. and Tyrrell, T., 1996. Importance of light for the formation of algal blooms by *Emiliania huxleyi*. *Mar. Ecol. Prog. Ser.* 136, 195-203.
- Nishida, S., 1979. Atlas of Pacific Nannoplanktons. *Micropaeontol. Soc. Osaka Spec. Pap.* 3, 1-31.
- Okada, H. and Honjo, S., 1973. The distribution of oceanic coccolithophorids in the Pacific. *Deep-Sea-Res.* 20, 355-374.
- Okada, H. and Matsuoka, M., 1996. Lower - photic nannoflora as an indicator of the late Quaternary monsoonal paleo - record in the tropical Indian Ocean In: A. M. & R. Whatley (Eds), *Microfossils and Oceanic Environments*. Aberystwyth Press, Aberystwyth, pp 231-245.
- Okada, H. and McIntyre, A., 1979. Seasonal distribution of modern coccolithophores in the western North Atlantic Ocean. *Mar. Biol.* 54, 319 - 328.
- Peterson, R. G. and Stramma, L., 1991. Upper-level circulation in the South Atlantic Ocean. *Prog. Oceanog.* 26,
- Roth, P. H. and Coulbourn, W. T., 1982. Floral and solution patterns of coccoliths in surface sediments of the North Pacific. *Mar. Micropaleontol.* 7, 1 -52.
- Rühlemann, C., Frank, M., Hale, W., Mangini, A., Mulitza, S., Müller, P. J. and Wefer, G., 1996. Late Quaternary productivity changes in the western equatorial Atlantic: Evidence from <sup>230</sup>Th-normalized carbonate and organic carbon accumulation rates. *Mar. Geol.* 135, 127-152.
- Samtleben, C., Schaefer, P., Andruleit, H., Baumann, A., Baumann, K.-H., Kohly, A., Matthiessen, J. and Schroeder-Ritzrau, A., 1995. Plankton in the Norwegian-Greenland Sea: From Living communities to Sediment Assemblages - an actualistic approach. *Geol. Rundsch.* 84, 108 - 136.
- Samtleben, C. and Schröder, A., 1992. Living coccolithophore communities in the Norwegian-Greenland Sea and their record in sediments. *Mar. Micropaleontol.* 19, 333-354.
- Sarnthein, M., Pflaumann, U., Ross, R., Tiedemann, R. and Winn, K., 1992. Transfer functions to reconstruct ocean paleoproductivity: a comparison In: C. P. ; Summerhayes, W. L. Prell and K. C. Emeis (Eds), *Upwelling Systems: Evolution since the early Miocene*. Geological Society Special Publication, London, pp 411-427.

- Schneider, R. R., Müller, P. J., Ruhland, G., Méinecke, G., Schmidt, H. and Wefer, G., 1996. Late Quaternary surface temperatures and productivity in the east-equatorial South Atlantic: response to changes in Trade / Monsoon wind forcing and surface water advection. In: G. Wefer, W. H. Berger, G. Siedler and D. Webb (Eds), *The South Atlantic: Present and Past Circulation..* Springer, Berlin, pp 527-551.
- Schulz, H., Bleil, U., Henrich, R. and Segel, M., 1995. Geo Bremen SOUTH ATLANTIC 1994, Cruise No. 29, 17 June - 5 September 1994. Meteor Berichte, Universität Hamburg 95-2, 323 pp.
- Shokati, I., Baumann, K.-H., Cepek, M. and Henrich, R., in press. Zur Sedimentation von Coccolithophoriden und ihrer Akkumulation in spätpleistozän-holozänen Sedimenten des östlichen Südatlantik. Zbl. Geol. Paläont. Teil I
- Sikes, C. S., Wierzbicki, A. and Fabry, V. J., 1994. From atomic to global scales in biomineralization. Bulletin de l'Institut Oceanographique (Monaco) SPEC. ISSUE 14, 1-47.
- Sprengel, C., Baumann, K.-H. and Neuer, S., subm. Seasonal and interannual variations of coccolithophore fluxes and species compositions in sediment traps north of Gran Canaria. Mar. Micropaleontol. this issue,
- Steinmetz, J. C., 1994. Sedimentation of coccolithophores In: A. Winter and W. G. Siesser (Eds), *Coccolithophores*. Cambridge University Press, Cambridge, pp 179-197.
- Struck, U., Sarnthein, M., Westerhausen, L., Barnola, J. M. and Raynaud, D., 1993. Ocean-atmosphere carbon exchange: impact of the "biological pump" in the Atlantic equatorial upwelling belt over the last 3330,000 years. *Paleogeogr., Paleoclimatol., Paleoecol.* 103, 41-56.
- van Andel, T. H., Heath, G. R. and Moore, T. C., 1975. Cenozoic history and paleoceanography of the central equatorial Pacific Ocean. 134 pp.
- Verardo, D. J. and McIntyre, A., 1994. Production and destruction: Control of biogenous sedimentation in the tropical Atlantic 0-300,000 years B.P. *Paleoceanography* 9, 63-86.
- Verardo, D. J. and Ruddiman, W. F., 1996. Late Pleistocene charcoal in tropical Atlantic deep sea sediments: Climatic and geochemical evidence. *Geology* 24, 855 - 857.
- Wefer, G., Berger, W. H., Bickert, T., Donner, B., Fischer, G., Kemle-von-Mücke, S., Meinecke, G., Müller, P. J., Mulitza, S., Niebler, H.-S., Pätzold, J., Schmidt, H., Schneider, R. R. and Segl, M., 1996. Late Quaternary surface circulation of the South Atlantic: The stable isotope record and Implications for Heat Transport and Productivity In: G. Wefer, W. H. Berger, G. Siedler and D. Webb (Eds), *The South Atlantic: Present and Past Circulation*. Springer, Berlin, pp 461-502.
- Westbroek, P., Brown, C. W., van Bleijswijk, J., Brownlee, C., Brummer, G. J., Conte, M., Egge, J., Fernández, E., Jordan, R., Knappertsbusch, M., Stefels, J., Veldhuis, M., van der Waal, P. and Young, J. R., 1993. A model system approach to biological climate forcing. The example of *Emiliania huxleyi*. *Global and Planetary Change* 8, 27-46.

- Winter, A., Reiss, Z. and Luz, B., 1979. Distribution of living coccolithophore assemblages in the Gulf of Elat (Aqaba). *Mar. Micropaleontol.* 4, 197 - 223.
- Young, J. R., 1994. Functions of coccoliths. In: A. Winter and W. G. Siesser (Eds), *Coccolithophores*. Cambridge Academic Press, Cambridge, pp
- Ziveri, P., Thunell, R. C. and Rio, D., 1995. Seasonal changes in coccolithophore densities in the Southern Californian Bight during 1991 - 1992. *Deep - Sea Research* 42, 1881 - 1903.

---

---

## **Calcareous plankton record in the Equatorial Atlantic: A 300 kyrs record of climate feedback and productivity**

Hanno Kinkel, Nicolas Dittert, and Rüdiger Henrich

*FB Geowissenschaften, Universität Bremen, Postfach 330 440, D-28334 Bremen,  
Germany*

**Abstract:** A sediment core from the southern equatorial Atlantic (GeoB 1117-2) was investigated to reconstruct the surface water circulation and its impact on productivity of calcareous plankton (planktic foraminifera and coccolithophores) during the last 300 kyrs.

The floral and faunal records show significant changes in surface water circulation which can be attributed (1) to advection of cool and nutrient rich water masses from higher southern latitudes and (2) to equatorial upwelling intensity. Cross-spectral analysis revealed that both processes show cyclic variations within the orbital frequency domains of eccentricity and precession, and to a minor degree within the obliquity band.

While the floral and faunal assemblages seem to be robust and only slightly affected by carbonate dissolution, the total numbers of planktic foraminifera and coccoliths, which should provide us with information on the productivity of calcareous plankton, partly seem to be biased by carbonate dissolution.

### **1. Introduction**

Surface water circulation and productivity changes in the equatorial Atlantic have been the focus of numeral studies (McIntyre et al., 1989; Mix, 1989; Molfino and McIntyre, 1990; Struck et al., 1993; Sikes and Keigwin, 1994; McIntyre and Molfino, 1996; Mix and Morey, 1996; Schneider et al., 1996). Usually stable isotopes, planktic foraminifera and calcium carbonate or organic carbon records are used to reconstruct the paleoceanography of the equatorial Atlantic.

The tropical Atlantic is a key area for understanding global thermohaline circulation as it transfers huge amounts of heat from the Southern to the Northern Hemisphere (Gordon, 1986; Gordon, 1996; Macdonald and Wunsch, 1996). Additionally, the equatorial upwelling area, associated with the South Equatorial Current, is a highly productive regime which contributes significantly to the global export productivity (Berger et al., 1989). Nowadays it may not be as productive in terms of carbon produced per area compared to the highly productive areas as the North Atlantic where massive

blooms occur regularly or the intensive upwelling zones of the continental margins along the eastern boundary currents. Since the tropical oceans cover by far the largest area, their contribution to the global carbon cycle is important (Longhurst, 1993; Monger et al., 1997). It was suggested that an increase in paleoproductivity in the equatorial Atlantic is likely to influence the global atmospheric CO<sub>2</sub> concentration as recorded in ice core inclusions (Mix, 1989; Struck et al., 1993; Mix and Morey, 1996).

Calcareous plankton contributes largely to the particle flux in the investigated area (Fischer and Wefer, 1996), thus, its sedimentary record should provide information on the productivity changes in the past. Yet, we have to keep in mind that the calcium carbonate record in the tropical Atlantic is susceptible to carbonate dissolution reflecting the glacial- interglacial fluctuations of deep-water circulation patterns (Verardo and McIntyre, 1994; Bickert and Wefer, 1996).

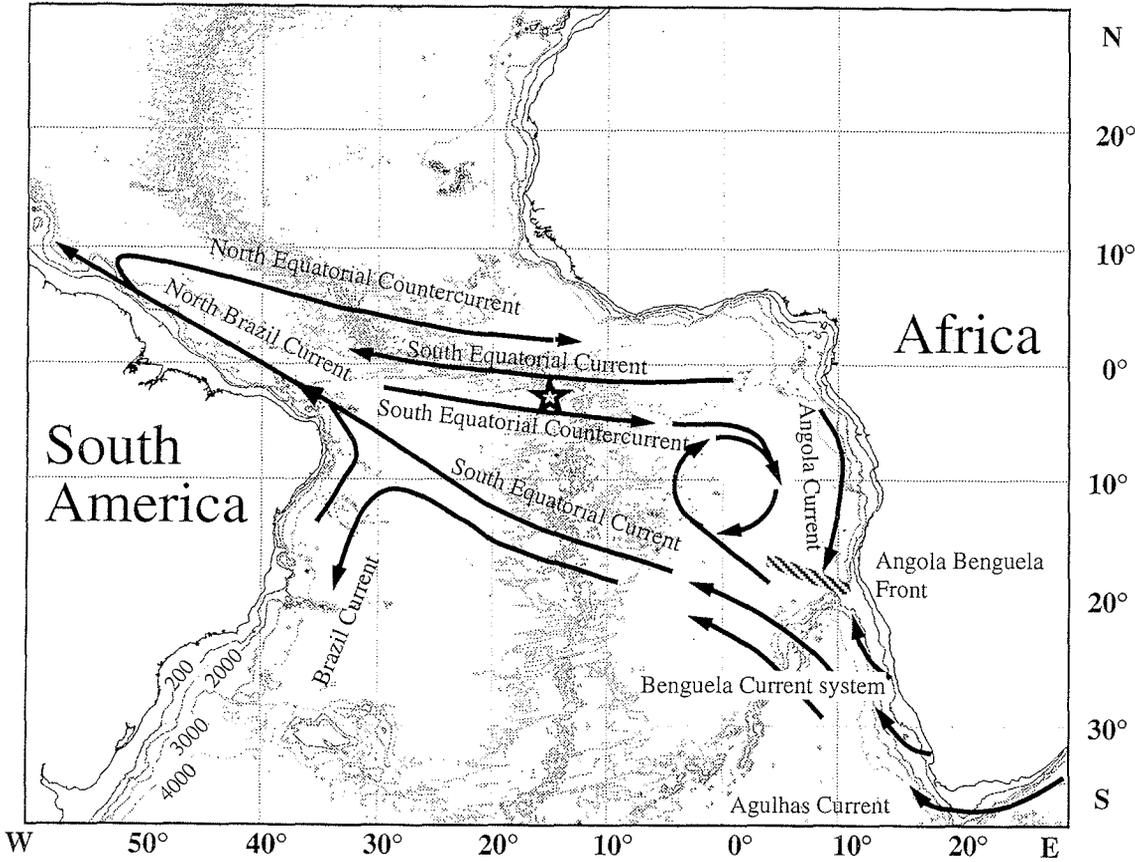
We have chosen a sediment core (GeoB 1117-2; 3°34'S - 14°54'W, 3,984 m; Fig. 1) from the southern rim of today's equatorial upwelling system and situated well above the modern Calcite Lysokline (CCL). Both surface- and deep-water circulation patterns are considered to have experienced significant changes during the last 300 kyrs in concert with global climate changes. We present data of the two dominant calcareous plankton groups, planktic foraminifera and coccolithophores, to reconstruct their faunal and floral response to changing surface water circulation as well as their productivity record.

## **2. Present and past equatorial Atlantic oceanography**

### *2.1. Surface water circulation*

The surface water oceanography of the equatorial Atlantic is characterized by the westward flowing South Equatorial Current (SEC) and the eastward flowing South Equatorial Counter Current (SECC), the North Equatorial Current (NECC) and the Equatorial Undercurrent (EUC). The westward flow of the SEC is mainly controlled by the intensification of westward directed tradewinds in boreal spring in the western tropical Atlantic (Philander and Pacanowski, 1986). This causes a massive transport of warm surface waters from the eastern tropical Atlantic, one of the major pathways of oceanic heat transport to the northern hemisphere within the Atlantic. As a result of the wind induced westward flow of the SEC, the thermocline is uplifted in the eastern tropical Atlantic and a corresponding deepening is observed in the western tropical Atlantic. The seasonal uplift of the thermocline which is at its maximum in boreal summer causes an elevated nutrient flux, which results in a productivity increase within the photic zone. Besides thermocline uplift, additional nutrient flux to the photic zone results from the a

wind driven equatorial divergence and shear mixing between the EUC and the SEC. During boreal autumn the thermocline has returned to its pre-upwelling state. More recently a comprehensive summary between the physical ocean dynamics and the observed phytoplankton response in the Equatorial Atlantic was given by Monger et al. (1997).



**Fig.1** Position of core GeoB 1117-2 and a sketch of the surface water circulation pattern, adapted from various authors.

This seasonal cycle in the surface water circulation of the equatorial Atlantic is an analogon for long-term variations by the precessional component of orbital forcing (Molfino and McIntyre, 1990). Perihelion centered on boreal winter (December) is equivalent to maximum divergence, while perihelion centered on boreal summer is equivalent to minimum divergence (McIntyre et al., 1989). The intensified heating of the African continent during June perihelion causes an uplift of air and relative low pressure in this region. As a result, a monsoonal effect is caused with meridional winds from the south.

The importance of the equatorial Atlantic's surface water circulation for northward

directed heat transport is a key for reconstructing and modeling past global climates (Webb et al., 1997). Discrepancies between the SST reconstruction for the tropical Atlantic (CLIMAP, 1981; 1984; Sikes and Keigwin, 1994) and terrestrial temperature records (Rind and Peteet, 1985; Stute et al., 1995) caused serious obstacles, as the significantly lowered temperatures on land (about 5 °C) and small changes in SST (<2 °C) in the tropics could not be explained by a conclusive model. More recently, CLIMAP's SST reconstructions were challenged by coral records from the Atlantic (Guilderson et al., 1994) as well as from the Pacific (Beck et al., 1997) which had the same magnitude as the terrestrial temperature records. SST display the same pattern for the investigated core position (Dittert et al. *subm.*).

## 2.2. *Deep-water circulation*

Today, the circulation in the deep South Atlantic Ocean is dominated by interactions between the AABW and the NADW in contrasting extent. NADW is indicated by oxygen enriched, nutrient depleted water masses of high  $\text{CO}_3^{2-}$  and low  $\text{CO}_2$  contents. AABW can be distinguished as an extremely cold, oxygen depleted and nutrient enriched water mass of low  $\text{CO}_3^{2-}$  and high  $\text{CO}_2$  contents (Kroopnick, 1985; Boyle, 1988). Today's mixing zone between AABW and NADW in the South Atlantic is close to the 90  $\mu\text{mol/kg}$   $\text{CO}_3^{2-}$  isopleth (Bainbridge, 1981). The relatively warm and saline NADW occupies the depth interval between 2,000 m and 4,000 m, while below 4,000 m AABW is encountered. However, the geometry deep-water masses in the South Atlantic is much more complex in detail. A strong east-west asymmetry in the deep water structure is observed, which is related to deflections along topographic barriers like the Mid Atlantic Ridge, the Walvis Ridge and the Rio Grande Rise. These barriers are partly incised by major deep water conducts like the Romanche Fracture Zone which enable the inflow of NADW to the equatorial eastern Atlantic Ocean. With respect to the modern South Atlantic Ocean, the border of AABW with NADW and the hydrographic lysokline coincide (Bickert and Wefer, 1996).

### 3. Material and methods

The gravity core was retrieved from the ocean floor during R/V METEOR cruise M9-4 (Wefer et al., 1989). In addition, a giant box corer was retrieved and sampled to achieve an undisturbed sediment surface which usually is not the case in the gravity core. To achieve a composite record all sediment parameters were used.

#### 3.1. Stratigraphy

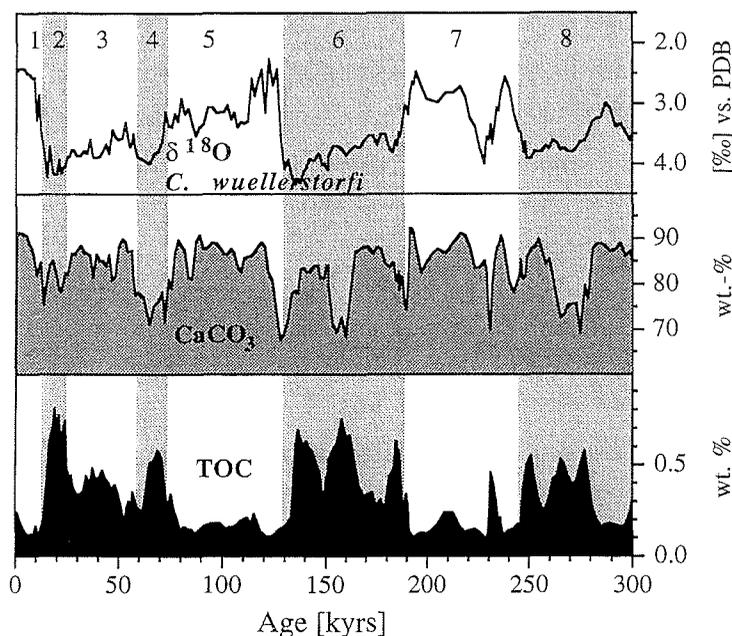
Stable oxygen and carbon isotopes of the epibenthic foraminifera *Cibicides wuellerstorfi* were analyzed at the University of Bremen (Bickert, 1992). All samples were analyzed using Finnigan MAT 251 micromass spectrometer coupled with a Finnigan automated carbonate device. The reproducibility of the measurements, as referred to an internal carbonate standard (Solnhofen limestone), is  $\pm 0.07\%$ . The conversion to the PDB - scale was performed using the international standards NBS 18, 19 and 20. To achieve a complete time series a composite record was established using all sediment parameters measured in the sediment sequences, in the giant box corer, and the gravity core. The age model is based on the graphic correlation between the  $\delta^{18}\text{O}$  record of the core and the SPECMAP standard record (Imbrie et al., 1984).

#### 3.2. Sedimentation and mass accumulation rates

Except transfer functions (Mix, 1989; Lebreiro et al., 1997) all methods for reconstructing paleoproductivity are based on mass accumulation rates of bulk parameters. Sedimentation rates were determined by linear interpolation between age control points of the  $\delta^{18}\text{O}$  record and the SPECMAP stack (Bickert, 1992). To elucidate the paleofluxes of various sediment components like calcium carbonate, organic carbon, planktic foraminifera, and coccolithophores, it is necessary to calculate their accumulation rates (AR). AR was calculated after the method of van Andel et al. (Van Andel et al., 1975). The accuracy of AR strongly depends on the preciseness of the age model applied. The correlation coefficient between the oxygen isotope record in core GeoB 1117-2 and the SPECMAP standard record is extremely high ( $r^2 > 0.98$ ). Nevertheless, there are a few outstanding maxima in sedimentation rates (Fig. 2) which are far above the expected variance. Since these maxima are also observed in the global distributed sediment cores that were used for the standard records, it is likely that they are artefacts due to a non-linear climate response to orbital forcing (Bickert, 1992).

### 3.3. Planktic foraminifera

For foraminiferal counts, samples were freeze-dried, weighed, and washed through a 63  $\mu\text{m}$  sieve under a gentle spray of water to prevent mechanical fragmentation. We base the faunal analysis on the fraction  $>150 \mu\text{m}$  according to the CLIMAP-conventions. After separating the fraction  $<150 \mu\text{m}$ , the samples were dry-sieved on a 212  $\mu\text{m}$ , 355  $\mu\text{m}$ , 500  $\mu\text{m}$ , and 1,000  $\mu\text{m}$  sieve-set in order to minimize sorting and to simplify counting. Each fraction was repeatedly split into subsamples using a microsplitter to obtain an aliquot of at least 300 non-fragmented planktic foraminiferal specimens (CLIMAP, 1984) which were identified and counted completely using an OLYMPUS SZ 40 binocular at 20I to 80I magnification. The taxonomy used follows that of Hemleben et al. (1989). Planktic foraminifera fragments, benthic foraminifera, radiolaria, and subordinately pteropods, rock fragments, and indeterminable particles were also counted on the same aliquot. All fauna-counts were converted into count percent and number of organisms per gram sediment (Mix, 1989).



**Fig. 2:** Downcore distribution of stable oxygen isotopes of the epibenthic foraminifera *C. wuellerstorfi* (from Bickert and Wefer, 1996),  $\text{CaCO}_3$  and organic carbon contents (wt.-%); from Bickert (1992).

### 3.4. Coccoliths

For preparation of sediment samples a combined dilution/filtering technique as described by (Andruleit, 1996) was used. A small amount of sediment was weighed and

brought into suspension. After dilution with a rotary splitter, the suspension was filtered through polycarbonate membrane filters (Schleicher&Schuell™, 50 mm diameter, 0.4 µm pore size). A monolayer of all sediment particles was successively studied by SEM. All coccoliths were recorded in numbers per gram dry sediment. In general, the taxonomy of Jordan and Kleijne (1994) was used.

Coccolith numbers were then converted to coccosphere units, assuming that coccospheres of *E. huxleyi* are covered by 24 coccoliths; coccospheres of the genus *Gephyrocapsa* bear 14 coccoliths, and coccospheres of *F. profunda* carry 75 coccoliths. This data contain own observations on living coccolithophores from the South Atlantic as well as from various other sources (e.g., Knappertsbusch, 1993; Young, subm.). Although it is known that the number of coccoliths per coccosphere is not constant, and that especially *E. huxleyi* is known to produce multiple layers of coccoliths and even to shed coccoliths during its life cycle, these values seem to be a reasonable average.

### 3.5. Spectral analysis

We performed spectral analysis with the software package "AnalySeries 1.1" (Paillard et al., 1996). The analyzed timeseries were evenly resampled at 3 kyr intervals and linearly detrended. As a record of global ice volume, we used the  $\delta^{18}\text{O}$  signal of the benthic foraminifer *C. wuellerstorfi* of the same core (Bickert and Wefer, 1996).

### 3.6. Carbonate and carbon content

Calcium carbonate and organic carbon contents of the bulk sediment were determined with a Leco - CS 244. Therefore, 100 mg of freeze-dried and homogenized sediment was analyzed. For determination of the organic carbon content, the same amount of sediment was acidified with 6n HCl and measured the same way. The carbonate content is calculated by subtracting the organic carbon content from the total carbon content.

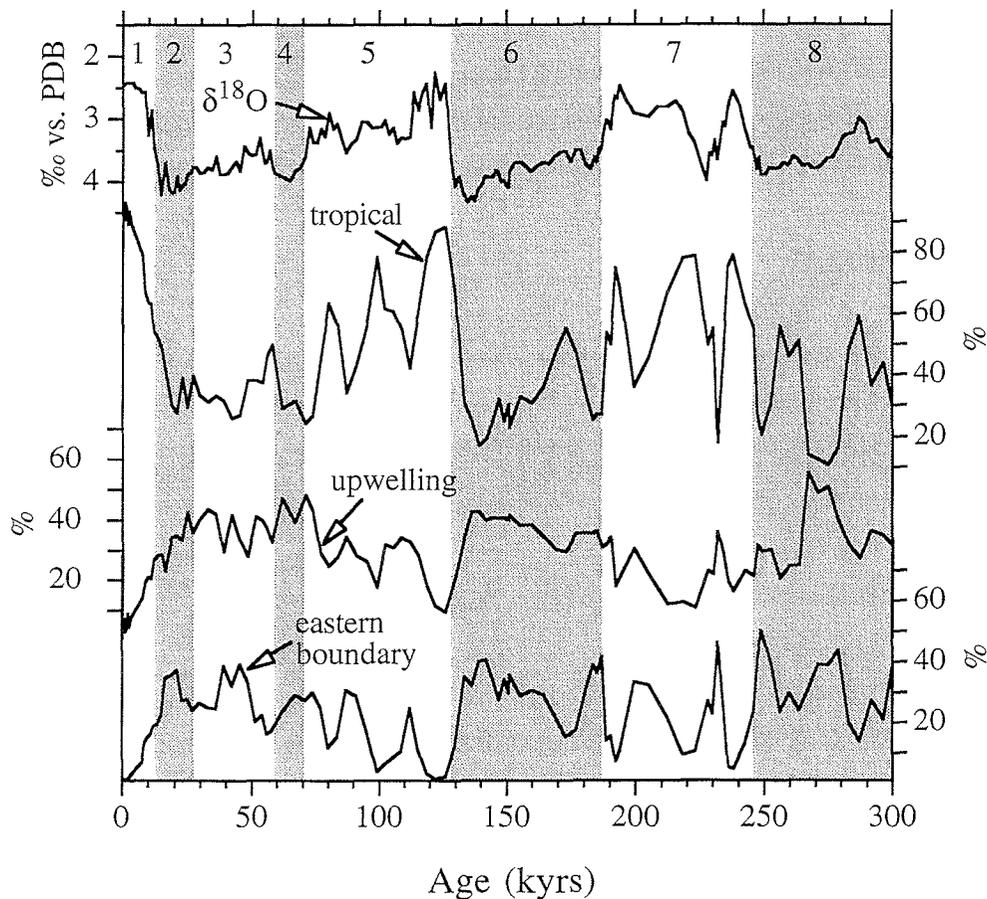
## 4. Results

### 4.1. Planktic foraminifera

The absolute number of planktic foraminifera per gram sediment varies from 27,000 to 191,000 specimens. Maximum numbers occur at the transition of isotope stages 8/7 and at the oxygen isotope events 7.1, 6.6, 6.4; minimum numbers occur at isotope events 6.3, 5.4, and 2.1. Relative abundances and absolute numbers of planktic foraminifera

show a distinct orbital-to-suborbital modification. Moreover, there is an obvious trend from 110,000 (300 ka) to 54,000 (Recent) planktic foraminifera per gram sediment.

The subtropical representative *G. ruber* (pink and white variety; 3 - 43 %) attains maxima at interglacial maxima, particularly at isotope stages 7, 5, and during the Holocene. Among the subpolar species, *N. pachyderma* dex. (0 - 49 %) has its maximum occurrence during the glacial maxima of isotope stage 8 and the isotope event 7.4; its abundance subsequently lowers. It is nearly absent during the Holocene. *Neogloboquadrina pachyderma* sin. (0 - 5 %) almost exclusively occurs at full glacial conditions. It is absent during the Holocene (cf. Dittert et al., subm.).



**Fig. 3:** Downcore distribution of the planktic foraminifera assemblages according to Mix and Morey (1996), species composition of the assemblages is listed in Table 1.

Mix and Morey (1996) distinguished three assemblages of planktic foraminifera, based on down core factor analysis of a set of sediment cores from the tropical Atlantic and Pacific Ocean. The use of down core sediment samples rather than surface sediment samples was chosen to avoid "no-analogue" situations, which are a general problem of modern analog and transfer techniques applied to foraminiferal counts. The three

assemblages are defined as: 1) warm-tropical-, 2) upwelling-, and 3) the eastern boundary assemblage. These assemblages are related to the major surface circulation processes in the tropical Atlantic. The first assemblage is representative for warm surface water masses with a deep thermocline; the second is attributed to an upwelling intensity with a shallow thermocline and reduced surface water temperature, whereas the third assemblage reflects the advection of cold and nutrient rich water masses via the eastern boundary currents.

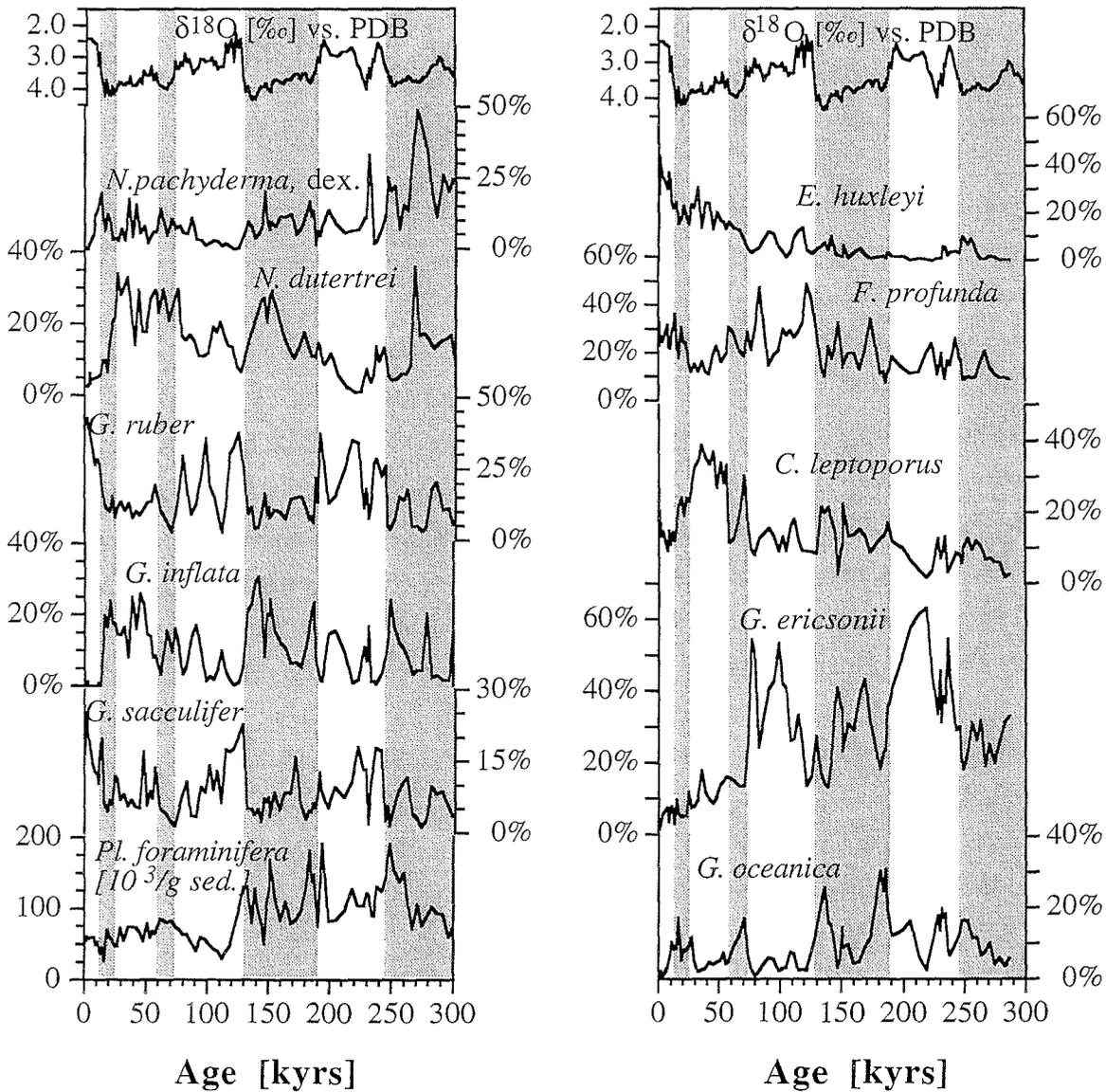


Fig. 4: Downcore distribution of the relative abundance of the most common coccolithophore and planktic foraminifera species. Mind the different scales!

Highest abundance of the tropical group occurs in isotope stages 7, 5, and during the Holocene which corresponds up to 96 % of the whole assemblage (Fig. 3). Lowest

values in general occur during all glacial stages and substages. The upwelling assemblage has maximum abundances in isotope stages 8, 6, and 4 which corresponds up to 55 % of the total assemblage (Fig.3). Minimum values occur during interglacials. The eastern boundary assemblage amounts up to 50.2 % of the total assemblage in isotope stage 8.1. Minimum values occur in isotope stage 5.5 and during the Holocene (Fig. 3).

#### 4.2. *Coccoliths*

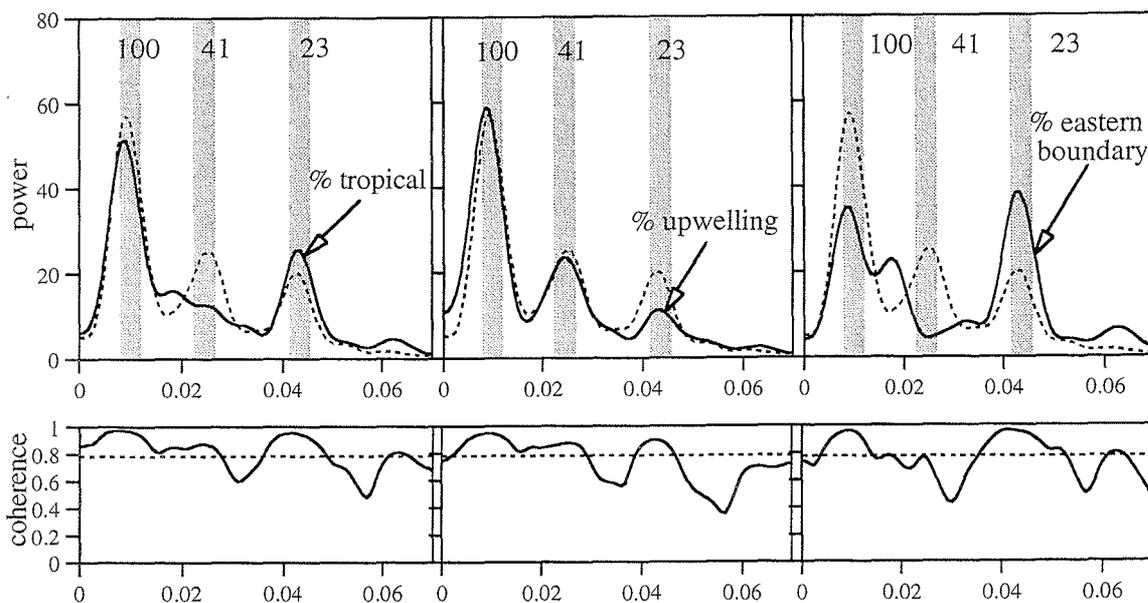
Coccolith numbers in core GeoB 1117-2 vary from about  $2.5 \times 10^9$  up to  $80 \times 10^9$  coccoliths/g sediment, while accumulation rates vary from  $60 \times 10^9$  up to  $1,500 \times 10^9$  coccoliths  $m^{-2} a^{-1}$  (Fig. 2). In general, variability in numbers of coccoliths resemble coccolith accumulation rates, with slight disagreement in isotope stage 4 and more larger disagreements in early isotope stage 6 and throughout stage 7. Highest numbers and highest accumulation rates occur during isotope stage 2 and 3. Lowest values are indicative for the Holocene as well as for oxygen isotope stage 5. During isotope stage 5 *G. ericsonii* and *F. profunda* dominate the assemblage (Fig. 4). Here, *G. ericsonii* reaches abundances of up to 54 %, while it shows subordinate abundance in Holocene sediments. A sharp drop in the abundance of this species is observed at the oxygen isotope stage boundary 5/4. Contemporaneously relative abundances of *E. huxleyi* began to rise until they reach their maximum values of 44 % in the Holocene. In addition, abundances of *F. profunda* show a cyclic variation throughout the record with values varying between 10 % and 48 %. Highest abundances with two significant peaks appear in isotope stage 5. In general, lower abundances of *F. profunda* are observed in the glacial intervals. *Calcidiscus leptoporus* reach almost 40 % in isotope stage 3, and additional maxima occur in glacial stages 6 and 4. A similar pattern can be seen in the abundance of *G. oceanica* which reveals significant maxima up to 26 % in glacial stages 6, 4, 2, and subordinate abundances in the rest of the record.

### 5. Discussion

Planktic foraminifera and coccoliths are the major components of the sediments in the investigated core, whereas siliceous microfossils (e.g. diatoms) are only a subordinated component (Gingele, 1992). Terrigenous sediments, in general eolian transported fine ( $< 2 \mu m$ ) and silt fraction ( $< 63 \mu m$ ), can reach 25 wt.-% of the total sediment in glacial periods (Gingele and Dahmke, 1994). Although these high percentages correlate well with low carbonate contents, and therefore a concentration effect due to carbonate

dissolution may be assumed, a two- to threefold increase in accumulation rates of terrigenous matter indicates stronger eolian transport during glacials, which has been reported by various authors from nearby sediment cores (Gingele, 1992; deMenocal et al., 1993; Ruddiman, 1997).

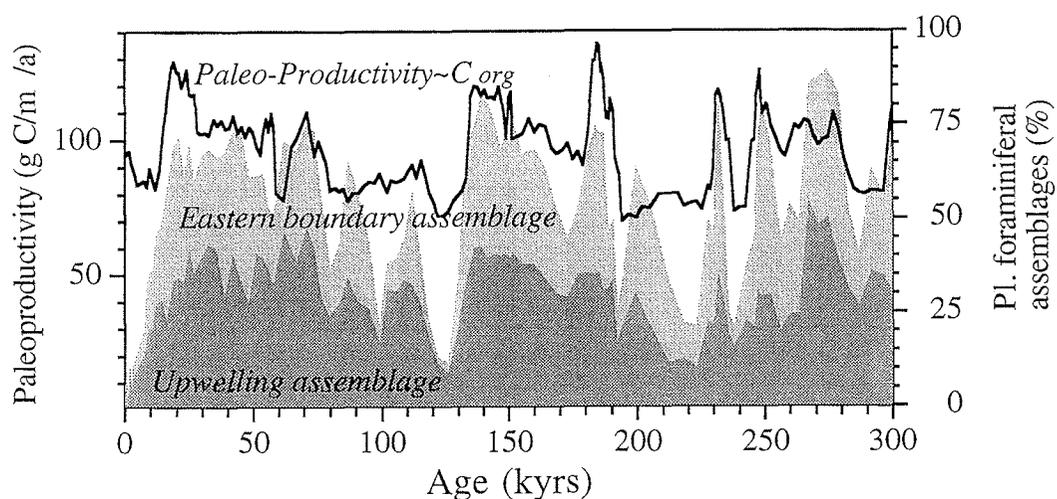
Since Imbrie and Kipp (1971) used planktic foraminifera to reconstruct past sea surface temperatures, a lot of authors turned to that method with different approaches (Mix et al., 1986a; 1986b; Pflaumann et al., 1996). Although the reliability of these methods increased with the growing numbers of calibration points (core top samples), the problem of "no-analogue" situations (Hutson, 1977) remained; a problem, that is unfortunately very apparent in the tropical oceans (Mix et al., 1986a; 1986b; Ravelo et al., 1990). Mix and Morey (1996) tried to avoid this problem by investigating planktic foraminiferal assemblages from a set of downcore samples from sites in the tropical Atlantic and Pacific Ocean instead of investigating surface sediments or core tops. This approach resulted in the establishment of three planktic foraminifera assemblages which allow to deduce long-term variations of the equatorial current system, as proposed before by Ravelo et al. (1990). Moreover these three assemblages are supposed to be relatively insensitive to carbonate dissolution (Mix and Morey, 1996, Dittert et al. subm.).



**Fig. 5:** Cross spectral analysis between the planktic foraminifera assemblages (solid line) and the stable oxygen isotope record of *C. wuellerstorfi* (dashed line). The coherency is plotted in the lower panel with the 80% confidence level indicated with the dashed line.

Cross-spectral analysis of the planktic foraminifera assemblages reveal cyclic variations within the main frequency domains of the earth's orbital parameters

(precession, obliquity, and eccentricity). However, it is obvious from the drawings of the downcore results, that the main periodicities between the assemblages are different (Fig. 3). Spectral analysis revealed significant differences in the main periodicities for each assemblage (Fig. 5). The tropical and eastern boundary assemblages are dominated by variations in the orbital eccentricity (100 kyrs) and precession (23 kyrs) periods coherent with global ice volume recorded in the  $\delta^{18}\text{O}$  of *C. wuellerstorfi*. It is apparent, that most variation within the tropical assemblage occurs in the 100 kyrs period with maxima aligned to a minimum in ice volume (Fig. 3). All three orbital periodicities (eccentricity, obliquity, and precession) are observed in the spectra of the upwelling assemblage with decreasing power from the longer to the shorter periods. In contrast, the eastern boundary assemblage spectra show most power in the precession band and weaker power in the eccentricity band, whereas no variation is observed in the obliquity band (Fig. 5). These results corroborate earlier studies in the equatorial Atlantic (McIntyre et al., 1989; Mix and Morey, 1996).



**Fig. 6:** Comparison between the relative abundance of the upwelling and eastern boundary assemblages (shaded areas) with the paleoproductivity estimations, based on organic carbon accumulation rates (from Bickert, 1992).

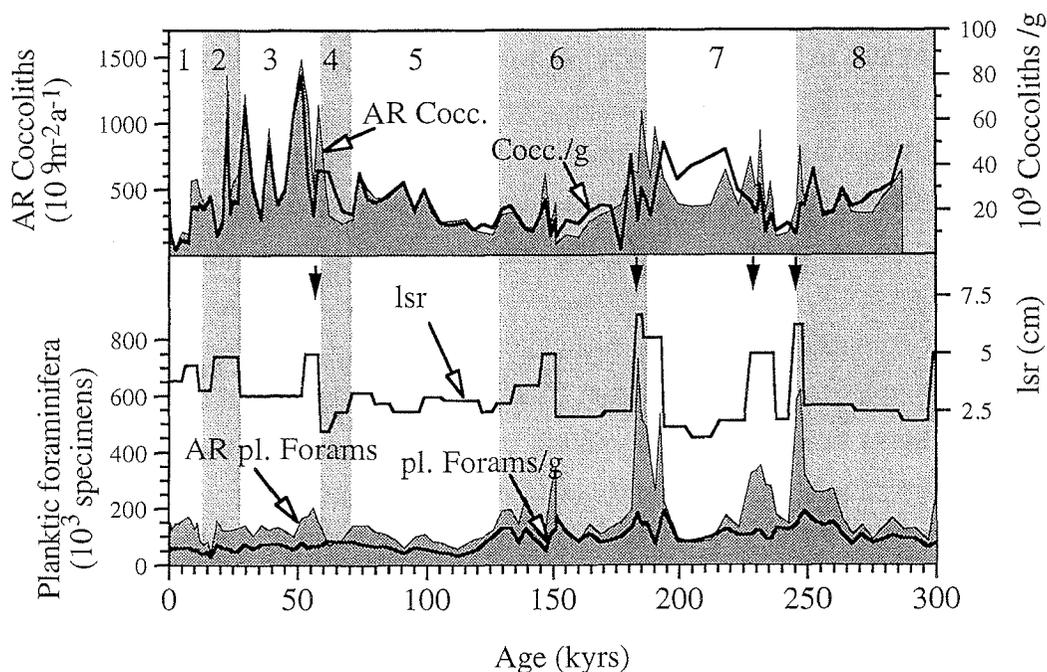
Comparison between the abundance of the three planktic foraminiferal assemblages to the numbers of planktic foraminifera per gram sediment does not reveal any significant linear correlation. However, we noticed obvious trends with high numbers of foraminifera per gram sediment being typical for higher abundances of the tropical assemblages (not plotted). The opposite is true for both, eastern boundary and upwelling assemblages. These results would severely bias productivity estimations based on AR  $\text{CaCO}_3$  (Brummer and Van Eijden, 1992; Rühlemann et al., 1996; Van Kreveld et al., 1996) if we assume that an increase in the abundance of upwelling and eastern boundary

assemblages should indicate higher productivity. However, in areas which remain more or less oligotrophic through time, this approach seems to provide reasonable results (Brummer and Van Eijden, 1992; Rühlemann et al., 1996). A more reasonable relationship is revealed by the comparison between the abundance of the upwelling and eastern boundary assemblages with the TOC record and the paleoproductivity estimations (Sarnthein et al., 1992) based on organic carbon accumulation rates (Fig. 6).

In addition, we tested the use of absolute numbers of coccoliths and coccolith accumulation rates to reconstruct paleoproductivity. An increase in coccolith numbers and accumulation rates should provide reliable information on an enhanced productivity in the surface water masses, although it remains questionable whether or not coccolithophores reflect the gross productivity of phytoplankton in surface water masses?

If we take a look at the data available on coccolithophore productivity in the modern oceans, it appears that coccolithophores do react to increased nutrient levels, due to upwelling or frontal systems in open and coastal oceans (Kleijne et al., 1989; Ziveri et al., 1994; Kinkel et al., in press.). Nevertheless, it seems to be obvious that coccolithophores may appear in second place within an ecological succession of phytoplankton groups in their ability to use nutrients in surface waters following fast growing phytoplankton like diatoms (Young, 1994). This is supported by results of plankton samples (Garcia-Soto et al., 1995; Giraudeau and Bailey, 1995) and sediment trap studies (Samtleben et al., 1995) which showed that coccolithophores began to thrive and dominate phytoplankton communities after diatoms utilized most of the nutrients and a postupwelling or seasonal stratification of the water column occurred. Today, coccolithophores react to upwelling activity in the tropical Atlantic along the equator which is documented in plankton and surface sediment samples (Kinkel et al., in press.). Albeit, the differences between the equatorial Atlantic upwelling area and the oligotrophic areas seem to be more distinguished by the composition of coccolith assemblages than by the numbers of coccoliths (Kinkel et al., in press.). Our downcore results indicate that enhanced coccolithophore productivity indeed did not occur simultaneously with maximum TOC-contents and paleoproductivity estimations (Figs. 7, 2, 6). However, we still assume that coccolith numbers and accumulation rates indicate increased productivity, at least of coccolithophores, during late isotope stage 8, early stage 7, at stage boundary 6/7, during substage 6.3, late stage 5, and stage 3. Moreover, the maximum in coccolith numbers and accumulation rates are observed just before and after TOC values reach their maximum. This leads to the conclusion that optimum growth conditions of coccolithophores may occur just before or after gross productivity was at its maximum. Yet, we have to keep in mind that productivity estimations based on TOC values in the

tropical Atlantic can be overestimated, as reasonable proportions of the organic carbon fraction may be added to the record by eolian transport of terrigenous organic matter (Verardo and Ruddiman, 1996; Wagner and Dupont, in press). The eolian transport of terrigenous matter is supposed to be increased during glacial times when wind speeds reach their maximum; nonetheless, the proportion of terrestrial organic carbon to total organic carbon is still under debate.

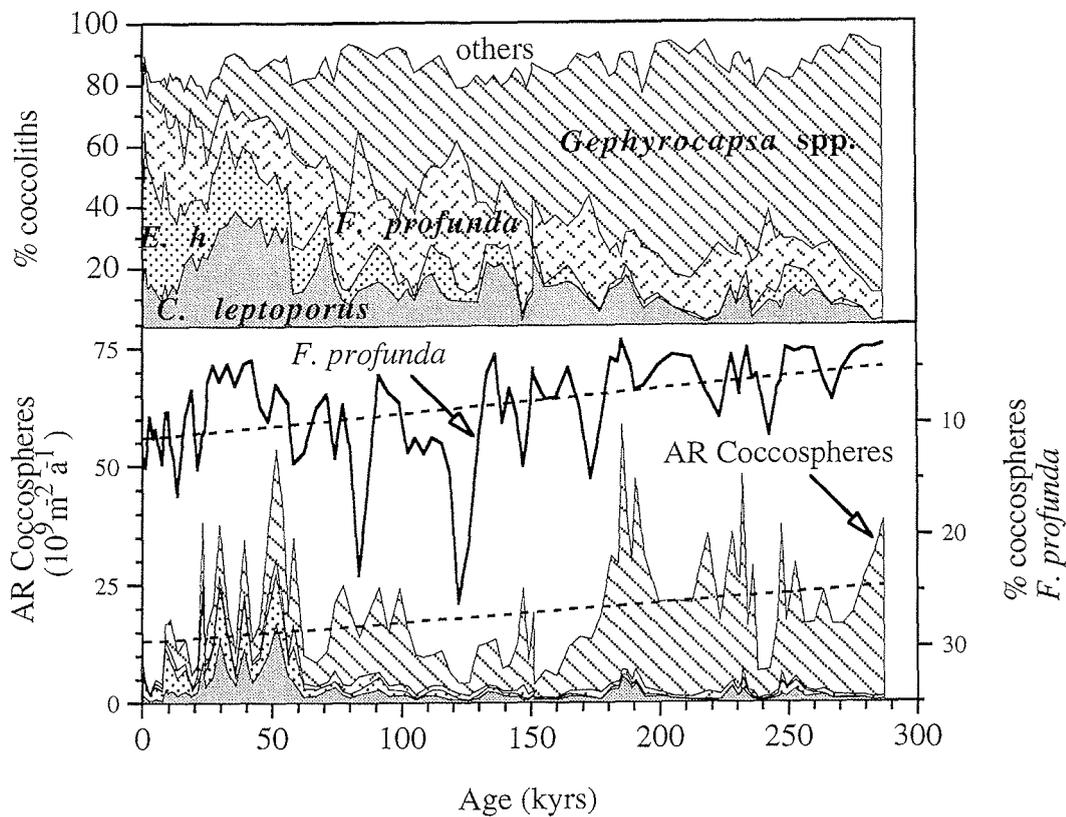


**Fig. 7:** Downcore distribution of the absolute numbers of coccoliths per gram sediment, coccolith accumulation rate, absolute numbers and accumulation rates of planktic foraminifera and the linear sedimentation rates (from Bickert, 1992).

The minima in coccolith numbers and accumulation rates in stages 6, 4 may correspond to a strong increase in diatom accumulation rates observed in core M 16772 (Abrantes et al., 1994), which is situated slightly east from our core position. This may indicate that diatoms rather than coccolithophores dominated the phytoplankton productivity at this intervals. No such trend is observed in the diatom record from Abrantes et al. (1994) for the stage 2, and therefore it is unclear what kind of phytoplankton caused the maxima in organic carbon at this time. Carbonate dissolution may have had a minor influence on the coccolith accumulation rates as no indication for strong carbonate dissolution is evident for this site (Dieter et al. subm.), though it can not

completely ruled out.

Comparison between the relative abundance of *F. profunda* and the numbers of coccoliths or coccolith accumulation rates reveal opposite trends with maxima in coccolithophore numbers and accumulation rates more or less coherent with minima in the relative abundance of *F. profunda* (Fig. 8). This gives further support to the conceptual model of Molfino and McIntyre (1990) who suggested that high abundances of *F. profunda* indicate a deep thermocline and nutricline leading to a decrease in coccolithophore productivity in the upper photic zone where the majority of coccolithophores grow. This conceptual model was applied successfully by other authors (Ahagon et al., 1993; Okada and Matsuoka, 1996; Bassinot et al., 1997; Beaufort et al., 1997) but it was never shown that other proxies reacted in the same manner or opposite to the *F. profunda* signal.



**Fig. 8:** Downcore distribution of the rel. abundance of coccoliths of the most common coccolithophore species (upper panel). The distribution pattern of the calculated coccosphere accumulation rate as well as the relative abundance of *F. profunda* after recalculating all coccoliths to coccospheres (lower panel).

Yet, an obstacle remains if we look at the relative abundance of *F. profunda* and the number of coccoliths or coccolith accumulation rates, respectively. It is obvious that on average, the relative abundance of *F. profunda* slightly increases over the last 300 kyrs

(Figs. 4, 8) while the same is true for the coccolith numbers and accumulation rates (Fig. 2) although an opposite trend would be expected. A similar trend can be observed in the abundance of *F. profunda* in a sediment core of the Indian Ocean (Beaufort et al., 1997) over the last 300 kyrs. We therefore converted the most common species (*E. huxleyi*, *C. leptoporus*, *F. profunda*, and *Gephyrocapsa* spp.) which in general make up more than 80 % of the total coccolith assemblage (Fig. 8) into coccosphere units. It was suggested before that ecological interpretation of coccolith assemblages may be biased if only coccoliths are taken into account instead of recalculating the organism level of entire cells (Giraudeau, 1992a; 1992b; Pujos, 1992). Our recalculations did not change the general picture but two significant modifications are notified: First of all, the increase in the coccosphere abundance of *F. profunda* over the last 300 kyrs is not as strong as in the coccolith abundance. Nevertheless, it is still notable. Second, the trend in the coccosphere accumulation rates of the most important species is opposite to that of the coccolith accumulation rates. This is reasonable as *C. leptoporus* and *E. huxleyi* are the major contributors to the coccosphere accumulation rates in sediments younger than oxygen isotope stage 4, whereas mainly species of the genus *Gephyrocapsa* contribute to the coccosphere accumulation rates in older sediments. Both *C. leptoporus* and *E. huxleyi* bear significantly more coccoliths per coccosphere (30 and 24, respectively) than coccospheres of the genus *Gephyrocapsa* which on an average only bear 14 coccoliths per coccosphere.

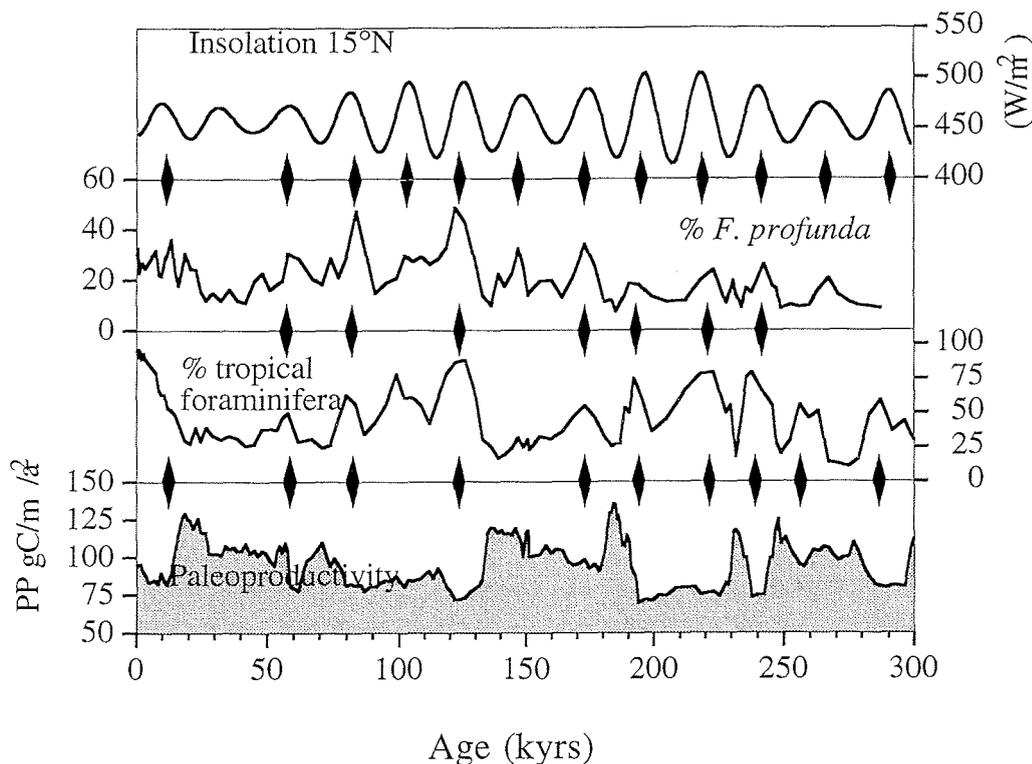
If we compare this result to our coccolith and foraminifera data we can conclude that the relative abundance data seem to be robust and generally are not influenced by carbonate dissolution. A stronger impact of carbonate dissolution may influence the absolute numbers calcareous microfossils.

## 6. Conclusions

The investigation of different faunal and floral assemblages together with a set of bulk parameters (TOC, CaCO<sub>3</sub>) in a sediment core from the southern Equatorial Atlantic provided details on the influence of surface water circulation patterns in the investigated area and its impact on the sedimentation of planktic foraminifera and coccolithophores.

Spectral analysis revealed significant variance at the 100 kyrs and the 23 kyrs periodicities which are typical for paleoceanographic reconstructions of the tropical Atlantic Ocean. As most variability and power is observed in the 23 kyrs band of the eastern boundary assemblage, we assume that advection of cold and nutrient rich water masses via the eastern boundary currents is the most important feature in surface water circulation above the investigated site. In addition, upwelling intensity is controlled by the

relationship between the meridional (monsoonal) and zonal (tropical easterlies) wind stress. Minima in upwelling intensity are monitored by the increase in the relative abundance of the coccolithophore *F. profunda* as well as the tropical planktic foraminiferal assemblage represented by (Fig. 9). Both are positively correlated to the insolation over the North African landmass with maxima indicating a warm and deep surface layer associated to a deep thermocline due to more meridional wind stress. In contrast, low insolation values leads to more zonal wind stress which will cause a thermocline uplift and increased nutrient supply leading to a rise in productivity.



**Fig. 9:** Comparison between the relative abundance of the *F. profunda* (coccolithophore), *G. ruber* (planktic foraminifer) and the insolation at 15°N (after Bergér and Loutre, 1991).

Our data do not allow a distinct separation between the eastern boundary and the upwelling mechanism. As there is much more variability in the eastern boundary dynamics, we assume that this is the driving force in the surface water circulation at this site that interacts with upwelling activity and provides it with additional nutrients.

Although carbonate sedimentation seems to be dominated by the tropical planktic foraminifera, coccolithophores contribute largely to the carbonate sedimentation in times of higher surface water productivity even though carbonate dissolution and the competition between diatoms and coccolithophores may reduce these signals during peak glacial times.

## 7. Acknowledgement

We like to thank C. Wienberg for technical assistance. P.J. Müller kindly provided the carbonate and organic carbon data, oxygen isotopes and stratigraphy were given by T. Bickert. We like to thank K.-H. Baumann and R. Huber for helpful comments on the manuscript. This is SFB 261 contribution No. xxx.

## 8. References

- Abrantes, F., Winn, K., Sarnthein, M. 1994. Late Quaternary paleoproductivity variation in the NE and equatorial Atlantic: diatom and C<sub>org</sub> evidence. In : Zahn, R., Pedersen, T.F., Kaminski, M.A., Labeyrie, L.(Eds.) *Carbon Cycling in the Glacial Ocean: Constrains on the Ocean's Role in Global Change*. Springer-Verlag, Berlin Heidelberg, pp. 425-480.
- Ahagon, N., Tanaka, Y., Ujiie, H., 1993. *Florisphaera profunda*, a possible nannoplankton indicator of late Quaternary changes in sea-water turbidity at the northwestern margin of the Pacific. *Mar. Micropal.* 22: 255-273.
- Andruleit, H., 1996. A filtration technique for quantitative studies of coccoliths. *Micropaleontology* 42: 403-406.
- Bainbridge, A.E., 1981. *GEOSECS Atlantic Expedition, Hydrographic Data, 1972-1973*. National Science Foundation, Superintendent of Documents, US Government Printing Office, Washington, DC, pp. 121.
- Bassinot, F.C., Beaufort, L., Vincent, E., Labeyrie, L., 1997. Changes in the dynamics of western equatorial Atlantic surface currents and biogenic productivity at the "Mid-Pleistocene Revolution" (930 ka). In: Shackleton, N.J., Curry, W.B., Richter, C., Bralower, T.J. (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results*. College Station, TX (Ocean Drilling Program), 154, pp. 269-284.
- Beaufort, L., Lancelot, Y., Camberlin, P., Cayre, O., Vincent, E., Bassinot, F., Labeyrie, L., 1997. Insolation cycles as a major control of equatorial Indian Ocean primary production. *Science* 278: 1451-1454.
- Beck, J.W., Récy, J., Taylor, F., Edwards, R.L., Cabioch, G., 1997. Abrupt changes in early Holocene tropical sea surface temperatures derived from coral records. *Nature* 385 705-707.
- Berger, W.H., Smetacek, V.S., Wefer, G., 1989. Ocean productivity and paleoproductivity - An overview. In: Berger, W.H., Smetacek, V.S., Wefer, G. (Eds.), *Productivity of the ocean: Present and past*. John Wiley & Sons, New York, NY, pp. 1-34.
- Bickert, T., 1992. Rekonstruktion der spätquartären Bodenwasserzirkulation im östlichen Südatlantik über stabile Isotope benthischer Foraminiferen. *Ber. Fachbereich Geowiss., Univ. Bremen* 27: 1-205.
- Bickert, T., Wefer, G., 1996. Late Quaternary deep water circulation in the South Atlantic: Reconstruction from carbonate dissolution and benthic stable isotopes. In: Wefer, G.,

- Berger, W.H., Siedler, G., Webb, D.J. (Eds.), The South Atlantic: Present and past circulation. Springer-Verlag, Berlin Heidelberg, pp. 599-620.
- Boyle, E.A., 1988. Vertical oceanic nutrient fractionation and glacial/interglacial CO<sub>2</sub> cycles. *Nature* 331: 55-56.
- Brummer, G.-J.A., Van Eijden, A.J.M., 1992. "Blue-ocean" paleoproductivity estimates from pelagic carbonate mass accumulation rates. *Mar. Micropal.* 19: 99-117.
- CLIMAP project members, 1981. Seasonal Reconstructions of the Earth's Surface at the last glacial maximum. *Geol. Soc. Am. Bull.*, MC Series 36: 1-18.
- CLIMAP project members, 1984. The last interglacial ocean. *Quat. Res.* 21: 123-224.
- Curry, W.B., Oppo, D.W., 1997. Synchronous, high frequency oscillations in tropical sea surface temperatures and North-Atlantic Deep Water production during the last glacial cycle. *Paleoceanography* 12: 1-14.
- deMenocal, P.B., Ruddiman, W.F., Pokras, E.M., 1993. Influences of high- and low-latitude processes on African terrestrial climate: Pleistocene eolian records from equatorial Atlantic Ocean Drilling Program Site 663. *Paleoceanography* 8: 209-242.
- Dittert, N., Niebler, H.-S., Henrich, R., *subm.* A 300 kyrs history of planktic foraminiferal distribution in the central equatorial Atlantic Ocean - paleo-environmental implications. *Mar. Micropal.*
- Fischer, G., Wefer, G., 1996. Seasonal and interannual particle fluxes in the eastern tropical Atlantic from 1989 to 1991: ITCZ migrations and upwelling. In: Ittekkot, V., Schäfer, P., Honjo, S., Depetris, P.J. (Eds.), *Particle Flux in the Ocean*. John Wiley & Sons, New York, NY.
- García-Soto, C., Fernández, E., Pingree, R.D., Harbour, D.S., 1995. Evolution and structure of a coccolithophore bloom in the Western English Channel. *Journal of Plankton Research* 17: 2011 - 2036.
- Gingele, F., 1992. Zur Klimaabhängigen Bildung biogener und terrigener Sedimente und ihrer Veränderung durch Frühdiagenese im zentralen östlichen Atlantik. *Berichte, Fachbereich Geowissenschaften* 202 S.
- Gingele, F.X., Dahmke, A., 1994. Discrete barite particles and barium as tracers of paleoproductivity in South Atlantic sediments. *Paleoceanography* 9: 151-168.
- Giraudeau, J., 1992a. Coccolith paleotemperature and paleosalinity estimates in the Caribbean Sea for the Middle-Late Pleistocene (DSDP Leg 68 - Hole 502 B). *Memorie di Scienze Geologiche* 43: 375 - 387.
- Giraudeau, J., 1992b. Distribution of recent nannofossil beneath the Benguela system: Southwest African continental margin. *Mar. Geol.* 108: 219-237.
- Giraudeau, J., Bailey, G.W., 1995. Spatial dynamics of coccolithophore communities during an upwelling event in the southern Benguela System. *Cont. Shelf Res.* 15: 1825-1852.
- Gordon, A.L., 1986. Interocean exchange of thermocline water. *J. Geophys. Res.* 91: 5037-5046.
- Gordon, A.L., 1996. Communication between oceans. *Nature* 382: 399-400.
- Guilderson, T.P., Fairbanks, R.G., Rubenstone, J.L., 1994. Tropical temperature variations
-

- since 20,000 years ago; modulating interhemispheric climate change. *Science* 263: 663-665.
- Hemleben, C., Spindler, M., Anderson, O.R., 1989. *Modern planktonic foraminifera*. Springer-Verlag, New York, NY, pp. 363.
- Hutson, W.H., 1977. Transfer functions under no-analog conditions: Experiments with Indian Ocean planktonic foraminifera. *Quat. Res.* 8: 355-367.
- Imbrie, J., Hays, J.D., Martinson, D.G., McIntyre, A., Mix, A.C., Morley, J.J., Pisias, N.G., Prell, W.L., Shackleton, N.J., 1984. The orbital theory of Pleistocene climate: Support from a revised chronology of the marine  $\delta^{18}\text{O}$  record. In: Berger, A., Imbrie, J., Hays, J., Kukla, G., Saltzman, B. (Eds.), *Milancovitch and climate - Part I*. D. Reidel, Dordrecht, pp. 269-305.
- Imbrie, J., Kipp, N.G., 1971. A new micropaleontological method for quantitative paleoclimatology: application to a Late Pleistocene Caribbean core. In: Turekian, K.K. (Ed.) *Late Cenozoic glacial ages*. (Memorial Lectures) Yale University Press, New Haven, 43, pp. 71-181.
- Jordan, R.W., Kleijne, A., 1994. A classification system for living coccolithophores. In: Winter, A., Siesser, W.G. (Eds.), *Coccolithophores*. Cambridge University Press, Cambridge, pp. 83-105.
- Kinkel, H., Baumann, K.-H., Cepek, M., in press. Living and Late Quaternary coccolithophores from the equatorial Atlantic: Response to surface water productivity. *Mar. Micropal.*
- Kleijne, A., Kroon, D., Zevenboom, W., 1989. Phytoplankton and foraminiferal frequencies in northern Indian Ocean and Red Sea surface waters. *Neth. J. Sea Res.* 24: 531-539.
- Knappertsbusch, M., 1993. Geographic distribution of living and Holocene coccolithophores in the Mediterranean sea. *Mar. Micropal.* 21 (1-3): 219-247.
- Kroopnick, P.M., 1985. The distribution of  $^{13}\text{C}$  of  $\Sigma\text{CO}_2$  in the World Oceans. *Deep-Sea Res.* 32: 57-84.
- Lebreiro, S.M., Moreno, J.C., Abrantes, F.F., Pflaumann, U., 1997. Productivity and paleoceanographic implications on the Tore Seamount (Iberian Margin) during the last 225 kyr: Foraminiferal evidence. *Paleoceanography* 12: 718-727.
- Longhurst, A., 1993. Seasonal cooling and blooming in tropical oceans. *Deep-Sea Res.* 40: 2145-2177.
- Macdonald, A.M., Wunsch, C., 1996. An estimate of global ocean circulation and heat fluxes. *Nature* 382: 436-439.
- McIntyre, A., Molfino, B., 1996. Forcing of Atlantic equatorial and subpolar millennial cycles by precession. *Science* 274: 1867-1870.
- McIntyre, A., Ruddiman, W.F., Karlin, K., Mix, A.C., 1989. Surface water response of the equatorial Atlantic Ocean to orbital forcing. *Paleoceanography* 4: 19-55.
- Mix, A.C., 1989. Influence of productivity variations on long-term atmospheric  $\text{CO}_2$ . *Nature* 337: 541-544.
- Mix, A.C., Morey, A.E., 1996. Climate feedback and Pleistocene variations in the Atlantic

- south equatorial current. In: Wefer, G., Berger, W.H., Siedler, G., Webb, D.J. (Eds.), *The South Atlantic: Present and past circulation*. Springer-Verlag, Berlin Heidelberg, pp. 503-525.
- Mix, A.C., Ruddiman, W.F., McIntyre, A., 1986a. Late Quaternary paleoceanography of the tropical Atlantic 1: Spatial variability of annual mean sea-surface temperatures, 0-20,000 Years B.P. *Paleoceanography* 1: 43-66.
- Mix, A.C., Ruddiman, W.F., McIntyre, A., 1986b. Late Quaternary paleoceanography of the tropical Atlantic 2: The seasonal cycle of sea-surface temperatures, 0-20,000 Years B.P. *Paleoceanography* 1: 339-353.
- Molfinio, B., McIntyre, A., 1990. Precessional forcing of nutricline dynamics in the equatorial Atlantic. *Science* 249: 766-769.
- Monger, B., McClain, C., Murtugudde, R., 1997. Seasonal phytoplankton dynamics in the eastern tropical Atlantic. *J. Geophys. Res.* 102: 12,389-12,411.
- Okada, H., Matsuoka, M., 1996. Lower-photic nanoflora as an indicator of the late Quaternary monsoonal paleo-record in the tropical Indian Ocean. In: Mokuilevsky, A., Whatley, R. (Eds.), *Microfossils and Oceanic Environments*. Aberystwyth Press, Aberystwyth, pp. 231-245.
- Paillard, D., Labeyrie, L., Yiou, P., 1996. Macintosh program performs time-series analysis. *AGU* 379.
- Pflaumann, U., Duprat, J., Pujol, C., Labeyrie, L.D., 1996. SIMMAX: A modern analog technique to deduce Atlantic sea surface temperatures from planktonic foraminifera in deep-sea sediments. *Paleoceanography* 11: 15-35.
- Philander, S.G.H., Pacanowski, R.C., 1986. The mass and heat budget in a model of the tropical Atlantic. *J. Geophys. Res.* 91: 14212-14220.
- Pujos, A., 1992. Calcareous nanofossils of Plio-Pleistocene sediments from the northwestern margin of tropical Africa. In: Summerhayes, C.P., Prell, W.L., Emeis, K.C. (Eds.), *Upwelling systems: Evolution since the Early Miocene*. (Geological Society Special Publication.) Geological Society of America, Avon, 64, pp. 343-358.
- Ravelo, A.C., Fairbanks, R.G., Philander, S.G.H., 1990. Reconstructing tropical Atlantic hydrography using planktonic foraminifera and an ocean model. *Paleoceanography* 5: 409-431.
- Rind, D., Peteet, D.M., 1985. Terrestrial conditions at the last glacial maximum and CLIMAP sea-surface temperature estimates; are they consistent? *Quat. Res.* 24: 1-22.
- Ruddiman, W.F., 1997. Tropical Atlantic terrigenous fluxes since 25,000 yrs B.P. *Mar. Geol.* 136: 189-207.
- Rühlemann, C., Frank, M., Hale, W., Mangini, A., Mulitza, S., Müller, P.J., Wefer, G., 1996. Late Quaternary productivity changes in the western equatorial Atlantic: Evidence from <sup>230</sup>Th-normalized carbonate and organic carbon accumulation rates. *Mar. Geol.* 135: 127-152.
- Samtleben, C., Schaefer, P., Andruleit, H., Baumann, A., Baumann, K.-H., Kohly, A., Matthiessen, J., Schröder-Ritzau, A., 1995. Plankton in the Norwegian-Greenland Sea:

- From living communities to sediment assemblages - an actualistic approach. *Geol. Rdschau* 84: 108-136.
- Sarnthein, M., Pflaumann, U., Ross, R., Thiedemann, R., Winn, K., 1992. Transfer functions to reconstruct ocean paleoproductivity: A comparison. In: Summerhayes, C.P., Prell, W.L., Emeis, K.C. (Eds.), *Upwelling systems: Evolution since the early Miocene*. Geological Society Special Publication, 64, pp. 411-427.
- Schneider, R.R., Müller, P.J., Ruhland, G., Meinecke, G., Schmidt, H., Wefer, G., 1996. Late Quaternary surface temperatures and productivity in the east-equatorial South Atlantic: response to changes in Trade / Monsoon wind forcing and surface water advection. In: Wefer, G., Berger, W.H., Siedler, G., Webb, D. (Eds.), *The South Atlantic: Present and Past Circulation*. Springer-Verlag, Berlin Heidelberg, pp. 527-551.
- Sikes, E.L., Keigwin, L.D., 1994. Equatorial Atlantic sea surface temperature for the last 30 kyr: A comparison of  $U^{k}_{37}$ ,  $\delta^{18}O$  and foraminiferal assemblage temperature estimates. *Paleoceanography* 9: 31-45.
- Struck, U., Sarnthein, M., Westerhausen, L., Barnola, J.M., Raynaud, D., 1993. Ocean-atmosphere carbon exchange: impact of the "biological pump" in the Atlantic equatorial upwelling belt over the last 330,000 years. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 103: 41-56.
- Stute, M., Forster, M., Frischkorn, H., Serejo, A., Clark, J.F., Schlosser, P., Broecker, W.S., Bonani, G., 1995. Cooling of Tropical Brazil (5°C) during the Last Glacial Maximum. *Science* 269: 379-383.
- Van Andel, T.H., Heath, G.R., Moore, T.C., 1975. Cenozoic history and paleoceanography of the central equatorial Pacific Ocean. *Geol. Soc. Am. Mem.* 143: 1-134.
- Van Kreveld, S.A., Knappertsbusch, M., Ottens, J., Ganssen, G.M., Van Hinte, J., 1996. Biogenic carbonate and ice-rafted debris (Heinrich Layer) accumulation in deep sea sediments from a North East Atlantic piston core. *Marine Geology* ??? xxx:
- Verardo, D.J., McIntyre, A., 1994. Production and destruction: Control of biogenous sedimentation in the tropical Atlantic 0-300,000 years B.P. *Paleoceanography* 9: 63-86.
- Verardo, D.J., Ruddiman, W.F., 1996. Late Pleistocene charcoal in tropical Atlantic deep-sea sediments: Climatic and geochemical significance. *Geology* 24: 855-857.
- Wagner, T., Dupont, L., in press. Terrestrial OM in marine sediments: analytic approaches and eolian-marine records of the central Equatorial Atlantic. In: Fischer, G., Wefer, G. (Eds.), *Proxies in paleoceanography*. Springer-Verlag, Berlin Heidelberg, pp.
- Webb, R.S., Rind, D.H., Lehman, S.J., Healy, R.J., Sigman, D., 1997. Influence of ocean heat transport on the climate of the Last Glacial Maximum. *Nature* 385: 695-699.
- Wefer, G., Bleil, U., Schulz, H.D., cruise participants, 1989. Bericht über die Meteor-Fahrt M9-4, Dakar-Santa Cruz, 19.2.-16.3.1989. *Ber. Fachbereich Geowiss., Univ. Bremen* 7: 1-103.
- Young, J.R., *subm.* Calculation of coccolith volume and its use in calibration of carbonate flux estimates. *Deep-Sea Res.*
- Young, J.R., 1994. Functions of coccoliths. In: Winter, A., Siesser, W.G. (Eds.),

Coccolithophores. Cambridge Academic Press, Cambridge, pp. 63-82.

Ziveri, P., Thunell, R.C., Rio, D., 1994. Export production of coccolithophores in an upwelling region: Results from San Pedro Basin, Southern California borderlands. *Mar. Micropal.* 24: 335-358.

---

---

## Carbonate dissolution in the deep-sea: Methods, quantification and paleoceanographic application

N. Dittert, K.-H. Baumann, T. Bickert, R. Henrich, R. Huber, H. Kinkel  
and H. Meggers

*Fachbereich Geowissenschaften, Universität Bremen,  
28334 Bremen, Germany*

**Abstract:** Understanding spatial and temporal changes in oceanic carbonate dissolution and preservation patterns is of key importance for testing models which seek to explain past changes in atmospheric  $p\text{CO}_2$  and surface water  $P\text{CO}_2$  through changes in the global carbon cycle.

As part of the *South Atlantic Dissolution Experiment*, three deep-sea transects covering areas above and below the calcite lysocline into the Brazil- and through the Cape Basin were investigated. Our work includes (1) determination of sediment surface assemblages of coccolithophores and planktic foraminifera; (2) SEM ultrastructure analysis of planktic foraminifera *Globigerina bulloides*; and (3) comparative assessment of different carbonate dissolution proxies.

We find that all dissolution proxies are able to distinguish the area above the top of the calcite lysocline from the area below. Moreover, some parameters are qualified to distinguish the upper continental margin of upwelling areas from the open ocean. Regarding three different oceanographic regimes, only the carbonate ion content and the percentage of sediment carbonate content put us in the position to determine the total scale of the lysocline. If these parameters are not available, a combination of the *Globigerina bulloides* Dissolution Index, the *Calcidiscus leptoporus* - *Emiliana huxleyi* Dissolution Index, and the rain ratio give the best approach to the authentic conditions.

### *Prologue*

By publishing his article "On the Distribution of the Pelagic Foraminifera at the Surface and on the Floor of the Ocean" as a monthly review of scientific progress, Murray (1897) laid the foundations of a topic that still occupies scientists 100 years later: he realized that the gradual disappearance of calcareous shells with increasing water depths is due to the solvent action of deep-sea water. The importance of the ocean as one principal global carbon reservoir and the close relationship between  $\text{CO}_2$  and climatic change led oceanographers and paleoceanographers to explore intensively the balance between

biogenic production and CaCO<sub>3</sub> accumulation-dissolution through time.

## Introduction

As early as in the late 19th century Murray and Renard (1891) realized that the distribution and character of *Globigerina* ooze are governed by the bio-/zoogeography of the living organisms in surface currents and by the chemistry of deep-sea water that is responsible for the modification of the sediment and organism assemblages. In particular, they noted that dissolution works selectively, and that below a depth of about 4,000 m in the central Pacific it destroys essentially all calcareous matter. In addition, Murray (1897) explained the different shell dissolution patterns observed by the powerful solvent action of decaying organic matter on carbonates. With expanded knowledge in micropaleontology, changes in faunal composition recorded in pelagic sequences could be explained to be dependent on both changes in the composition of the living assemblages and in the intensity of dissolution and resulting fragmentation of the tests (Schott 1935). Even before this, Philippi (1910) already had established the hypothesis of increased activity of Antarctic Bottom Water during glacials based on an enhanced carbonate dissolution. However, one obstacle in recognizing that carbonate dissolution in the eastern tropical Pacific was in fact less important during glacials than during interglacials was the (mistaken) notion of *Globigerina* sp. as being highly resistant to dissolution and of *Globorotalia* sp. as being highly susceptible to it (Arrhenius 1952). The reverse has been shown to be correct (Berger 1967). In contrast to the situation in the equatorial Pacific, Olausson (1965) showed that interglacials can be assigned to high-carbonate stages and glacials to low-carbonate stages in the Atlantic.

The first demonstration that the long-term exposure of calcite crystals to sea water on deep-sea moorings revealed information on the depth dependence of dissolution rate and calcite saturation was given by Peterson (1966). Milliman (1975) repeated Peterson's experiment in the North Atlantic using aragonite, low and high Mg calcite and confirmed that each of these carbonate varieties had its own lysocline occurrence at critical levels of undersaturation.

Berger (1967, 1968) ranked planktic foraminifera species collected from sediment samples according to dissolution resistance as a basis for forming dissolution indices. Furthermore, he exposed samples which were derived from sediment and from plankton tows on a taut wire buoy (same mooring as that used by Peterson 1966) at different depths in the central Pacific, in order to assess the effects of dissolution on foraminiferal shells. Additional information on the dissolution of planktic organisms were delivered by

investigations on coccolithophores (Hay 1970) as well as on pteropods (Berner 1977). Comparison of laboratory experiments with surface sediment samples indicated differential preservation of coccolithophore species in oceanic sediments (McIntyre and McIntyre 1971). Further evidence of differential dissolution among shells from analyses of living specimens and fossil shells has been obtained by in-situ experiments using sediment traps (Honjo and Erez 1978) and by laboratory experiments (Bé et al. 1975); comparisons between water column communities and sediment assemblages (including in-situ investigations) were performed by Vilks (1975).

With technological progress and the invention of scanning electron microscopy, Bé et al. (1975) started investigations of foraminiferal ultrastructure reaction to carbonate dissolution. They elaborated various species-specific SEM dissolution indices. This approach has been evaluated for *Neogloboquadrina pachyderma* (Henrich 1989; Baumann and Meggers 1996) and for *Globigerina bulloides* (Van Kreveld 1996; Dittert and Henrich subm). For both species the progressive ultrastructural breakdown with increasing dissolution could be shown.

In order to outline the essentials for carbonate dissolution in the deep-sea, a brief review on the carbon dioxide system and on the deep-water circulation in the world oceans will be presented. Many different methodical approaches were established as dissolution proxies in the past. We will contemplate the most important ones regarding the use of bulk sediment parameters and the use of calcareous micro- and nannoplankton. Since the history of "*Carbonate dissolution in the deep-sea*" covers more than one hundred years, only a few scientists who improved the comprehension of that complex topic can be mentioned. An excellent summary on previous studies is given by Boltovskoy (1991).

This leads up to the *South Atlantic Dissolution Experiment*, where the mentioned parameters are tested for their usefulness at three surface sediment transects into the Brazil Basin and through the Cape Basin. At last, we will elucidate the advantages and disadvantages of several dissolution proxies.

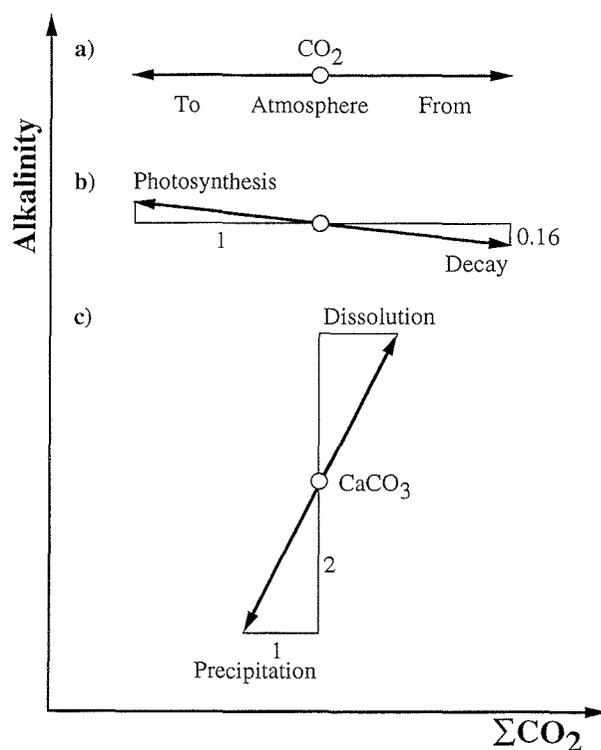
### **Some aspects on the carbon dioxide system and carbonate dissolution**

The carbon dioxide flux between atmosphere and ocean surface water is governed by molecular diffusion. Thereby the direction and magnitude of the CO<sub>2</sub> flux depend on the gas exchange coefficient of carbon, the thickness of the surface water boundary layer, the solubility coefficient, and the partial pressure difference between sea water and air (Liss 1973; Millero 1979; Liss and Merlivat 1986; Maier-Reimer and Hasselmann 1987). Only

about 1% of dissolved  $[\text{CO}_2]_{\text{aqua}}$  occurs as  $\text{H}_2\text{CO}_3$ , the rest of the  $\text{CO}_2$  exists in the form of different ions. Representatives of inorganic carbon are carbonic acid, bicarbonate and carbonate. Coccolithophores, foraminifers, pteropods, and a few other organisms build calcium carbonate shells or skeletons. Calcification can proceed both from carbonate and bicarbonate ions. In any case, it tends to drive  $\text{CO}_2$  from the ocean to the atmosphere (Gattuso et al. 1993).

The transfer of calcium carbonate particles from the mixed layer to the deep ocean was introduced as carbonate pump or alkalinity pump (Berger 1982). The vertical distribution of organic carbon in the ocean is mainly controlled by photosynthesis, feeding, respiration, and decay (Berger et al. 1989) which contribute to the biological pump (Revelle 1944). With respect to the water column,  $\text{Ca}^{2+}$  varies relatively little, hence the calcite saturation state is controlled by the concentration of  $\text{CO}_3^{2-}$ , temperature, and water pressure. Position and thickness of the saturation horizon in the water column can be defined as the difference  $\Delta\text{CO}_3^{2-}$  between the concentration of carbonate *in situ* and the concentration of saturated carbonate ion for the mineral phase calcite (Broecker and Takahashi 1978).

Carbonate dissolution in the water column (Culkin 1965; Edmont 1970; Murray and Riley 1971) and at the sediment pore water interface (Santschi et al. 1983; Le and Shackleton 1992) depend on the disequilibrium of the total carbon dioxide content ( $\Sigma\text{CO}_2$ ). It is balanced with  $\text{HCO}_3^-$  and  $\text{CO}_3^{2-}$  and driven by the alkalinity (Fig. 1; Baes 1982). The water depth in which the sea water carbonate ion content and the concentration of carbonate ions in equilibrium with sea water for calcite mineral phase intercept was introduced as the hydrographic calcite lysocline (Broecker and Takahashi 1978) - also known as "Peterson's level" (Berger 1975). It is stated that an undersaturation of about  $10 \mu\text{mol}/\text{kg}$  is enough to dissolve almost all the calcite descending to the sea-floor (Broecker and Peng



**Fig. 1.**  $\Sigma\text{CO}_2$ -alkalinity-vector-diagram which describes changing alkalinity and total carbon content according to a) supply and withdrawal of  $\text{CO}_2$  to/from the atmosphere; b) enhanced photosynthesis or decay; c) increased  $\text{CaCO}_3$  precipitation or dissolution (modified after Baes 1982).

1982). The depth at which the effects of dissolution first appear in the sediments is termed sedimentary lysocline (Berger 1975), foraminiferal lysocline (Berger 1968), or coccolith lysocline (Berger 1973a), respectively. Keir (1980) discovered that dissolution becomes progressively more intense in proportion to the fourth power of  $\Delta\text{CO}_3^{2-}$  below the lysocline. Where undersaturation is large enough so that the rate of calcite sedimentation is totally compensated for by the rate of calcite dissolution, the carbonate compensation depth (CCD) is attained (Bramlette 1961), which is described by Archer (1996) as the zero intercept of the %CaCO<sub>3</sub> versus  $\Delta\text{CO}_3^{2-}$  relation.

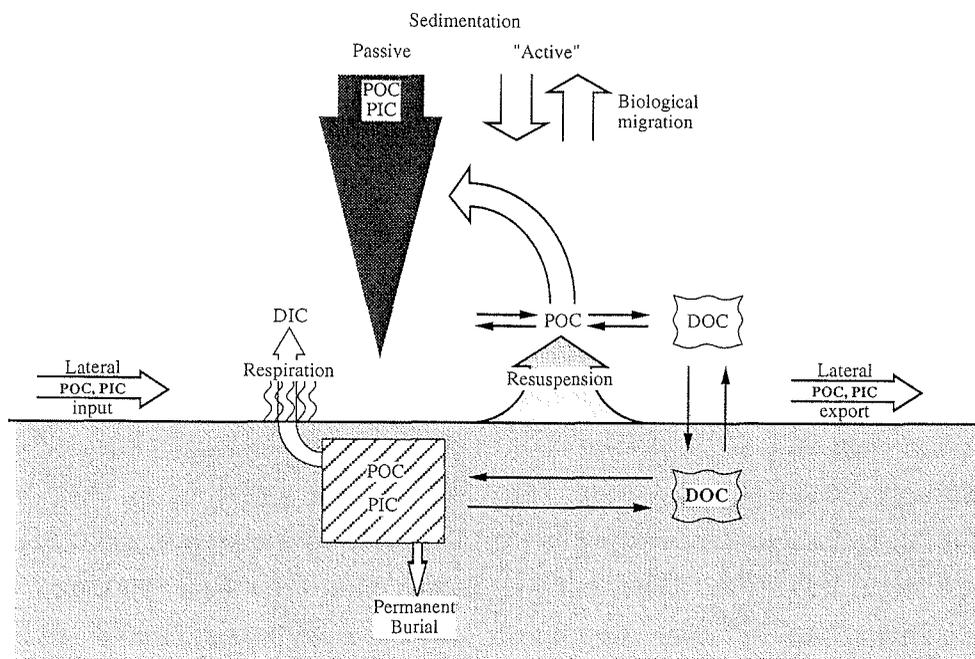


Fig. 2. Carbon fluxes at the benthic boundary layer (from JGOFS 1989).

I ... Inorganic; O ... Organic; C ... Carbon; P ... Particulate; D ... Dissolved

The by far greatest fraction of the organic carbon arriving at the sea-floor is respired as CO<sub>2</sub> or remineralized to other organic compounds by benthic organisms (Reimers 1989). This metabolic CO<sub>2</sub> generated by organisms which live within the sediment may contribute to the dissolution of calcite even above the lysocline, known as supralysoclineal dissolution (Emerson and Bender 1981; Jahnke et al. 1994; Freiwald 1995). Other parts of the vertical and horizontal flux to the sediment are degraded or resuspended and recycled back into the ocean (Fig. 2). The remaining material is perturbed in the uppermost centimeters and decimeters of the sediment by benthic organisms. Molecular diffusion alone, coupled with the low solubility of calcite, would yield extremely low dissolution rates. The benthic mixing process continually accumulates new calcite into the

sediment eliminating the necessity for a long diffusion path (Broecker and Peng 1982). At last, the benthic boundary layer (Santschi et al. 1983) is the site of carbon removal from the ocean-atmosphere system and constitutes the historical record of the carbon flux - perhaps distorted by the process of diagenesis - from which paleoceanographic and paleoclimatic changes are deciphered (Jumars et al. 1989). Long records of carbonate fluctuations exhibit long-term trends in dissolution (e. g., the Mid-Brunhes dissolution cycle) which are thought to be associated with global changes in the carbon reservoir of the oceans (Vincent 1981; Farrell and Prell 1991; Bassinot et al. 1994; Bickert et al. 1997). Thus, for reconstructing the deep-water chemistry in the past, both the respiratory effect and the global trend have to be considered to extract the true deep-water properties from dissolution records.

### **The use of bulk sediment parameters as dissolution proxies**

Quantitative reconstruction of carbonate dissolution to times of the past is not a simple matter. It requires the determination of the fraction of calcite rained to the sea-floor which survived dissolution. Unfortunately, among the several criteria used to judge the state of preservation of the calcite most remain qualitative. One indicator is the weight percentage of the coarse fraction ( $>63 \mu\text{m}$ ). The sand content of deep-sea carbonates decreases as dissolution progresses (Johnson et al. 1977; Berger et al. 1982; Wu et al. 1990). The reason for this is that foraminiferal shells are weakened by dissolution and tend to break down into small fragments. Thus, material moves from the coarse fraction into finer fractions. Inspection of other dissolution indices, such as calcareous micro- and nannoplankton dissolution proxies (see chapter below), investigated in deep-sea sediments by several authors (e.g., Hebbeln et al. 1990; Yasuda et al. 1993), shows a good agreement with the sand content records of each study. However, other sediment related studies on the deep-sea rise reveal that foraminiferal fragmentation and hence the percentage of the fine fraction increases before the significant overall loss of carbonate begins, and thus may be more sensitive to changes in bottom water or pore water corrosiveness than bulk carbonate. For instance, Peterson and Prell (1985) showed that about 60 % of the non-fragmented sand-sized planktic foraminifera were already broken at the lysocline level, whereas no more than 20 % to 30 % of carbonate has been lost. This mismatch in sensitivities may be due to the transfer of carbonate during the fragmentation from larger to smaller size fractions. Furthermore, changes in the rain ratio between nannofossil placoliths and foraminiferal shells could bias the relative portion of the coarse fraction without any changes in dissolution (e.g., Bickert and Wefer 1996).

Therefore, the sand content is not an unambiguous proxy for dissolution and requires calibration with other dissolution indices prior to the interpretation of its variation with time.

A potentially more quantitative index of calcite dissolution is the percentage of  $\text{CaCO}_3$  in the sediment. Of course, variations in the percentage of  $\text{CaCO}_3$  in a single core cannot be simply interpreted as an index of preservation because the relative abundance of carbonate is controlled by the balance of productivity over dissolution and by dilution due to the influx of non-carbonate sedimentary components. Only in the ideal situation, where the rain rate of calcitic and of noncalcitic material are constant in space and time, the amount of calcite lost to dissolution could be calculated from the percentage  $\text{CaCO}_3$  in the sediment. Otherwise, for each time interval of interest, the calcite content of the sediment from above the lysocline has to be used as the reference for the amount of dissolution which has occurred in cores from the transition zone (the "depth-transect approach"; e.g., Farrell and Prell 1989; Curry and Lohmann 1990; Bickert et al. 1997). However, the fact that  $\text{CaCO}_3$ -contents of supralysoclinical sediment average to about 90 % in the world ocean (Archer 1996) raises the problem that quite large amounts of dissolution create only very small changes in the carbonate content. For example, if a sediment which, in the absence of dissolution, would have a calcite content of 90 % were to lose half of its calcite to dissolution, its  $\text{CaCO}_3$ -content would drop to only 82 %. Because of this, even small variations in the ratio of the rain rate of calcite to the rain rate of non-calcite would lead to substantial errors in the extent of dissolution.

One way out of this dilemma could be the conversion of  $\text{CaCO}_3$  % (w/w) to  $\text{CaCO}_3$  mass accumulation rate (MAR), which corrects for the effect of dilution in the sediment. According to van Andel et al. (1975) the  $\text{CaCO}_3$ -MAR is calculated as:

$$\text{CaCO}_3\text{-MAR (g/cm}^2\text{/ky)} = \text{CaCO}_3 \text{ \% (w/w)} \cdot \text{DBD (g/cm}^3\text{)} \cdot \text{SR (cm/ky)} \quad (1)$$

This calculation requires estimates of dry bulk densities (DBD) for the sediments and sedimentation rates (SR). DBD, if not measured directly, might be calculated using the empiric equation of Ruddiman and Janecek (1989). The major problem comes from the SR, which is commonly derived by linear interpolation between stratigraphic datums based on oxygen isotope, paleomagnetic and biostratigraphic events. Especially, if the variance of the carbonate content is low, the  $\text{CaCO}_3$ -MAR will be dominated by the SR changes, which depend on the resolution of the age model and which are mostly difficult to reproduce the sediment accumulation variability with time.

Two other processes are at work which could bias the interpretations based on the  $\text{CaCO}_3$ -content. The first of these consists in the winnowing of sediment by currents which carry away the fine material and thereby enrich the coarse material (mainly shells). This raises the  $\text{CaCO}_3$ -content (Wu et al. 1990). The other is deposition by turbidity and

boundary currents. As currents often originate along the continental margins, the debris they carry is usually very low in  $\text{CaCO}_3$ . To avoid the impacts of these processes, quiet zones on the sea-floor must be carefully chosen as the localities for such studies.

Regarding all these potential complications, how should one carry out a reliable quantification of calcite dissolution in the deep-sea? Significant progress has been made in modelling the diagenesis of  $\text{CaCO}_3$  in sediments, on diagenetic scales of centimeters (Emerson and Bender 1981; Archer et al. 1989; Keir 1990; Hales et al. 1994), basin-wide scales (Emerson and Archer 1990), and global scales (Keir 1990; Archer and Maier-Reimer 1994). The models have reached the point where even small variations of the carbonate distribution on the sea-floor might be interpretable or serve to differentiate model formulations and assumptions. Archer (1996) converted available sedimentary data into a format suitable for validating models of  $\text{CaCO}_3$ -dynamics in the ocean. He related the distribution of sedimentary calcite in the deep-sea to a new gridded field of water column  $\Delta\text{CO}_3^{2-}$  in an attempt to reveal regional variations in calcite preservation and thus the shape of the calcite lysocline. As a result, the lysocline has been found thicker (i.e., has a greater contrast in  $\Delta\text{CO}_3^{2-}$  between the high- and low-calcite sediments) in the western Pacific and in the Atlantic Oceans than it is in the eastern equatorial Pacific. This pattern is consistent with the model's response to varying rates of dilution caused by terrigenous material. In low latitudes, calcite can be preserved to  $-30 \mu\text{mol/kg CO}_3^{2-}$ , whereas calcite is depleted from higher latitude sediments by a rate of  $-10 \mu\text{mol/kg CO}_3^{2-}$ . This gradient is smaller than the glacial/interglacial shift as required by the "rain ratio model" for generating lower atmospheric  $p \text{CO}_2$  (Archer and Maier-Reimer 1994). This implies that the model requires an application of conditions in glacial times which have no analog in today's ocean. This conclusion rules out that the modern ocean carbonate system not necessarily validates models of  $\text{CaCO}_3$ -dynamics in the past. This is especially true for the preservation events at the onset of each interglaciation and for the dissolution events at the onset of each glaciation, recorded in dissolution records in the deep of the Indian and Pacific Ocean, which require the additional examination of compensation processes in the carbonate system on different time scales.

### **The use of calcareous micro- and nannoplankton as dissolution proxies**

#### *Comparative analysis of dissolution proxies derived from planktic and benthic foraminifera*

The preservation potential of planktic foraminifera strongly depends on the internal wall

---

structure, which consists of small, anhedral crystals on the proximal side, larger crystals toward the distal side, and in some partially deep-living species, large crystals, forming the calcite crust (Bé et al. 1975). The shell containing the largest crystals is the most resistant one. In some cases, a very smooth distal calcite layer ("cortex"; e.g., *Pulleniatina obliquiloculata*) covers the outside of the test. It retards dissolution for some time, protecting the underlying crust.

Berger (1967; 1968) investigated samples from a mooring (Peterson 1966) as well as plankton and sediment samples. He finds that carbonate dissolution changes species diversity, test size distribution, content of damaged shells, and average particle weight of an assemblage. Moreover, he establishes the ranking of planktic foraminiferal species with respect to their preservation potential. Investigations on the shell calcite show that the ratio of elements such as Na, Mg, Sr, F, V, U versus Ca decrease in the course of dissolution in some planktic foraminiferal species (Bender et al. 1975; Rosenthal and Boyle 1993; Hastings 1994; Russell et al. 1994; Nürnberg 1995). The reason is that chambers, keel and "cortex" are each secreted in different depths displaying a distinct chemical water composition, and dissolution removes the most "impure" calcite parts first and faster than pure calcite (Brown and Elderfield 1996). As the foraminiferal assemblage is changed qualitatively and quantitatively due to dissolution, the perturbation of the record makes the interpretation difficult, and some method must be found to indicate the extent of bias caused by dissolution (Hemleben et al. 1989).

There are routinely measured micropaleontological and sedimentological methods considered to be linked to carbonate dissolution and preservation. These methods include determination of (1) percentage of fragmented planktic foraminifera tests (e.g., Keigwin 1976; Le and Shackleton 1992); (2) proportions of solution susceptible and solution resistant planktic foraminifera species (e.g., Schott 1935; Berger 1979; Boltovskoy and Totah 1992); (3) the ratio of benthic to planktic foraminifera (e.g., Parker and Berger 1971; Hooper et al. 1991); (4) the ratio of agglutinating to calcifying foraminifera (e.g., Kennett 1966; Murray 1989); (5) the ratio of radiolaria to foraminifera (Peterson and Prell 1985); (6) the ratio of pteropods to foraminifera (Berner 1977); (7) the ratio of coccoliths to foraminifera (e.g., Hay 1970; Hsü and Andrews 1970). Each of these parameters is a potential dissolution index, but their variations may partly be controlled by ecological or other factors (e.g., productivity, winnowing). Thus mostly, a multi-method approach was used in carbonate dissolution-studies.

Several similar rankings of the solubility of planktic foraminifera (Table 1) were derived from sediment samples, from taut wire buoys, from mooring experiments, and from laboratory experiments. This ranking depends on chamber structure, test size, thickness of the shell, development of a "cortex", dimension of aperture, existence of spines, width

of pores, fragility of sutures (Berger 1979; Henrich and Wefer 1986). It is stated that *Globigerinoides ruber* is one of the most solution-susceptible species whereas *Neogloboquadrina* sp. belongs to the rather solution-resistant species.

**Table 1.** Dissolution ranking of planktic foraminifera based on previous work by several authors: low numbers correspond to least resistance and vice versa. If data of all authors are standardized, genus-dependent resistance with respect to dissolution becomes obvious:

(least resistant)

*Globigerinoides* sp. < *Globigerina* sp. < *Globigerinella* sp. < *Globigerinita* sp. < *Globorotalia* sp.

(most resistant)

Species	Way of investigation:	SCHOTT	PARKER	BERGER	MALMGREN	BERGER	THUNELL	BOLTOVSKOY
		(1935)	&BERGER (1971)	(1979)	(1983)	(1970)	& HONJO (1981)	& TOTAH (1992)
		Sediment ranking			Taut wire buoy	Mooring	Laboratory	
<i>Hastigerina</i>	<i>pelagica</i>		3	4			6	
<i>Globigerina</i>	<i>bulloides</i>		31	21	63	36	17	
	<i>fulconensis</i>		49	43				
<i>Turborotalita</i>	<i>humilis</i>		100	89		100		
	<i>quinqueloba</i>		29	25	13	41		
<i>Globoturborotalita</i>	<i>rubescens</i>		11	11		18		
	<i>tenella</i>		14	18		27		
<i>Globigerinella</i>	<i>adamsi</i>		20					
	<i>calida</i>		34	46			33	
	<i>digitata</i>		63	61			11	
	<i>siphonifera</i>		17	36		14	22	45
<i>Orbulina</i>	<i>universa</i>	50	54	39		9	39	
<i>Globigerinita</i>	<i>glutinata</i>		43	50	50	45		18
	<i>wvula</i>		40		25			
	<i>Candeina nitida</i>		51			50	28	
	<i>Tenuitella iota</i>		46	54				
<i>Globigerinoides</i>	<i>conglobatus</i>		26	32		32	61	64
	<i>ruber</i>		9	14		5	44	9
	<i>sacculifer</i>	25	23	29		23	56	55
	<i>(trilobus)</i>							27
	<i>Sphaeroidinella dehiscens</i>		94	75		91	100	82
<i>Globoquadrina</i>	<i>conglomerata</i>		66	64				73
	<i>(Neo-) dutertrei</i>		83	86		73	67	36
	<i>(Neo-) pachyderma</i>		86	100	37 (dex.) / 100 (sin.)	77		
<i>Globorotalia</i>	<i>crassaformis</i>		77	82		86	94	
	<i>hirsuta</i>		69			55		
	<i>inflata</i>		74	96	88	64	72	
	<i>menardii</i>	75		68			50	
	<i>scitula</i>		57	57				
	<i>truncatulinooides</i>		71	93	75	59	78	
	<i>tumida</i>	100	97	79		95	89	91
<i>Berggrenia</i>	<i>pumilio</i>		89					
	<i>Globorotaloides hexagonus</i>		60					
	<i>Pulleniatina obliquiloculata</i>		91	71		82	83	100

According to Berger (1973b), benthic foraminifera are approximately three times less susceptible to dissolution than planktic foraminifera. Unfortunately, the information available on the dissolution of benthic foraminifera is scarce and fragmentary. Corliss and Honjo (1981) compiled a table of the relative susceptibility of benthic foraminifera to

dissolution. It should be noted that at least some planktic foraminifera are more resistant than certain benthic ones (Adelseck 1977; Boltovskoy and Totah 1992).

Another method is based on the ratio of the number of insoluble organic linings of five benthic foraminifera species to the number of calcareous shells of the same species (De Vernal et al. 1992). Maximum concentrations of organic linings correspond with a minimum of well-preserved shells and vice versa. The known relation between calcareous shells and their organic linings may lead to a dissolution index.

#### *Dissolution of calcareous nannoplankton assemblages*

Due to their small size, delicate ultrastructure, and complex sedimentation processes, relatively little work was done on coccolith dissolution as compared to planktic foraminifera. An early attempt to establish a preservation index was made by Roth and Thierstein (1972) who set up four categories of etching to express the preservation state of a coccolith assemblage. Among others, Hay (1970) stated that coccoliths show the best resistance to dissolution in deep waters especially compared with planktic foraminifera and other carbonate secreting invertebrates. He found - confirmed by early results of the Deep Sea Drilling Project - coccoliths to be more abundant close to the CCD than foraminifera. However, the results of Berger (1973b), Roth and Coulbourn (1982), and Paull et al. (1988) suggest that the dissolution behavior of coccoliths and foraminifera is rather similar, although differences in range of resistance cannot be excluded.

The occurrence of well-preserved coccoliths far below the CCD was then explained by protective chemosorptive coatings (Chave and Suess 1970) or organic membranes (McIntyre and McIntyre 1971). Fecal pellet transport is the most likely explanation for this phenomenon (Honjo 1975). Moreover, transport by fecal pellets is the most important process in transferring small phytoplankton skeletons from the photic zone to the ocean floor and therefore is a major component in the global carbon, carbonate, and silica cycles (Honjo 1976; Honjo et al. 1982). On the other hand, almost no information is available whether and how digestion processes in the guts of copepods or other zooplankton could lead to the dissolution of calcium carbonate after incorporation (Nejstgaard et al. 1994). Investigations on living coccolithophore communities have shown that malformation is a common feature in the biomineralization of coccoliths (Kleijne 1990; Giraudeau et al. 1993).

This incomplete formation of coccoliths already influences their preservation within the water column. In addition, heavily corroded specimens often occurred as well (Young 1994; Baumann et al. 1997).

Roth and Coulbourn (1982) explained the problems of defining a coccolith lysocline via the composition of a coccolith assemblage with the predominance of solution resistant species in both well and badly preserved coccolith assemblages. This is in contrast to foraminiferal assemblages that are usually predominated by more fragile forms should they be well preserved. All studies on coccolith dissolution are based on visual examination or ranking of the coccolith assemblages according to their preservation state. More recently Matsouoka et al. (1991) tried to use the disintegration of the distal and proximal shields of *Calcidiscus leptoporus* to establish a dissolution index.

### The South Atlantic dissolution experiment

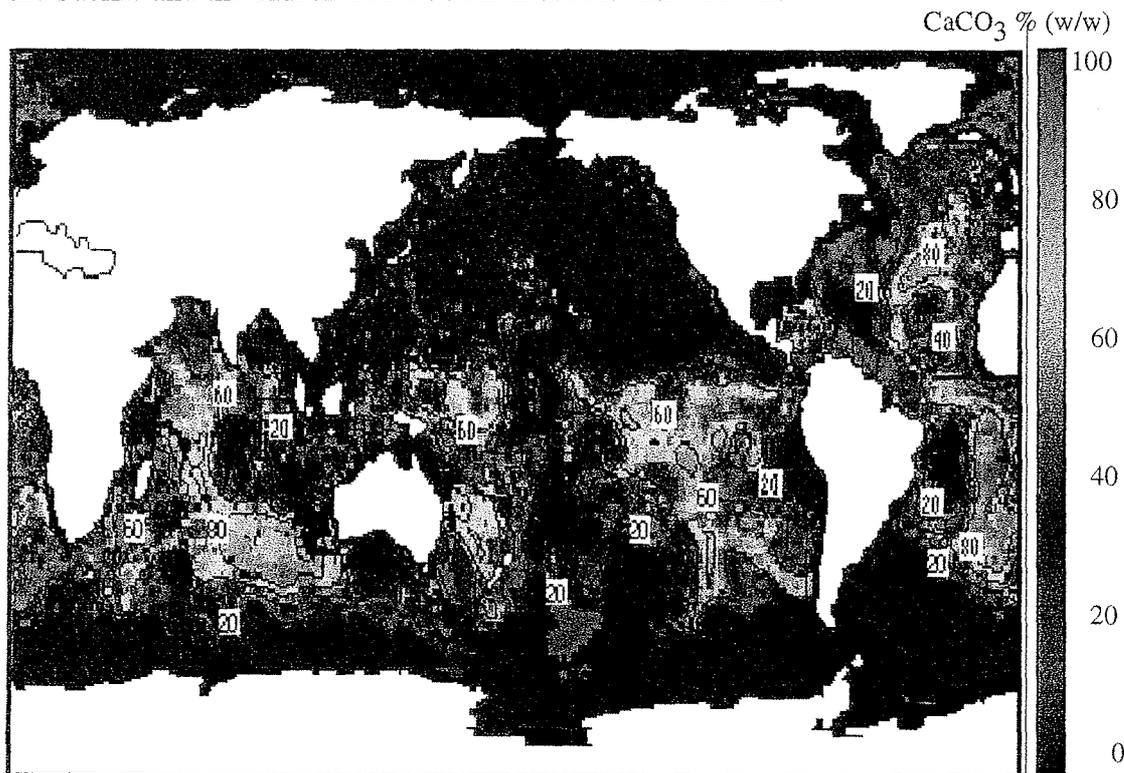
In the following, several of the methods presented in the first part of this publication were applied on three depth transects in the South Atlantic extending a) from the Mid-Atlantic Ridge into the Brazil Basin, b) from the Walvis Ridge into the Cape Basin, and c) from the Namibian Continental Margin into the Cape Basin (Fig. 7, Table 2). In particular, these methods include the bulk sediment parameters, i.e. absolute and relative weights of the coarse fraction ( $>63 \mu\text{m}$ ), rain ratio, and carbonate content. With respect to planktic foraminifera, the number of fragments of single species and the number of fragments of all species, the ratio of dissolution resistant to dissolution susceptible species, the weighted occurrence and the ratio of several species, the ultrastructural breakdown of a single species, the ratio of planktic foraminifera to radiolaria as well as benthic foraminifera were applied as investigation methods. Furthermore, the carbonate ion content of the water column versus the saturation state of calcite in sea water and a nannofossil dissolution index were used. The purpose of the dissolution experiment was to compare the pattern of carbonate dissolution in both the open ocean and the coastal upwelling zones in particular consideration of the applicability of dissolution proxies.

**Table 2.** Locations and water depths of the investigated core-top samples (0-1 cm) and GEOSECS stations 48,103.

Giant box core	Latitude	Longitude	Water depth [m]
Transect 1: MOR - Brasil Basin			
GeoB 1115-4	3°33.5'S	12°34.8'W	2.921
GeoB 1116-1	3°37.4'S	13°11.2'W	3.471
GeoB 1117-3	3°49.0'S	14°54.2'W	3.977
GeoB 1118-2	3°33.6'S	16°25.9'W	4.675
GeoB 1119-2	2°59.9'S	18°22.7'W	5.213
GEOSECS 48	4°00.0'S	29°00.0'W	11 - 5,075
Transect 2: Walvis Ridge - Cape Basin			
GeoB 1217-1	24°56.7'S	6°43.5'E	2.007
GeoB 1207-2	24°35.9'S	6°51.3'E	2.593
GeoB 1208-1	24°29.5'S	7°06.8'E	2.971
GeoB 1209-1	24°30.7'S	7°17.0'E	3.303
GeoB 1211-1	24°28.4'S	7°32.2'E	4.089
GeoB 1212-2	24°19.9'S	8°15.0'E	4.669
GEOSECS 103	23°59.7'S	8°30.2'E	5 - 4,572
Transect 3: Cape Basin - Namibia Continental Margin			
GeoB 1709-3	23°35.3'S	10°45.5'E	3.837
GeoB 1710-2	23°25.8'S	11°42.2'E	2.987
GeoB 1711-5	23°19.0'S	12°22.7'E	1.964
GeoB 1712-2	23°15.3'S	12°48.2'E	1.007

### Deep-water circulation and carbonate dissolution

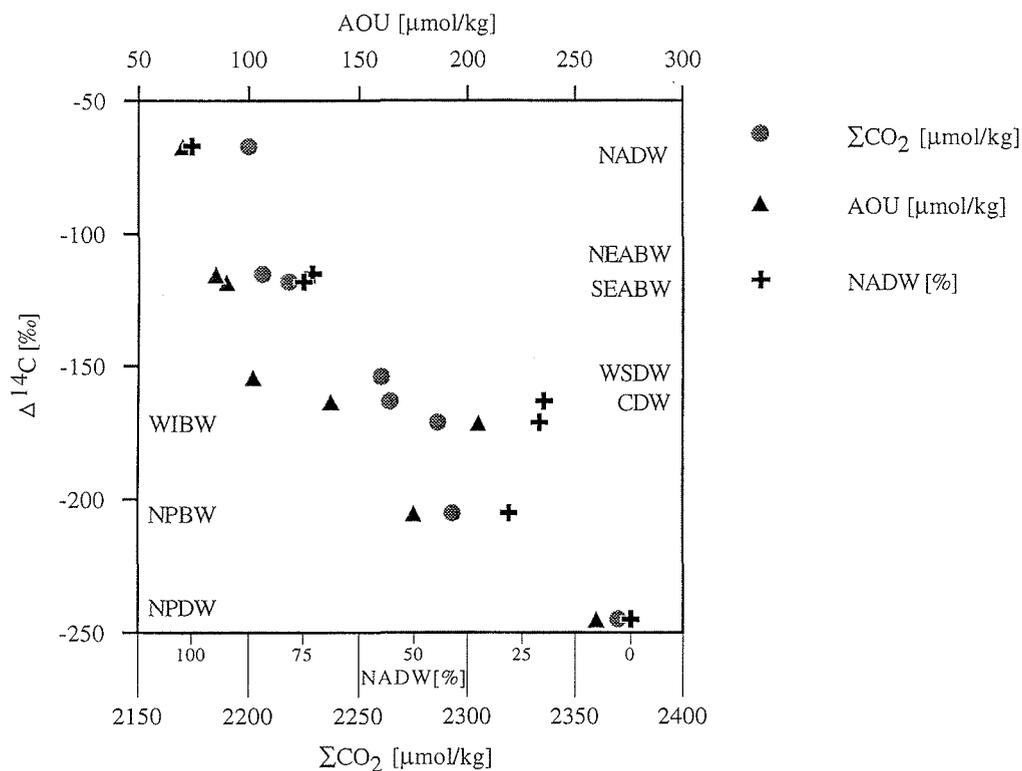
Regarding the modern distribution patterns of  $\text{CaCO}_3$  in deep-sea sediments (Fig. 3), the Atlantic Ocean (Biscaye et al. 1976) generally exhibits a better calcium carbonate preservation in deeper waters than the Pacific (Berger et al. 1976) and the Indian Oceans (Kolla et al. 1976). Accordingly, the saturation horizon is deepest in the western Atlantic Ocean (~4,500 m), intermediate in the western Indian Ocean (~3,500 m) and shallowest in the northernmost Pacific Ocean (~1,000 m) due to different vertical mixing processes within the water column (Broecker and Peng 1982). Additionally, the CCD is shallower in the Pacific and the Indian Oceans than in the Atlantic Ocean.



**Fig. 3.** Calcium carbonate ( $\text{CaCO}_3$  % (w/w)) distribution in surface sediments of the Atlantic, Pacific and Indian Oceans (from Archer 1996).

The global deep-waters are driven by thermohaline processes, characterized and separated by unambiguous water features. The overriding factor is the age of each water mass. It strongly depends on both the distance to the source area and the alteration of the water mass on the pathway to and through the deep ocean. Plots of  $\text{C}^{14}\text{C}$  (Fig. 4) versus apparent oxygen utilization (AOU), versus North Atlantic Deep Water (NADW) share in the deep-water, and versus inorganic carbon ( $\Sigma\text{CO}_2$ ) for various deep-water types show

a strong dependence of each parameter on the distance to the deep-water source area (Broecker and Peng 1982). The water mass alterations result from molecular diffusion (Liss 1973), turbulent mixing (Liss and Merlivat 1986), and respiration activity of benthic organisms (Reimers 1989; Berelson et al. 1990).

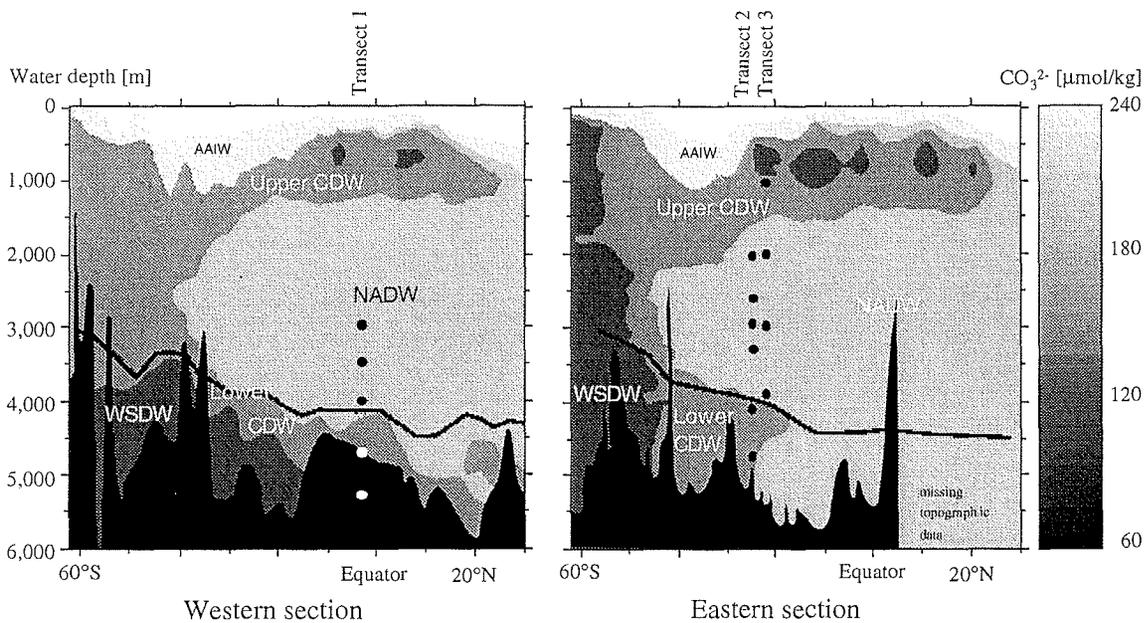


**Fig. 4.** Plots of  $\Delta^{14}\text{C}$  versus apparent oxygen utilization (AOU), versus North Atlantic Deep Water (NADW) proportion in the deep water, and versus inorganic carbon content ( $\Sigma\text{CO}_2$ ) for various deep water types show strong correlation ( $r^2 > 0.9$ ): The more distant a distinct deep water type from the source area, the lower the amount of NADW, the more oxygen is respired, and the higher the content of  $\Sigma\text{CO}_2$  will be (modified after Broecker and Peng 1982).

NADW...North Atlantic Deep Water, NEABW/SEABW ... North-, Southeast Atlantic Bottomwater, WSDW ... Weddell Sea Bottom Water, CDW ... Circumpolar Deep Water, WIBW ... West Indian Bottom Water, NPBW/NPDW ... North Pacific Bottom/Deep Water

NADW is characterized by oxygen enriched, nutrient depleted water masses of high  $\text{CO}_3^{2-}$  and low  $\text{CO}_2$  contents. Antarctic Bottom Water (AABW) can be distinguished as an extremely cold, oxygen depleted and nutrient enriched water mass of low  $\text{CO}_3^{2-}$  and high  $\text{CO}_2$  contents (Reid 1989; Boyle 1988). Today's mixing zone between AABW and NADW in the South Atlantic is close to the  $90 \mu\text{mol/kg}$   $\text{CO}_3^{2-}$  isoline (Fig. 5; Bainbridge 1981). The carbonate ion content of GEOSECS station 48 ranges from  $235 \mu\text{mol/kg}$  at 11 m to  $77 \mu\text{mol/kg}$  at 5,075 m with a distinct minimum of  $69 \mu\text{mol/kg}$  at 512 m water depth. According to equation (2), values for calcite saturation increase from  $48 \mu\text{mol/kg}$

at 11 m to 107  $\mu\text{mol/kg}$  at 5,075 m water depth. The carbonate ion content curve intersects the calcite saturation at about 4,150 m. At these points  $\Delta\text{CO}_3^{2-}$  becomes zero. The carbonate ion content of GEOSECS station 103 ranges from 219  $\mu\text{mol/kg}$  at 5 m to 84  $\mu\text{mol/kg}$  at 4,572 m with a distinct minimum of 63  $\mu\text{mol/kg}$  at 613 m water depth. The carbonate ion content curve intersects the calcite saturation at about 4,000 m. It has been known since the studies of Wüst (1935) that the water characteristics of the corrosive AABW are responsible for the pronounced abyssal calcium carbonate dissolution. Furthermore, the asymmetry in deep-water distribution is responsible for the modern pattern of carbonate dissolution driving the positions of the calcite lysocline and the CCD (Berger 1968).

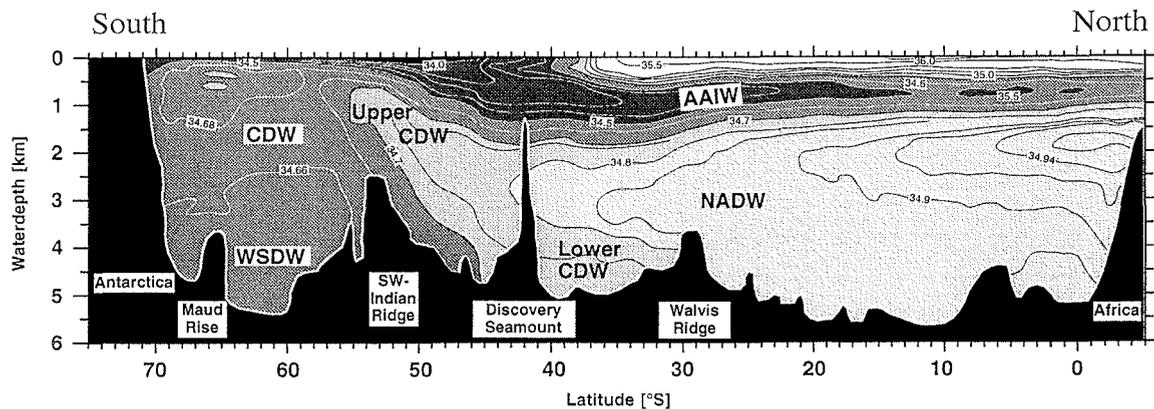


**Fig. 5.** Present-day stratification of the main water masses in the South Atlantic as displayed by  $\text{CO}_3^{2-}$  ion content. Carbonate ion distribution refers to Geochemical Ocean Section Study data (GEOSECS; Bainbridge 1981). The lysocline depth (black line) was calculated according to Broecker and Takahashi (1978). In the western section of the South Atlantic, the carbonate ion content continually decreases southwards due to the strong influence of AABW. Consequently, the lysocline raises from 4,000 m up to 3,000 m. In the eastern section of the South Atlantic, North Atlantic Deep Water (NADW) is stopped in the South at the Walvis Ridge and at the SW Indian Ridge. Hence, the lysocline rises in steps. Dots indicate the position of the sample locations.

CDW...Circumpolar Deep Water; AAIW...Antarctic Intermediate Water; NADW...North Atlantic Deep Water; WSDW ... Weddell Sea Deep Water; AABW ... Antarctic Bottom Water (WSDW + Lower CDW)

Today, two domains of deep-water production can be distinguished. NADW is formed in the Baffin Bay, the Labrador Sea, and the Norwegian-Greenland Sea. The advected warm water evaporates, becomes more saline, cools and sinks down, carrying

atmospheric carbon with it. From there, NADW extends far southwards across the equator into the South Atlantic and is subsequently distributed into the Indian and the Pacific Oceans via the Antarctic Circumpolar Current (ACC). The second major deep-water source is subdivided into the dense Weddell Sea Deep Water (WSDW) - which is derived from surface water and after making contact with air is cooled and becomes more saline when sea ice is formed - and the lighter Circumpolar Deep Water (CDW) which is derived from the upwelled currents recirculated around Antarctica (Rhein et al. 1996). The density characteristics of these water masses cause the NADW to divide the CDW into an upper and a lower branch (UCDW, LCDW; (Reid 1989). WSDW and LCDW form the AABW which is distributed into the Atlantic, the Indian, and the Pacific Oceans via the ACC (McCartney 1992).



**Fig. 6.** Present-day stratification of main ocean water masses in the South Atlantic as displayed by salinity contour lines [‰] at a north-south transect along the Greenwich Meridian (modified after Reid 1989).

CDW...Circumpolar Deep Water; AAIW...Antarctic Intermediate Water; NADW...North Atlantic Deep Water; WSDW ... Weddell Sea Deep Water; AABW ... Antarctic Bottom Water (WSDW + Lower CDW)

The western Atlantic ocean receives deep-water directly both from the northern and the southern production area. The relatively warm and saline NADW occupies the depth interval between 2 km and 4 km, whereas AABW is located below 4 km (Fig. 6). The only path where AABW can enter the western North Atlantic is on the route through the Equatorial Channel into the Guiana Basin. In the eastern Atlantic, the Walvis Ridge and the Mid-Atlantic Ridge bar AABW from entering the Angola Basin. Only small quantities of AABW pass the sills eastwards through the Romanche- (Van Bennekom and Berger 1984; Warren and Speer 1991), the Chain Fracture Zone (Mercier et al. 1994), and the Walvis Passage (Connary and Ewing 1972; Shannon and Chapman 1991). Thus, even the deepest parts of these basins are filled almost exclusively by NADW. In contrast, the Cape Basin, although located east of the Mid-Atlantic Ridge, is dominated by AABW

below 4,000 m due to a bottom water passage which allows AABW to enter the basin from the South.

The Indian and the Pacific Oceans are supplied mainly from the southern source whereas NADW is added only secondary via the ACC. The North Pacific Deep Water (NPDW) is the abyssal water mass most abroad from the two domains of deep-water production. Hence, it carries almost no NADW. Likewise, NPDW contains the largest amount of CO<sub>2</sub>, because oxygen is respired almost totally on its abyssal way to the northern edges of the Pacific Ocean, which results in sub- to anoxic pore water.

### Samples and methods

All sediment surface samples from giant box cores were collected on R/V *Meteor* cruises (Wefer et al. 1989; Wefer et al. 1990; Schulz et al. 1992) at water depths from 1,007 m down to 5,213 m (Fig. 7; table 2).

The first transect (GeoB 1115-1119) extends from 3°33'S - 12°35'W over about 345 nm to the West (2,921 m to 5,213 m water depth) and belongs to the tropical biogeographic faunal province sensu Bé (1977). The second transect (GeoB 1207-1217) stretches from 24°57'S - 6°44'E over about 85 nm to the East (2,007 m to 4,669 m water depth); the third transect (GeoB 1709-1712) ranges from 23°15'S - 12°48'E over about 120 nm to the West (1,007 m to 3,837 m water depth). Transect 2 and transect 3 belong to the subtropical biogeographic faunal province. Hence, all samples within each transect should be characterized by a more or less identical faunal association except for the easternmost sample (GeoB 1712), which is located beneath the cold, nutrient rich, and highly productive Benguela Coastal Current system.

The top of the hydrographic lysocline horizon was determined sensu Takahashi et al. (1980) and Broecker and Takahashi (1978) given by the relationship:

$$(\text{CO}_3^{2-})_{\text{calcite}} [\mu\text{mol/kg}] = 90 \cdot e^{[0.16 \cdot (\text{Water depth [km]} - 4)]} \quad (2)$$

The thickness of the calcite lysocline covers the range from 10 μmol/kg (sensu Broecker and Peng 1982) to the ΔCO<sub>3</sub><sup>2-</sup> at the CCD (ΔCO<sub>3</sub><sup>CCD</sup>) sensu Archer (1996a).

A LECO CS-125 infrared analyzer was used in order to measure the total carbon (TC) and the total organic carbon (TOC) content of bulk sediments. Calcium carbonate content was calculated in weight percentage of the bulk sample according to the following equation:

$$\text{CaCO}_3 \text{ \% (w/w)} = (\text{TC \% (w/w)} - \text{TOC \% (w/w)}) \cdot 8.33 \quad (3)$$

The rain ratio (Berger and Keir 1984) is determined by the molar ratio of organic (C<sub>org</sub>) to inorganic (C<sub>carb</sub>) carbon.

For grain-size analysis as well as for foraminiferal counts, samples were washed through a 63  $\mu\text{m}$  sieve under a gentle spray of water to prevent additional fragmentation. The whole sample  $>63 \mu\text{m}$  was sieved on a 150  $\mu\text{m}$ , 212  $\mu\text{m}$ , 355  $\mu\text{m}$ , 500  $\mu\text{m}$ , and a 1,000  $\mu\text{m}$  sieve-set according to the CLIMAP-conventions (Imbrie and Kipp 1971). Each fraction was repeatedly split into subsamples using a microsplitter to obtain an aliquot of at least 300 non-fragmented planktic foraminifera specimens (CLIMAP 1984) that were identified and counted completely; fragments, benthic foraminifera and radiolaria were also counted on the same aliquot. Meanwhile, it is common to examine the  $>150 \mu\text{m}$  fraction in paleoceanographic and paleoclimatic investigations (CLIMAP 1976). The taxonomy used follows that of Hemleben et al. (1989).

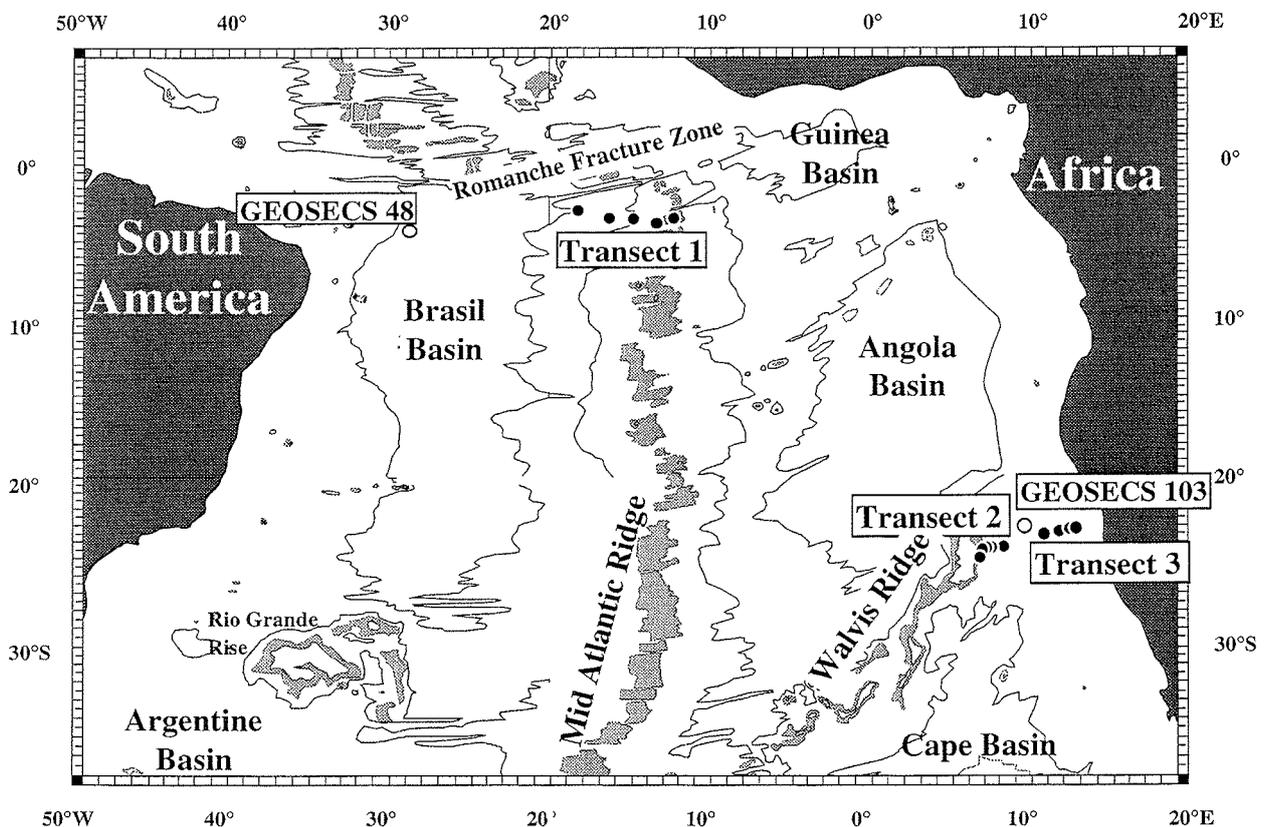


Fig. 7: General map of the investigated areas; for data consult table 2.

For the determination of dissolution stages according to ultrastructural breakdown, in each of the 5 fractions at least 40 *Globigerina bulloides* specimens were hand-picked and mounted on a carbon tape, glued onto a SEM stub, and then coated with Au-Pd. The apertural side of the non-fragmented test, the last and the penultimate chambers were examined using ZEISS Digital Scanning Microscope 940 A. The five dissolution stages correspond to "undissolved test surface" (stage 0) until "preserved not even as fragments" which is equivalent to "absent due to dissolution" (stage 5). Each *G. bulloides*

Dissolution Index (BDX) between zero and five was calculated weighted on the frequency of appearance per sample according to Dittert and Henrich (subm):

$$\text{BDX} = \sum (\text{BDX}') / \text{number of investigated tests} \quad (4)$$

$$\text{BDX}' = \sum (A_{0-5}) / \text{number of aspects per test obtained}$$

$A_{0-5}$  ... dissolution aspects of stage 0 to 5 per test

Fragments are counted if at least 50 % of the single chamber is preserved. The absolute and relative frequencies of skeletal fragments, the ratio of benthic to planktic foraminifera, and the ratio of radiolaria to planktic foraminifera were calculated according to Diester-Haass and Rothe (1987):

$$\text{Fragmentation Index} = F / (F+W) \quad (5.1)$$

$$\text{Benthic to planktic foraminifera Index} = B / (B+P) \quad (5.2)$$

$$\text{Radiolaria to planktic foraminifera Index} = R / (R+P) \quad (5.3)$$

F ... number of fragmented planktic foraminifera tests

W ... number of non-fragmented planktic foraminifera tests

B ... number of benthic foraminifera

P ... number of planktic foraminifera

R ... number of radiolaria

According to the dissolution-resistance, Berger (1979) defined a foraminiferal dissolution index (FDX; Table 1):

$$\text{FDX} = \sum (R_i \cdot P_i) / \sum P_i \quad (6)$$

$R_i$  ... rank of species  $i$

$P_i$  ... percentage of species  $i$

Ecological factors may bias results referring to faunal investigations; nevertheless, the loss of foraminifera was estimated on the assumption that the initial association within a transect is invariant and altered only by dissolution, not by changing productivity.

In order to describe the effect of carbonate dissolution on calcareous nannoplankton, the ratio of two coccolithophore species, *Emiliana huxleyi* and *Calcidiscus leptoporus*, was chosen. Both species occur frequently in modern sediments of the investigation area and appear to have a similar biogeographic distribution pattern (see Baumann et al., this volume). Hence, ecological factors that could influence this ratio are more or less excluded. The coccoliths formed by both species are placoliths, i.e., they consist of a proximal and a distal shield joined by a central column. *E. huxleyi* is a relatively fragile form with slots separating the single elements of the proximal shield, a large central pore, and a distal shield that is build up of delicate T-shaped elements. In contrast, *C. leptoporus* is a very solution-resistant form with heavily calcified distal and proximal shields, where no slots between the single elements occur and the connecting central tube is very narrow. Carbonate dissolution will have a stronger effect on *E. huxleyi* than on *C. leptoporus* and, therefore, the ratio of these two species will change with increasing carbonate dissolution. This *Calcidiscus leptoporus* - *Emiliana huxleyi* Dissolution Index

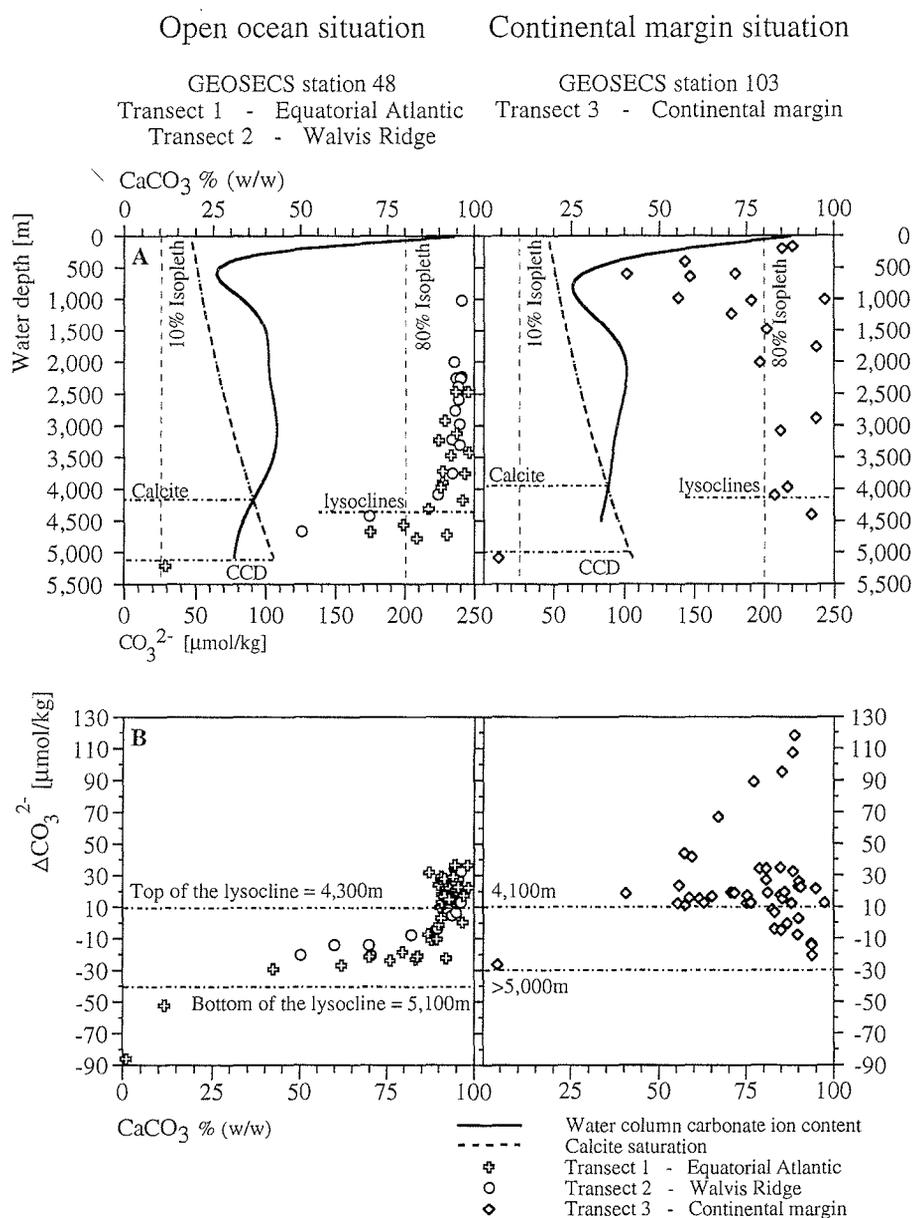
(CEX) is calculated as: 
$$\text{CEX} = \%E. \text{ huxleyi} / (\%E. \text{ huxleyi} + \%C. \text{ leptoporus}) \quad (7)$$

## Results

*Bulk parameters.* The sediment CaCO<sub>3</sub>-content extends from 94.6 % (w/w) at 2,471 m to 0.9 % (w/w) at 7,622 m (transect 1 - equatorial Atlantic) and from 96.4 % (w/w) at 1,023 m to 50.3 % (w/w) at 4,669 m water depth (transect 2 - Walvis Ridge). The 80 % isopleth intersects CaCO<sub>3</sub>-values of transect 1 and 2 at about 4,300 m, whereas the 10 % isopleth crosses CaCO<sub>3</sub>-values of transect 1 at about 5,100 m water depth (Fig. 8A, left side). Transect 3 (continental margin) CaCO<sub>3</sub>-values amount to 88.3 % (w/w) at 167 m, reach a first minimum at 603 m with 40.6 % (w/w), attain a distinct maximum at 1,006 m with 97.5 % (w/w) and lastly come down to 4.2 % (w/w) at 5,086 m water depth. The 80 % isopleth crosses CaCO<sub>3</sub>-values three times at about 200 m, 2,000 m, and at about 4,100 m, whereas the 10 % isopleth intersects transect 3 at about 5,000 m (Fig. 8A, right side).

With respect to GEOSECS station 48, the top of the hydrographic calcite lysocline can be set to 4,150 m, whereas the top of the sediment calcite lysocline appears at about 4,300 m; the bottom of the sediment calcite lysocline can be obtained at about 5,100 m water depth (transect 1) which corresponds to -40 μmol/kg ΔCO<sub>3</sub><sup>2-</sup> (Fig. 8A, B, left side). According to transect 2, the bottom of the lysocline cannot be estimated due to absent sediment samples. Regarding GEOSECS station 103, the top of the hydrographic calcite lysocline can be set to 4,000 m, whereas the top of the sediment calcite lysocline appears at about 4,100 m (transect 3); the bottom of the sediment calcite lysocline is considered to be located at about 5,000 m water depth which corresponds to -30 μmol/kg ΔCO<sub>3</sub><sup>2-</sup>. Because there are no values below -30 μmol/kg ΔCO<sub>3</sub><sup>2-</sup>, this estimation is somewhat uncertain (Fig. 8A, B, right side). We should note, that GEOSECS station 103 possibly belongs to the pelagic ocean rather than to the continental margin and consequently CO<sub>3</sub><sup>2-</sup>-values may bias our results to some extent.

With respect to transect 1, the grain size fraction 63 μm - 150 μm increases from 15 % at 2,921 m to 70 % at 5,213 m water depth, the fractions 150 μm - 355 μm remain mostly unchanged, and the fractions >355 μm decrease from 60 % to about 10 %. In transect 2 as well as in transect 3, size fractions do not vary greatly. Fluctuations amount to 10 % maximum (Fig. 9, above). Dry bulk density decreases from 0.6 g/cm<sup>3</sup> to 0.2 g/cm<sup>3</sup> (transect 1) and from 0.9 g/cm<sup>3</sup> to 0.3 g/cm<sup>3</sup> (transect 2). Only in transect 3 could a significant increase be detected. Values rise from 0.4 g/cm<sup>3</sup> to 0.8 g/cm<sup>3</sup> (Fig. 9, above). The rain ratio increases from 0.002 to about 0.07 with a distinct shift at 4,779 m water



**Fig. 8.** The top of the hydrographic lysocline is determined by the intercept of seawater carbonate ion content ( $\text{CO}_3^{2-}$ ) and the concentration of carbonate ions in equilibrium with seawater (saturation state) for calcite mineral phase. The top of the lysocline as obtained from the sediment can be described as the 80 %  $\text{CaCO}_3$  isopleth (A) sensu Farrell and Prell (1989). The top of the calcite lysocline at the continental margin is higher than in the open ocean due to stronger influence of the AABW and due to the respiration effects at the continental margin of the coastal ocean within the classical upwelling area of the Benguela system induced by enormous productivity, high export and rapid sedimentation.

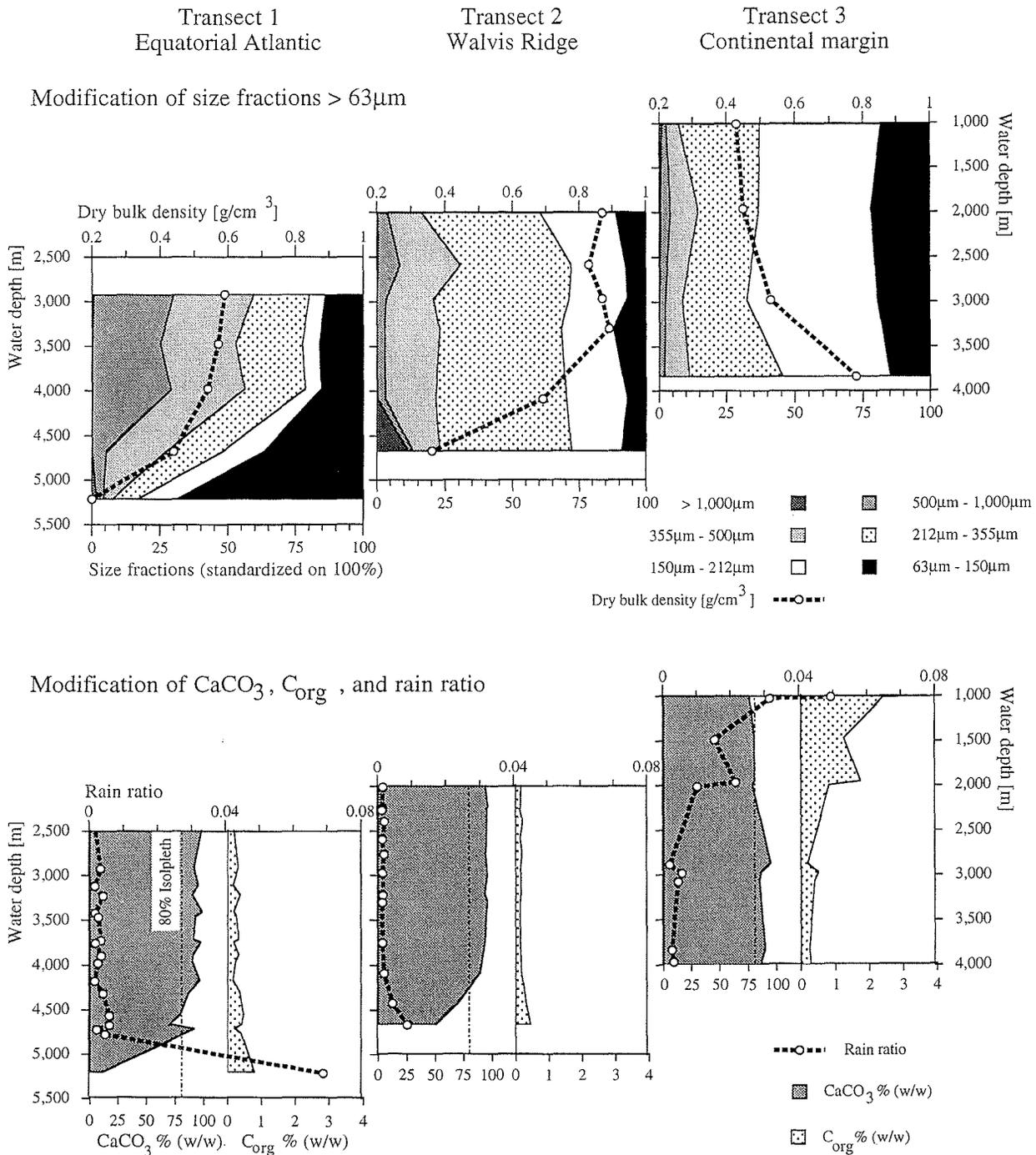
The thickness of the calcite lysocline (B) covers the range from 10  $\mu\text{mol/kg}$  sensu Broecker and Peng (1982) to the  $\Delta\text{CO}_3^{2-}$  at the CCD ( $\Delta\text{CO}_3^{\text{CCD}}$ ) which is the zero intercept of the  $\text{CaCO}_3$  % (w/w) versus  $\Delta\text{CO}_3^{2-}$  relation sensu Archer (1996), i.e.  $\Delta\text{CO}_3^{2-}$  (% $\text{CaCO}_3$  = 0). The calcite lysocline at the continental margin (transect 3) is thicker than in the open ocean (transects 1, 2) due to the higher calcium carbonate production and dissolution within the Benguela system. Water carbonate ion content refers to GEOSECS stations 48, 103 (Takahashi et al. 1980). Sediment calcite content ( $\text{CaCO}_3$  % (w/w)) refers to GeoB locations.

depth (transect 1). In transect 2, modifications are not that sharp. The shift occurs at about 4,089 m towards 0.01. The most recognizable changes occur in transect 3, where the rain ratio decreases from 0.05 to about 0.002 building an interim maximum of 0.02 at 1,964 m water depth (Fig. 9 below; Fig. 13C).

*Planktic foraminifera parameters.* The modification of organism assemblages can be expressed by the number of radiolaria, benthic and planktic foraminifera >150  $\mu\text{m}$  per gram sediment (Fig. 10, above). Transect 1 is characterized by a strong decrease in planktic foraminifera from 15,000 down to 4,000 tests; benthic foraminifera increase from 500 to 3,000 tests, and radiolaria increase from 150 to 360,000 tests per gram sediment. The most vigorous shift can be seen at about 3,977 m water depth. A similar picture is given in transect 2. Planktic foraminifera decrease from 14,000 to 4,500 tests, benthic foraminifera increase from 600 to 1,100 tests, and radiolaria increase from 100 to about 4,000 tests per gram sediment. A totally different situation occurs in transect 3: Planktic foraminifera increase from 17,000 to 45,000 tests, benthic foraminifera decrease from 1,800 to 500 tests, and radiolaria drop from 600 to 200 tests per gram sediment.

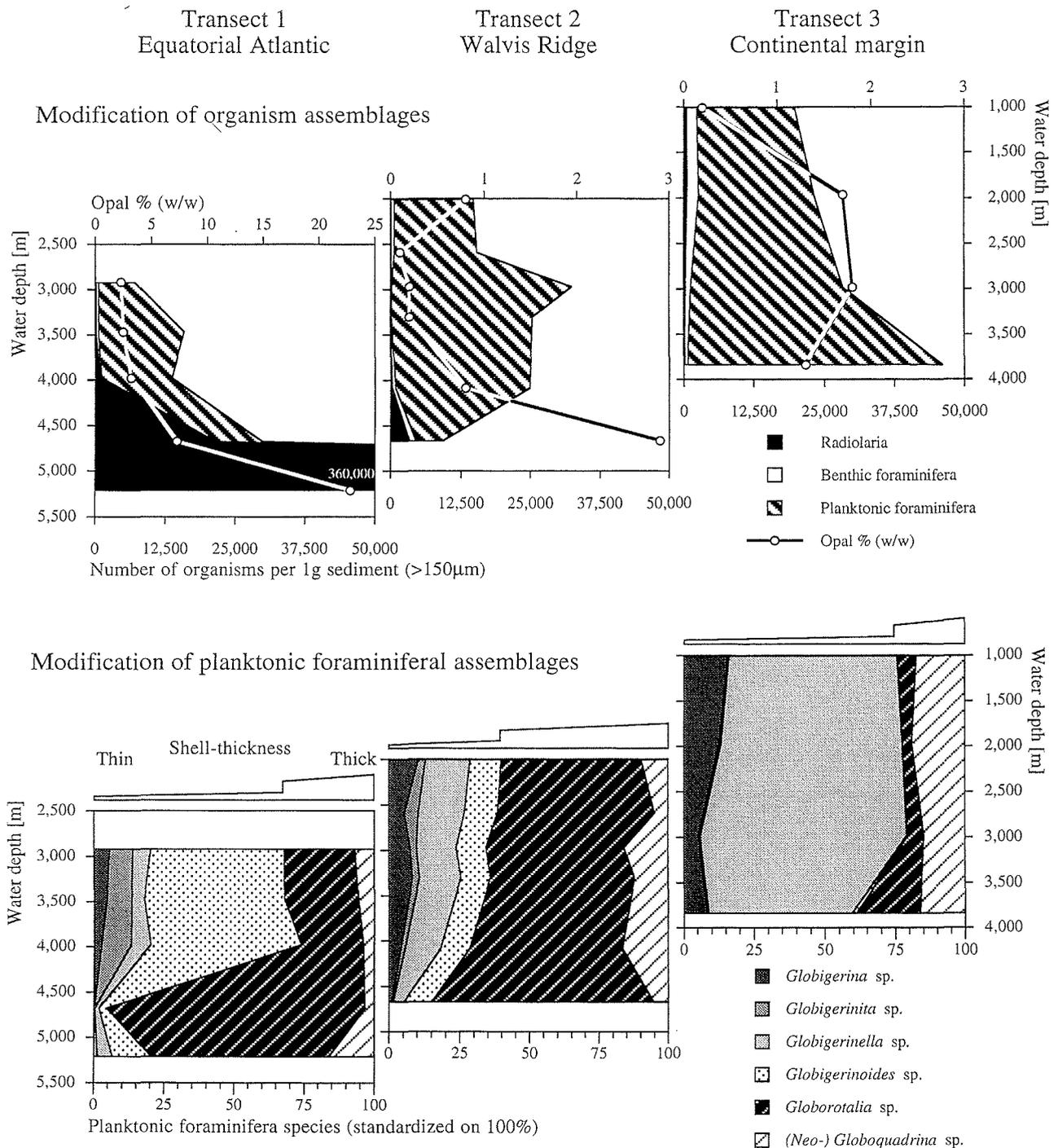
Looking at the modification of planktic foraminiferal assemblages, thick- and thin shelled varieties can be related to each other (Fig. 10, below). In transect 1, thick-shelled planktic foraminifera amount to 25 % at 2,921 m and increase to about 80 % at 5,213 m with an interim peak of 95 % at 4,675 m water depth. In transect 2, the amount of 60 % thick-shelled varieties at 2,007 m rises to 85 % at 4,669 m water depth. A similar picture appears in transect 3 where 25 % thick-shelled tests at 1,007 m increase to 40 % at 3,837 m water depth.

The ratio of dissolution susceptible to resistant planktic foraminifera shows a consistent trend in all three transects. Values remain consistently low from 1,007 m to 4,089 m, shift from about 0.2 to 0.6 and 0.8 at 4,670 m and drop then to 0.6 at 5,213 m water depth (Figs. 11A, F). The ratio of radiolaria to planktic foraminifera starts with about zero at 1,007 m and shifts at 4,089 m to about 1 at 5,213 m water depth (Fig. 11C). In a similar manner, the ratio of benthic to planktic foraminifera begins with about zero at 1,007 m and jumps at 4,089 m to about 0.5 at 5,213 m water depth (Fig. 11D). The foraminiferal dissolution index (FDX) commences at about 4.5 at 1,007 m rises at 4,089 m to 7 at 4,675 m and decreases to about 6 at 5,213 m water depth with respect to transects 1 and 3. Transect 2 starts on a higher level with 6 at 2,007 m and increases with a low slope to about 7 at 4,669 m water depth (Fig. 11B). Likewise, the fragmentation index of the sum of planktic foraminifera remains mostly unchanged from 1,007 m to 3,977 m and then shifts from 0.3 to 0.8 at 4,675 m, then decreasing to 0.4 at 5,213 m water depth according to transects 1 and 3. Values of transect 2 increase from 0.2 at 2,007 m to 0.8 at 4,089 m, then drop to 0.2 at 4,700 m water depth (Fig. 11E). Looking



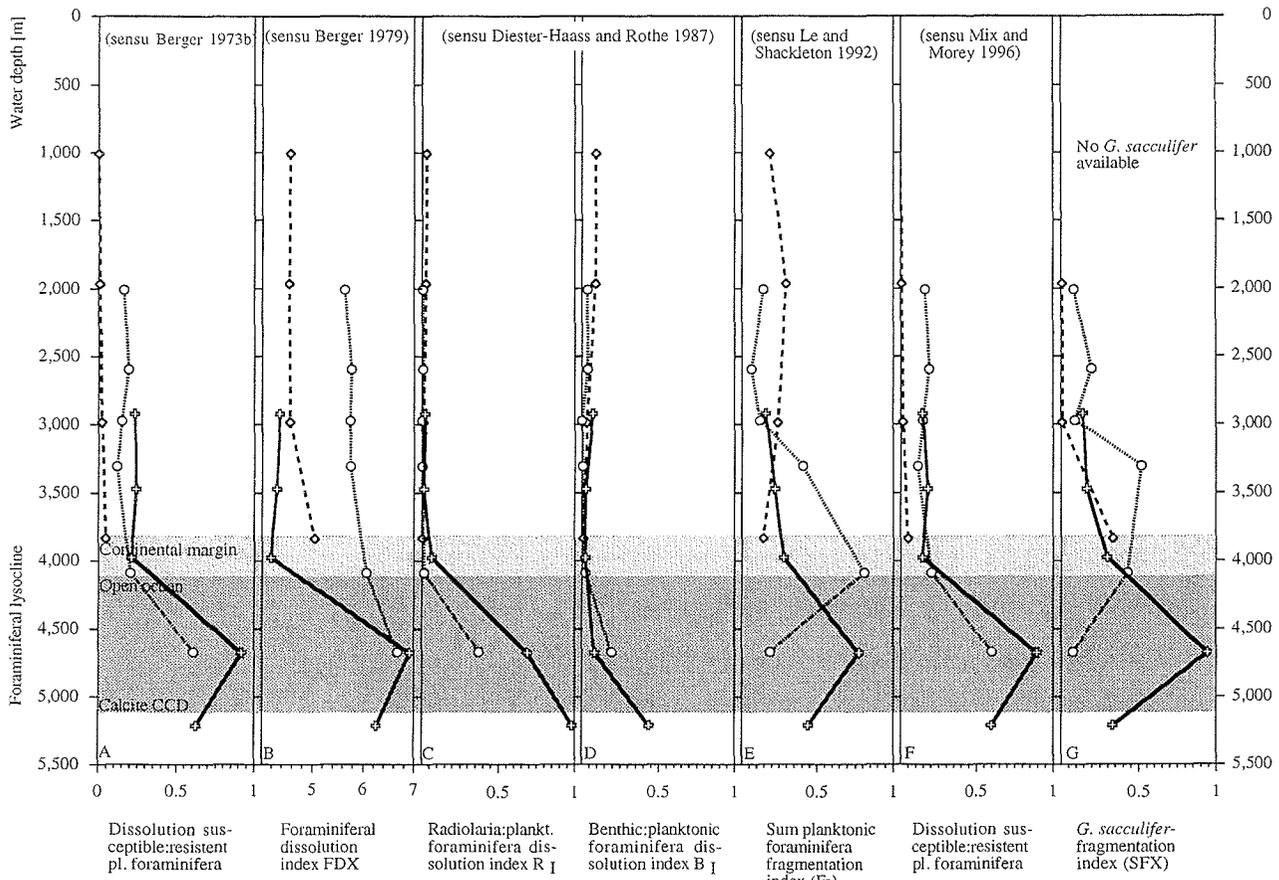
**Fig. 9.** Above. Modification of the grain size fractions (>63 μm) and the dry bulk density show that at the top of the calcite lysocline size fractions are partly dominated by smallest fractions. Dry bulk density decreases due to the lower part of calcareous (2.7 g/cm<sup>3</sup>) tests and the higher amount of opal skeletons (2.1 g/cm<sup>3</sup>).

Below. Modification of CaCO<sub>3</sub> % (w/w), C<sub>org</sub> % (w/w), and rain ratio. High rain ratio may be attributed to the fact that a) productivity of organic carbon is enlarged vigorous what leads to supralysoclineal dissolution, and b) CaCO<sub>3</sub> values decrease due to sublysoclineal dissolution. Where the rain rate of calcitic and noncalcitic material are constant and neither productivity nor dilution are enhanced, rain ratio of organic to inorganic carbon remains constant and low.



**Fig. 10.** Upper panel. Modification of organism assemblages show that the number of planktic foraminifera decreases whereas the number of benthic foraminifera and radiolaria increases at the top of the calcite lysocline. Furthermore, this is reflected by the rising amount of opal % (w/w). In the area of enhanced supralysoclineal dissolution the same picture is given resulting from respiration effects at the continental margin of the coastal ocean. This may be explained with enormous productivity, high export and rapid sedimentation of organic carbon.

Lower panel. Modification of planktic foraminiferal assemblages, expressed by the ratio of thick- to thin-shelled species. At the top of the calcite lysocline the amount of thick-shelled varieties increases drastically. Towards the CCD, the ratio is disturbed due to the deteriorated data base.



**Fig. 11.** Foraminiferal dissolution parameters which distinguish the area above the calcite lysocline from the area below, irrespective of whether they are derived from the open ocean or the continental margin transects. Increase of dissolution can be obtained at the top of the lysocline; towards the CCD, the parameters are disturbed due to the deteriorated data base.

at the fragmentation of *Globigerina sacculifer* tests, the values of all transects slightly increase from about zero at 2,007 m to 0.9 at 4,089 m. Transect 2 values drop to 0.1 at 4,669 m whereas transect 1 values rise to 0.9 at 4,675 m and then drop to 0.3 at 5,213 m water depth (Fig. 11G).

Regarding the development of fragmentation, about 60 percent of the sand-sized planktic foraminifera assemblage may be fragmented, whereas just 20 percent or less of the initial  $\text{CaCO}_3$ -content are lost (Fig. 12).

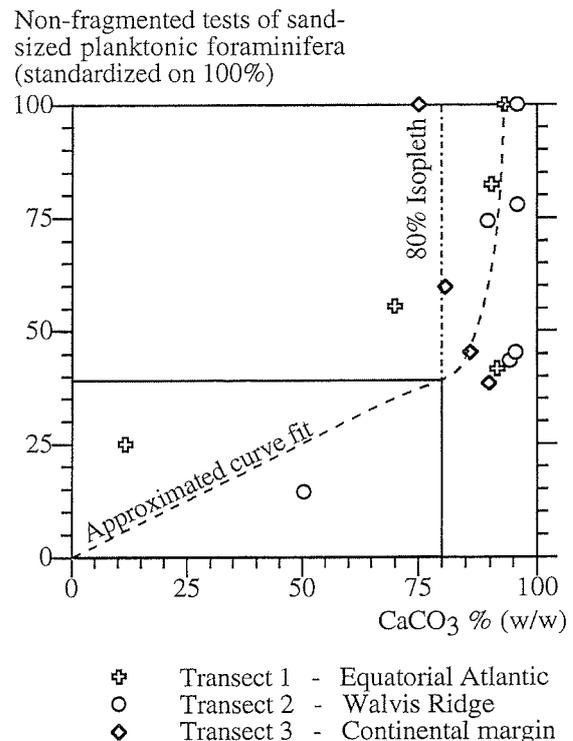
*New approaches.* The *Globigerina bulloides* Dissolution Index (BDX) increases from 1 at 2,007 m to about 2 at 4,089 m with respect to transects 1 and 2. Below, the values increase to 5 at 5,213 m water depth. According to transect 3, values increase from 1 at 1,007 m to about 3 at 3,837 m water depth (Fig. 13A). The *Calcidiscus leptoporus* - *Emiliana huxleyi* Dissolution Index (CEX) decreases from 0.8 at 2,007 m to 0.5 at 4,089 m and then shifts to about 0.2 at 5,213 m water depth with respect to transects 1 and 2. According to transect 3, values drop from 0.8 at 1,007 m to about 0.6 at 3,977 m

water depth (Fig. 13B).

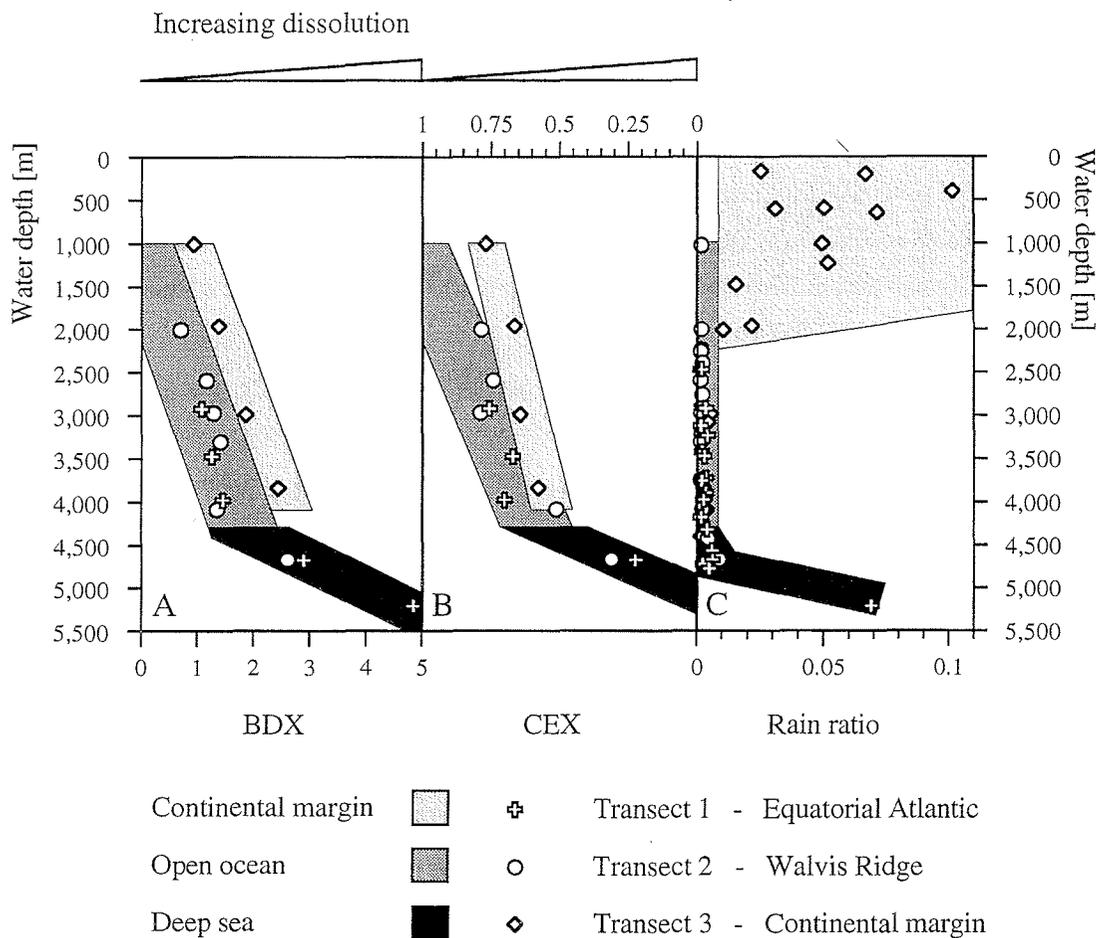
## Discussion

In general, all parameters applied to the carbonate dissolution in the deep ocean contain both striking advantages and limiting handicaps. First of all, we were able to distinguish three quite different environments. The open ocean realms refer to the environments above and below the top of the lysocline, which is reflected by all parameters of each transect, no matter whether they are derived from the equatorial Atlantic, the Walvis Ridge or the continental margin samples. The continental margin realm is characterized by the strong productivity of the surface waters due to the coastal upwelling which is connected to the Benguela Current.

The best lysocline reconstruction is obtained on the basis of the carbonate ion content measured within the water column. This leads to the exact determination of the hydrographic lysoclines with respect to calcite (Fig. 8A). GEOSECS data position the hydrographic lysocline with respect to calcite at a depth of 4,150 m for the open ocean and at a depth of 4,000 m for the continental margin. Our results corroborate the calculations by Broecker and Takahashi (1978) who concluded that the hydrographic lysoclines are located where carbonate ion concentration in the water column plotted against the water depth intersects the carbonate saturation curve. Moreover, the same depths are attained following the concept by Broecker and Peng (1982) who set the top of the lysocline at  $10 \mu\text{mol/kg } \Delta\text{CO}_3^{2-}$ . On the other hand, our investigations show, that the 'sedimentary' lysocline which coincides with the bend in the slope of the sediment  $\text{CaCO}_3$ -content versus water depth curve (Berger 1975), is positioned at 4,300 m for the open ocean and 4,100 m water depth for the continental margin realm (Fig. 8A).



**Fig. 12.** The plot of  $\text{CaCO}_3$  % (w/w) versus the number of non-fragmented tests of sand-sized planktonic foraminifera clarifies that about 60 % of the assemblage is fragmented, whereas only 20 % or less of the initial  $\text{CaCO}_3$  content are lost.



**Fig. 13.** A. *Globigerina bulloides* dissolution index (BDX) intensifies with increasing water depths and steady decrease of  $\Delta\text{CO}_3^{2-}$  within the water column. BDX increases by about one dissolution stage towards the calcite lysocline. BDX values increase drastically in samples below the lysocline. However, the investigated tests of the equatorial Atlantic and the Walvis Ridge transect above the lysocline show an offset of about one dissolution stage less than at comparable depths of the continental margin.

B. *Calcidiscus leptoporus* - *Emiliania huxleyi* dissolution index (CEX) shows the same pattern as BDX.

C. The rain ratio of organic to inorganic carbon can serve as a useful tool. Low values (<0.01) above the lysocline and strongly increasing values (>0.01) below represent the open ocean situation, whereas high values (>>0.01) in the upper few thousand meters of the water column stand for the continental margin realm. The high rain ratio may be explained as follows: a) the productivity of organic carbon is enlarged leading to supralysoclineal dissolution, and b) the carbonate values decrease due to sublysoclineal dissolution. Where the rain rate of calcitic and noncalcitic material are constant and neither productivity nor dilution are enhanced, rain ratio of organic to inorganic carbon remains constant and low.

Additionally, these results comply to the concept by Farrell and Prell (1989) who define the top of the sediment lysocline by the 80 %  $\text{CaCO}_3$ -isopleth (Fig. 8A). At the same depths, we observed the 'foram' lysocline (Figs. 10, 11) which is based upon morphology and association of planktic foraminifera (Berger 1968). We put that offset

between the hydrographic lysocline and the sedimentary and the 'foram' lysocline due to the fact that dissolution mostly occurs at the sediment pore water interface rather than in the water column. That is, at this interface  $[\text{CO}_3^{2-}]$  is very likely to be higher than at the equivalent water depths in the water column (Le and Shackleton 1992). Nevertheless, we are not able to give any evidence for the position of the aragonite lysocline due to missing indicators such as pteropods. The bottom of the lysocline was determined by two different concepts which both set it to a depth of 5,100 m for the open ocean and at about 5,000 m water depth for the continental margin. Here, carbonate undersaturation reaches such low values that the rate of calcite sedimentation is nearly totally compensated for by the rate of calcite dissolution (Bramlette 1961; Archer 1996). Hence, the thickness of the lysocline is calculated as about 800 m for the open ocean and more than 900 m water depth for the continental margin (Fig. 8B). Where the carbonate content falls below 10 % (w/w), we can ascertain that both the geochemical and the sedimentary reconstructions of each transect lead to a corresponding depth of the bottom of the lysocline. Presumably, this accordance is due to the fact that the 10 % isopleth and the zero intercept of the  $\% \text{CaCO}_3$  versus  $\Delta \text{CO}_3^{2-}$  relation coincide approximately with the progressive dissolution increase to the fourth power of  $\Delta \text{CO}_3^{2-}$  (Keir 1980) below the top of the lysocline. But it has to be emphasized that the percentage of  $\text{CaCO}_3$  as a single dissolution parameter cannot be simply interpreted as an index of preservation. Some general aspects must be regarded: 1) the rain rate and the accumulation rate of carbonate and non-carbonate particles; 2) the extent to which sea water is saturated with  $\text{CaCO}_3$ ; 3) the amount of organic matter buried with  $\text{CaCO}_3$ ; 4) whether the carbonate particles have an organic coating to retard dissolution; 5) whether there are currents to stir the layer of dissolution around the  $\text{CaCO}_3$ -particles (Le and Shackleton 1992). Only in the ideal situation, where the rain rate of carbonate and non-carbonate material is constant, can the amount of calcite lost to dissolution be calculated from the percentage  $\text{CaCO}_3$  in the sediment (Farrell and Prell 1989; Curry and Lohmann 1990; Bickert et al. 1997).

Another method to distinguish the three environments leads to the new approaches made here. The continuous increase of dissolution stages of *Globigerina bulloides* ultrastructure with increasing water depths complies to the concept of perpetual decrease of  $\Delta \text{CO}_3^{2-}$  within the water column (Broecker and Takahashi 1978). For all transects, dissolution increases by about one dissolution stage towards the calcite lysocline. Samples below the lysocline drastically increase in BDX values. However, the investigated tests of the equatorial Atlantic and the Walvis Ridge transect above the lysocline show an offset of about one dissolution stage less than at comparable depths of the continental margin (Fig. 13A). This is due to the strong productivity of organic and inorganic carbon within the Benguela upwelling system which yields higher benthic

respiration rates and hence a larger contribution to carbonate dissolution (Berger et al. 1987). However, each realm can be distinguished by discrete clusters. The important point is that this parameter does not depend on the ecology of the surface water, i.e., if there are tests broken without being affected by dissolution - whatever the reason may be - they will raise micropaleontological parameters and additionally they even will change the fragmentation index towards stronger dissolution (Dittert and Henrich *subm*).

The *Calcidiscus leptoporus* - *Emiliana huxleyi* Dissolution Index (CEX) shows comparable results. Considering the investigated areas, *Emiliana huxleyi* and *Calcidiscus leptoporus* show rather similar ecological behavior in response to nutrient distribution and temperature. Consequently, the changing ratio of these two species can be attributed to their different dissolution susceptibility. Hence, we are able to form clusters which separate the continental margin from the open ocean realm above and below the lysocline. That is, CEX values rise steadily with increasing water depths above the lysocline and then turn to stronger dissolution below the lysocline. Due to higher productivity, CEX values are offset by about 0.1 towards stronger dissolution above the lysocline at the continental margin (Fig. 13B). However, in surface waters which are distinctly more nutrient-depleted or cooler, CEX may fail.

The rain ratio of organic to inorganic carbon can serve as a useful tool. Our results show, that rain ratio forms clusters which are comparable to BDX and CEX. Low values ( $<0.01$ ) above the lysocline and strongly increasing values ( $>0.01$ ) below represent the open ocean situation, whereas high very values ( $>>0.01$ ) in the upper few thousand meters of the water column stand for the continental margin realm. This supports the concept of Berger (1991) who describes maximum values of organic carbon for the upper continental margin of the coastal ocean within the classical upwelling areas on the basis of a combination of enormous productivity, high export and rapid sedimentation (Fig. 9, below). On the other hand, oxidation of such an immense amount of organic carbon deposits results in (1) a successive  $\text{CO}_2$  release which lowers the pH of pore water; (2) reduced oxygen content; and (3) supralysoclineal dissolution of carbonates. Consequently, a high rain ratio may be attributed to the fact that a) productivity of organic carbon is intensified which leads to supralysoclineal dissolution, and b) carbonate values decrease due to sublysoclineal dissolution. Where the rain rate of carbonate and non-carbonate material is constant and neither productivity nor dilution are enhanced, the rain ratio of organic to inorganic carbon remains constant and low. All three situations can clearly be distinguished in separate clusters (Fig. 13C). Questions on the origin of organic carbon may arise if the eolian supply of terrigenous organic material related to the trade winds was of some importance in the deep Equatorial Atlantic (Verardo and Ruddiman 1996); furthermore, riverine particulate organic carbon deposited nearshore might enforce the

total organic carbon signal (Emerson and Hedges 1988). However, extended input of land-derived organic carbon would raise the total organic carbon content and consequently also increase the rain ratio towards higher values with respect to both the open ocean and the continental margin.

In contrast, most of the parameters dealing with planktic foraminifera are only qualified to determine the position of the lysocline. No matter whether it concerns the modification of grain size distribution of the sand fraction (Fig. 9, above), the modification of organism assemblages (Fig. 10, upper panel), the variation of planktic foraminifera assemblages (Fig. 10, lower panel), the ratio of dissolution susceptible to resistant planktic foraminifera (Figs. 11A, B, F), the ratio of radiolaria to planktic foraminifera (Fig. 11C), the ratio of benthic to planktic foraminifera (Fig. 11D), or the fragmentation of planktic foraminifera (Figs. 11E, G), the calcite lysocline can be positioned at about 4,300 m for the open ocean transects and at about 4,100 m water depth for the continental margin transect. The reasons why the continental margin situation cannot be distinguished are diverse. If there were intermediate water currents they might blow out lighter particles, i.e. finer grain-size fractions, fragments, and radiolaria. This would bias the results of grain-size investigations as well as the results of micropaleontological examinations towards less dissolution (Diester-Haass and Müller 1979). In a similar way, most samples below 4,675 m water depth (Fig. 11) present a distorted picture of less dissolution. We ascribe this to the fact that the number of organisms to be investigated is too small due to the effects of dissolution, i.e. the total decreases under the minimum that is required for statistical relevance (CLIMAP 1984).

In order to establish BDX and CEX as global dissolution proxies, we will apply these parameters on further realms which include continental margin situations outside the upwelling areas and regions with modified bottom water influence.

## Conclusions

Carbonate dissolution in the deep ocean was determined by using sea water carbonate ion data, bulk sediment parameters, and calcareous micro- and nannoplankton parameters as dissolution proxies. Investigation areas were the open ocean regime specified by two transects into the western Brazil Basin and the western Cape Basin. The continental margin realm is characterized by one transect into the eastern Cape Basin. Carbonate ion contents were measured between 5 m and 5,075 m water depth. The sediment surface samples are derived from water depths between 1,007 m and 5,213 m.

We can conclude that all parameters are capable of distinguishing the area above from the

area below the top of the calcite lysocline. Beyond that, some parameters are suited to distinguish the upper continental margin of the coastal ocean within an upwelling area controlled by enormous productivity, high export and rapid sedimentation. In detail, these are the carbonate ion content of the water column and the weight percentage of sediment  $\text{CaCO}_3$ -content (Fig. 8), the rain ratio (Fig. 9, below; Fig. 13C), the *Globigerina bulloides* Dissolution Index (BDX; Fig. 13A), and the *Calcidiscus leptoporus* - *Emiliania huxleyi* Dissolution Index (CEX; Fig. 13B).

Regarding the three different oceanographic regimes, only the carbonate ion content and the percentage of sediment carbonate content put us in the position to determine top, bottom, and thickness of the lysocline. If these parameters are not available, a combination of BDX, CEX and rain ratio (Fig. 13) gives the best approach to the authentic conditions.

According to the investigated transects, the top of the calcite lysocline can be set to about 4,300 m in the open ocean realm of the Brazil- and the western Cape Basin. It reflects the modern boundary between the North Atlantic Deep Water and the corrosive Antarctic Bottom Water, subsequently leading to sublysoclinal dissolution. The thickness of the lysoclines amount to about 800 m. With respect to the continental margin of the eastern Cape Basin, the lysocline is situated at about 4,100 m water depth; the lysocline thickness becomes >900 m. It reflects the high amount of organic matter buried with  $\text{CaCO}_3$ , induced by coastal upwelling processes of the Benguela Current, subsequently leading to sublysoclinal dissolution as well as to supralysoclineal dissolution.

## Acknowledgements

We appreciate the kind assistance of the crews and masters of R/V METEOR on numerous cruises to The South Atlantic. The authors are indebted to M. Matthies and R. Schlotte, who assisted the processing of the GEOSECS data set, as well as to H. Heilmann, R. Henning, and C. Wienberg for technical collaboration. B. Diekmann contributed Fig. 6. This research benefitted from many discussions with colleagues at Bremen University. Finally, we are grateful to W. H. Berger for constructive comments. The investigations were funded by the Deutsche Forschungsgemeinschaft. This is SFB 261 contribution no. xxx at Bremen University.

## References

- Adelseck CG (1977) Dissolution of deep-sea carbonate: Preliminary calibration of preservational and morphological aspects. *Deep-Sea Res* 25:1167-1185
- Archer DE (1996) An Atlas of the distribution of calcium carbonate in sediments of the deep-sea. *Global Biogeochem Cycles* 10(1):159-174
- Archer DE, Emerson S, Reimer C (1989) Dissolution of calcite in deep-sea sediments: pH and O<sub>2</sub> microelectrode results. *Geochim Cosmochim Acta* 53:2831-2846
- Archer DE, Maier-Reimer E (1994) Effect of deep-sea sedimentary calcite preservation on atmospheric CO<sub>2</sub> concentration. *Nature* 367:260-264
- Arrhenius GOS (1952) Sediment Cores from the East Pacific - Fasc. 1. Rep Swed Deep-Sea Exped 1947-1948 5:1-227
- Baes CFJ (1982) Effects of ocean chemistry and biology. In: Clark WC (ed) Carbon dioxide Review 1982. Oxford University Press, Oxford, 488 pp
- Bainbridge AE (1981) GEOSECS Atlantic Expedition, Hydrographic Data, 1972-1973. National Science Foundation, Superintendent of Documents, US Government Printing Office, Washington, DC, 121 pp
- Bassinot FC, Beaufort L, Vincent E, Labeyrie LD, Rostek F, Müller PJ, Quidelleur X, Lancelot Y (1994) Coarse fraction fluctuations in pelagic carbonate sediments from the tropical Indian Ocean: A 1,500 kyr record of carbonate dissolution. *Paleoceanography* 9(4):579 - 600
- Baumann K-H, Andrulleit H, Schröder-Ritzrau A, Samtleben C (1997) Spatial and temporal dynamics of coccolithophore communities during low production phases (spring-early summer) in the Norwegian-Greenland Sea. In: Hass HC, Kaminski MA (eds) Contributions to the micropaleontology and paleoceanography of the northern North Atlantic. Grzybowski Foundation Special Publication, Kraków, 5:227-243
- Baumann K-H, Meggers H (1996) Paleoceanographical change in the Labrador Sea during the last 3.1 MY: Evidence from calcareous plankton records. In: Mogailevsky A, Whatley R (eds) Microfossils and Oceanic Environments. Aberystwyth-Press, Aberystwyth, 131-154
- Bé AWH (1977) An ecological, zoogeographic and taxonomic review of recent planktonic foraminifera. In: Ramsay ATS (ed) Oceanic Micropaleontology. Academic Press, London, 1:1-100
- Bé AWH, Morse JW, Harrison SM (1975) Progressive dissolution and ultrastructural breakdown of planktonic foraminifera. In: Sliter WV, Bé AWH, Berger WH (eds) Dissolution of Deep-Sea Carbonates. Cushman Found. Foram. Res. Spec. Publ., Ithaca, NY, 13:27-55
- Bender ML, Lorens RB, Williams DF (1975) Na, Mg, Sr in the tests of planktonic foraminifera. *Micropaleontology* 21:448-459
- Berelson WM, Hammond DE, Cutter GA (1990) *In situ* measurements of calcium carbonate dissolution rates in deep-sea sediments. *Geochim Cosmochim Acta* 54:3013-3020

- Berger WH (1967) Foraminiferal ooze: Solution at depths. *Science* 156(3773):383-385
- Berger WH (1968) Planktonic foraminifera: Selective solution and paleoclimatic interpretation. *Deep-Sea Res* 15:31-43
- Berger WH (1970) Planktonic foraminifera: Selective solution and the lysocline. *Mar Geol* 8:111-138
- Berger WH (1973a) Deep-sea carbonates: Evidence for a coccolith lysocline. *Deep-Sea Res* 20:917-921
- Berger WH (1973b) Deep-sea carbonates: Pleistocene dissolution cycles. *J Foraminif Res* 3(4):187-195
- Berger WH (1975) Deep-sea carbonates: Dissolution profiles from foraminiferal preservation. In: Sliter WV, Bé AWH, Berger WH (eds) Cushman Foundation For Foraminiferal Research Special Publication. Cushman Found Foramin Res Spec Publ, Ithaca, NY, 13:82-86
- Berger WH (1979) Preservation of foraminifera. In: Lipps JH, Berger WH, Buzas MA, Douglas RG, Ross CA (eds) Foraminiferal Ecology and Paleocology. Society of Economic Paleontologists and Mineralogists, Houston, 6:105-155
- Berger WH (1982) Increase of carbon dioxide in the atmosphere during deglaciation: the coral reef hypothesis. *Naturwissenschaften* 69:87-88
- Berger WH (1991) Produktivität des Ozeans aus geologischer Sicht: Denkmodelle und Beispiele. *Z Dt Geol Ges* 142:149-178
- Berger WH, Adelseck CG, Mayer LA (1976) Distribution of carbonate in surface sediments of the Pacific Ocean. *J Geophys Res* 81(C):2617-2627
- Berger WH, Bonneau M-C, Parker FL (1982) Foraminifera on the deep-sea floor: lysocline and dissolution rate. *Oceanol Acta* 5(2):249-258
- Berger WH, Fischer K, Lai C, Wu G (1987) Ocean productivity and organic carbon flux. Part I. Overview and maps of primary production and export production. *Scripps Inst. Oceanogr., Univ. Calif.*, 67 pp
- Berger WH, Keir RS (1984) Glacial-Holocene changes in atmospheric CO<sub>2</sub> and the deep-sea record. In: Hansen JE, Takahashi T (eds) Climate processes and climate sensitivity. *Geophys. Monogr.* 29, Maurice Ewing Series, Washington, DC, 5:337-351
- Berger WH, Smetacek VS, Wefer G (1989) Ocean productivity and paleoproductivity - An overview. In: Berger WH, Smetacek VS, Wefer G (eds) *Productivity of the Ocean: Present and Past*. John Wiley & Sons, New York, NY, 1-34
- Berner RA (1977) Sedimentation and dissolution of pteropods in the ocean. In: Andersen NR, Malahoff A (eds) *The Fate of Fossil Fuel CO<sub>2</sub> in the Oceans*. Plenum Press, New York, NY, 243-260
- Bickert T, Cordes R, Wefer G (1997) Late Pliocene to Mid-Pleistocene (2.6-1.0 M.Y.) carbonate dissolution in the western equatorial Atlantic: Results of Leg 154, Ceara Rise. *Proc ODP, Sci Results* 154:229-237

- Bickert T, Wefer G (1996) Late Quaternary deep water circulation in the South Atlantic: Reconstruction from carbonate dissolution and benthic stable isotopes. In: Wefer G, Berger WH, Siedler G, Webb DJ (eds) *The South Atlantic: Present and past circulation*. Springer-Verlag, Berlin Heidelberg, 599-620
- Biscaye PE, Kolla V, Turekian KK (1976) Distribution of calcium carbonate in surface sediments of the Atlantic Ocean. *J Geophys Res* 81(C5):2595-2603
- Boltovskoy E (1991) La destruction des tests de foraminifères (expériences de laboratoire). *Revue de Micropaléontologie* 34(1):19-25
- Boltovskoy E, Totah VI (1992) Preservation index and preservation potential of some foraminiferal species. *J Foram Res* 22(3):267-273
- Boyle EA (1988) Vertical oceanic nutrient fractionation and glacial/interglacial CO<sub>2</sub> cycles. *Nature* 331:55-56
- Bramlette MN (1961) Pelagic sediments. In: Sears M (ed) *Oceanography*. AAAS Publication, New York, NY, 67:345-366
- Broecker WS, Peng TH (1982) *Tracers in the Sea*. Eldigio Press, New York, NY, 689 pp
- Broecker WS, Takahashi T (1978) The relationship between lysocline depth and in situ carbonate ion concentration. *Deep-Sea Res* 25F(1):65-95
- Brown SJ, Elderfield H (1996) Variations in Mg/Ca and Sr/Ca ratios of planktonic foraminifera caused by postdepositional dissolution: Evidence of shallow Mg-dependent dissolution. *Paleoceanography* 11(5):543-551
- Chave KE, Suess E (1970) Calcium carbonate saturation in sea water: Effects of dissolved organic matter. *Limnol Oceanogr* 15:633-637
- CLIMAP Project members (1976) The surface of the ice-age earth. *Science* 191(4232):1131-1137
- CLIMAP Project members (1984) The last interglacial ocean. *Quat Res* 21:123-224
- Connary SD, Ewing M (1972) The nepheloid layer and bottom circulation in the Guinea and Angola Basins. In: Gordon AL (ed) *Studies in physical oceanography: a tribute to Georg Wüst on his 80th birthday*. Gordon and Breach, New York, NY, 2:169-184
- Corliss BH, Honjo S (1981) Dissolution of deep-sea benthic foraminifera. *Micropaleontology* 27(4):356-378
- Culkin F (1965) The major ion components of seawater. In: Riley JP, Skirrow G (eds) *Chemical oceanography*. Academic Press, New York, NY, 1:121-162
- Curry WB, Lohmann GP (1990) Reconstructing past particle fluxes in the tropical Atlantic Ocean. *Paleoceanography* 5:487-506
- De Vernal A, Bilodeaul G, Hillaire-Marcel C, Kassou N (1992) Quantitative Assessment of Carbonate Dissolution in Marine Sediments from Foraminifer Linings vs. Shell Ratios: Davis Strait, Northwest North Atlantic. *Geology* 20:527-530

- Diester-Haass L, Müller PJ (1979) Processes influencing sand fraction composition and organic matter content in surface sediments off W Africa (12-19°N). "Meteor" Forsch-Ergebn C 31:21-47
- Diester-Haass L, Rothe P (1987) Plio-Pleistocene sedimentation on the Walvis Ridge, Southeast Atlantic (DSDP Leg 75, Site 532) - Influence of surface currents, carbonate dissolution and climate. Mar Geol 77:53-85
- Dittert N, Henrich R (subm) Carbonate dissolution in the South Atlantic Ocean: Evidence by *Globigerina bullloides*' ultrastructure breakdown: Deep-Sea Res
- Edmont JM (1970) High precision determination of titration alkalinity and total carbon dioxide content of seawater by potentiometric titration. 17:737-750
- Emerson S, Archer D (1990) Calcium carbonate preservation in the ocean. Phil Trans R Soc Lond A 331:29-40
- Emerson S, Bender M (1981) Carbon fluxes at the sediment-water interface of the deep-sea: calcium carbonate preservation. J Mar Res 39:139-162
- Emerson S, Hedges JI (1988) Processes controlling the organic carbon content of open ocean sediments. Paleoceanography 3(5):621-634
- Farrell JW, Prell WL (1989) Climatic change and CaCO<sub>3</sub> preservation: An 800,000 year bathymetric reconstruction from the central equatorial Pacific Ocean. Paleoceanography 4(4):447-466
- Farrell JW, Prell WL (1991) Pacific CaCO<sub>3</sub> preservation and  $\delta^{18}\text{O}$  since 4 Ma: paleoceanographic and paleoclimatic implications. Paleoceanography 6(4):485-498
- Freiwald A (1995) Bacteria-induced carbonate degradation: A taphonomic case study of *Cibicides lobolatus* from a high-boreal carbonate setting. Palaios 10:337-346
- Gattuso J-P, Pichon M, Delesalle B, Frankignoulle M (1993) Community metabolism and air-sea CO<sub>2</sub> fluxes in a coral reef ecosystem (Moorea, French Polynesia). Mar Ecol Prog Ser 96:259-267
- Giraudeau J, Monteiro PMS, Nikodemus K (1993) Distribution and malformation of living coccolithophores in the northern Benguela upwelling system off Namibia. Mar Micropal 22:93-110
- Hales B, Emerson S, Archer D (1994) Respiration and dissolution in the sediments of the western North Atlantic: estimates from models of *in situ* microelectrode measurements of pore water oxygen and pH. Deep-Sea Res 41(4):695-719
- Hastings DW (1994) Vanadium in the ocean: A marine mass balance and paleoseawater record. PhD Thesis:1-177
- Hay WW (1970) Calcareous nannofossils from cores recovered on Leg 4. DSDP, Initial Reports 4:455-501
- Hebbeln D, Wefer G, Berger WH (1990) Pleistocene dissolution fluctuations from apparent depth of deposition in core ERDC-127P, West-Equatorial Pacific. Mar Geol 92:165-176

- Hemleben C, Spindler M, Anderson OR (1989) Modern planktonic foraminifera. Springer, New York, NY, 363 pp
- Henrich R (1989) Glacial/interglacial cycles in the Norwegian Sea: Sedimentology, paleoceanography, and evolution of late Pliocene to Quaternary northern hemisphere climate. In: Eldholm O, Thiede J, Taylor E (eds) Proceedings of the Ocean Drilling Program, Scientific Results. College Station, TX, 104:189-232
- Henrich R, Wefer G (1986) Dissolution of biogenic carbonates: Effects of skeletal structure. *Mar Geol* 71:341-362
- Honjo S (1975) Dissolution of suspended coccoliths in the deep-sea water column and sedimentation of coccolith ooze. In: Sliter WV, Bé AWH, Berger WH (eds) Dissolution of Deep-Sea Carbonates. Cushman Found Foramin Res Spec Publ, Ithaca, NY, 13:114-120
- Honjo S (1976) Coccoliths: production, transportation and sedimentation. *Mar Micropal* 1(1):65-79
- Honjo S, Erez J (1978) Dissolution rates of calcium carbonate in the deep ocean; an in-situ experiment in the North Atlantic Ocean. *Earth Planet Sci Lett* 40:287-300
- Honjo S, Manganini SJ, Cole JJ (1982) Sedimentation of biogenic matter in the deep ocean. *Deep-Sea Res* 29(5A):609-625
- Hooper PWP, Funnell BM, Weaver PPE (1991) Late Miocene-Early Pliocene planktonic foraminifera and paleoceanography of the North Atlantic. *J Micropaleontol* 9:145-152
- Hsü KJ, Andrews JE (1970) Lithology. In: Bader RG (ed) Initial Report DSDP. National Science Foundation, Superintendent of Documents, US Government Printing Office, Washington, DC, 3:445-453
- Imbrie J, Kipp NG (1971) A new micropaleontological method for quantitative paleoclimatology: application to a Late Pleistocene Caribbean core. In: Turekian KK (ed) Late Cenozoic glacial ages. (Memorial Lectures) Yale University Press, New Haven, 43:71-181
- Jahnke RA, Craven DB, Gaillard JF (1994) The influence of organic matter diagenesis on  $\text{CaCO}_3$  dissolution at the deep-sea floor. *Geochim Cosmochim Acta* 58:2799-2809
- JGOFS (1989) Canadian National Programme for the Joint Global Ocean Flux Study. The Canadian Committee for JGOFS, Halifax, 28 pp
- Johnson TC, Hamilton EL, Berger WH (1977) Physical properties of calcareous ooze: Control by dissolution at depth. *Mar Geol* 24:259-277
- Jumars PA, Altenbach AV, De Lange GJ, Emerson SR, Hargrave BT, Müller PJ, Prah FG, Reimers CE, Steiger T, Suess E (1989) Transformation of Seafloor-arriving Fluxes into the Sedimentary Record. In: Berger WH, Smetacek VS, Wefer G (eds) Productivity of the Ocean: Present and Past. John Wiley & Sons, New York, NY, 291-311
- Keigwin LD (1976) Late Cenozoic planktonic foraminiferal biostratigraphy and paleoceanography of the Panama Basin. *Micropaleontology* 22:419-422

- Keir RS (1980) The dissolution kinetics of biogenic calcium carbonates in seawater. *Geochim Cosmochim Acta* 44:241-252
- Keir RS (1990) Reconstructing the ocean carbon system variation during the last 150,000 years according to the Antarctic nutrient hypothesis. *Paleoceanography* 5(3):253-276
- Kennett JP (1966) Foraminiferal evidence of a shallow calcium carbonate solution boundary, Ross Sea, Antarctica. *Science* 153(3732):191-193
- Kleijne A (1990) Distribution and malformation of extant calcareous nannoplankton in the Indonesian Seas. *Mar Micropal* 16:293-316
- Kolla V, Bé AWH, Biscaye PE (1976) Calcium carbonate distribution in surface sediments of the Indian Ocean. *J Geophys Res* 81(C15):2605-2616
- Le J, Shackleton NJ (1992) Carbonate dissolution fluctuations in the western equatorial Pacific during the Late Quaternary. *Paleoceanography* 7:21-42
- Liss PS (1973) Process of gas exchange across an air-water interface. *Deep-Sea Res* 20:221-238
- Liss PS, Merlivat L (1986) Air-sea gas exchange rates: introduction and synthesis. In: Ménard-Buat P (ed) *The role of air-sea exchange in geochemical cycling*. NATO ASI Series, Dordrecht Boston, C185:113-127
- Maier-Reimer E, Hasselmann K (1987) Transport and storage of CO<sub>2</sub> in the Ocean - An inorganic ocean-circulation carbon cycle model. *Clim Dyn* 2:63-90
- Malmgren BA (1983) Ranking of dissolution susceptibility of planktonic foraminifera at high latitudes of the South Atlantic Ocean. *Mar Micropal* 8:183-191
- Matsuoka H, McIntyre A, Molfino A, Verardo B (1991) A sensitive dissolution indicator *Calcidiscus leptoporus*: Concordance with climate-forced dissolution at orbital time scales. *EOS* 72(44):271
- McCartney MS (1992) Recirculating components to the Deep Boundary of the Northern North Atlantic. *Prog Oceanog* 29:283-383
- McIntyre A, McIntyre R (1971) Coccolith concentrations and differential solution in Oceanic Sediments. In: Funnell BM, Riedel WR (eds) *The micropaleontology of oceans*. Cambridge University Press, London, 253-261
- Mercier H, Speer KG, Honnorez J (1994) Tracing the Antarctic Bottom Water through the Romanche and Chain Fracture Zones. *Deep-Sea Res* 41:1457-1477
- Millero FJ (1979) The thermodynamics of the carbonate system in seawater. *Geochim Cosmochim Acta* 43:1651-1661
- Milliman JD (1975) Dissolution of aragonite, Mg-calcite, and calcite in the North Atlantic Ocean. *Geology* 3(8):461-462
- Mix AC, Morey AE (1996) Climate feedback and Pleistocene variations in the Atlantic south equatorial current. In: Wefer G, Berger WH, Siedler G, Webb DJ (eds) *The South Atlantic: Present and Past Circulation*. Springer-Verlag, Berlin Heidelberg, 503-525

- Murray CN, Riley JP (1971) The solubility of gases in distilled water and seawater. IV. Carbon dioxide. *Deep-Sea Res* 18:533-541
- Murray J (1897) On the distribution of the pelagic foraminifera at the surface and on the floor of the ocean. *Nat Sci* 11(65):17-27
- Murray J, Renard AF (1891) Deep-sea deposits based on the specimens collected during the voyage of H.M.S. *Challenger* in the years 1872-1876. London, 525 pp
- Murray JW (1989) Syndepositional dissolution of calcareous foraminifera in modern shallow-water Sediments. *Mar Micropal* 15:117-121
- Nejstgaard JC, Witte HJ, Van-der-Wal P, Jacobsen A (1994) Copepod grazing during a mesocosm study of an *Emiliana huxleyi* (Prymnesiophyceae) bloom. *Sarsia* 79(4):369-377
- Nürnberg D (1995) Magnesium in tests of *Neogloboquadrina pachyderma*, sinistral from high northern and southern latitudes. *J Foram Res* 25(4):350-368
- Olausson E (1965) Evidence of climatic changes in North Atlantic deep-sea cores, with remarks on isotopic paleotemperature analysis. In: Sears M (ed) *Progress in Oceanography*. Pergamon Press, London, 3:221-252
- Parker LF, Berger WH (1971) Faunal and solution patterns of planktonic foraminifera in surface sediments of the South Pacific. *Deep-Sea Res* 18:73-107
- Paul CK, Hills SJ, Thierstein HR (1988) Progressive dissolution of fine carbonate particles in pelagic sediments. *Mar Geol* 81:27-40
- Peterson LC, Prell WL (1985) Carbonate dissolution in recent sediments of the eastern equatorial Indian Ocean: Preservation patterns and carbonate loss above the lysocline. *Mar Geol* 64:259-290
- Peterson MNA (1966) Calcite: Rates of dissolution in a Vertical profile in the central Pacific. *Science* 154(3756):1542-1544
- Philippi E (1910) Die Grundproben der Deutschen Südpolar-Expedition 1901-1903. *Deutsch Südpolar-Exped 1901-1903* 2:411-616
- Reid JL (1989) On the total geostrophic circulation of the South Atlantic Ocean: Flow patterns, tracers and transports. *Prog Oceanog* 23:149-244
- Reimers CE (1989) Control of benthic fluxes by particulate supply. In: Berger WH, Smetáček VS, Wefer G (eds) *Productivity of the Ocean: Present and Past*. John Wiley & Sons, New York, NY, 217-233
- Revelle R (1944) Marine bottom samples collected in the Pacific Ocean by the 'Carnegie' on its seventh cruise. *Carnegie Inst Wash Publ* 556(2-1):1-133
- Rhein M, Schott F, Fischer J, Send U, Stramma L (1996) The deep water regime in the equatorial Atlantic. In: Wefer G, Berger WH, Siedler G, Webb DJ (eds) *The South Atlantic: Present and past circulation*. Springer-Verlag, Berlin Heidelberg, 261-271
- Rosenthal Y, Boyle EA (1993) Factors controlling the fluoride content of planktonic

- foraminifera: An evaluation of its paleoceanographic applicability. *Geochim Cosmochim Acta* 57:335-346
- Roth PH, Coulbourn WT (1982) Floral and solution patterns of coccoliths in surface sediments of the North Pacific. *Mar Micropal* 7:1-52
- Roth PH, Thierstein HR (1972) Calcareous nannoplankton. DSDP, Initial Reports 14:421-486
- Ruddiman WF, Janecek TP (1989) Pliocene-Pleistocene biogenic and terrigenous fluxes at equatorial Atlantic Sites 662, 663 and 664. *Proc ODP, Sci Results* 108:211-240
- Russell AD, Emerson S, Nelson BK, Erez J, Lea DW (1994) Uranium in foraminiferal calcite as a recorder of seawater uranium concentrations. *Geochim Cosmochim Acta* 58:671-681
- Santschi PH, Bower P, Nyffeler UP, Azevedo A, Broecker WS (1983) Estimates of the resistance to chemical transport posed by the deep-sea benthic boundary layer. *Limnol Oceanogr* 28:899-912
- Schott W (1935) Die Foraminiferen in dem Äquatorialen Teil des Atlantischen Ozeans. *Wiss Ergebn d Deutschen Atl Exp Meteor 1925-1927* 3:1-135
- Schulz HD, cruise participants (1992) Bericht und erste Ergebnisse über die Meteor-Fahrt M20/2, Abidjan-Dakar, 27.12.1991-3.2.1992. *Ber FB Geo Univ Bremen* 25:1-173
- Shannon LV, Chapman P (1991) Evidence of Antarctic Bottom Water in the Angola Basin at 32°S. *Deep-Sea Res* 38:1299-1304
- Takahashi T, Broecker WS, Bainbridge AE, Weiss RF (1980) Carbonate chemistry of the Atlantic, Pacific and Indian Oceans: The results of the GEOSECS expeditions 1972-1978. Lamont-Doherty Geological Observatory, Palisades, NY, 211 pp
- Thunell RC, Honjo S (1981) Calcite dissolution changes in the South Atlantic Ocean: Response to initiation of northern hemisphere glaciation. *Paleoceanography* 4:565-583
- Van Andel TH, Heath GR, Moore TC (1975) Cenozoic history and paleoceanography of the central equatorial Pacific Ocean. *Geol Soc Am Mem* 143:1-134
- Van Bennekom AJ, Berger GW (1984) Hydrography and silica budget of the Angola Basin. *Neth J Sea Res* 17:149-200
- Van Kreveland SA (1996) Calcium carbonate dissolution indices on the northeast Atlantic sea floor. In: Van Kreveland-Alfane SA (ed) Late Quaternary sediment records of mid-latitude Northeast Atlantic calcium carbonate production and dissolution. FEBO B.V., Enschede, 135-184
- Verardo DJ, Ruddiman WF (1996) Late Pleistocene charcoal in tropical Atlantic deep-sea sediments: Climatic and geochemical significance. *Geology* 24(9):855-857
- Vilks G (1975) Comparison of *Globorotalia pachyderma* (EHRENBERG) in the water column and sediments of the Canadian Arctic. *J Foram Res* 5:313-325
- Vincent E (1981) Carbonate stratigraphy of Hess Rise, Central North Pacific and paleoceanographic implications. *Mar Biol* 62:571-606

- Warren BA, Speer KG (1991) Deep circulation in the eastern South Atlantic Ocean. Deep-Sea Res 38(Suppl. 1):281-322
- Wefer G, Bleil U, cruise participants (1990) Bericht über die Meteor-Fahrt M12/1, Kapstadt-Funchal, 13.3.1990-14.4.1990. Ber FB Geo Univ Bremen 11:1-66
- Wefer G, Bleil U, Schulz HD, cruise participants (1989) Bericht über die Meteor-Fahrt M9-4, Dakar-Santa Cruz, 19.2.-16.3.1989. Ber FB Geo Univ Bremen 7:1-103
- Wu G, Herguera JC, Berger WH (1990) Differential dissolution: Modification of late Pleistocene oxygen isotope records in the western Equatorial Pacific. Paleoceanography 5(4):581-594
- Wüst G (1935) Die Stratosphäre. Wiss Ergebn d Deutschen Atl Exp Meteor 1925-1927 6(1-2):1-288
- Yasuda M, Berger WH, Wu G, Burke S, Schmidt H (1993) Foraminiferal preservation record for the last million years: Site 805, Ontong Java Plateau. Proc ODP, Sci Results 130:491-508
- Young JR (1994) Variations in *Emiliana huxleyi* coccolith morphology in samples from the Norwegian EHUX experiment. Sarsia 79:417-425

## COMPARISON OF COCCOLITHOPHORE NUMBERS AND ALKENONE CONCENTRATIONS IN LATE QUATERNARY SEDIMENTS FROM THE SOUTH ATLANTIC

Hanno Kinkel \*, Karl-Heinz Baumann, Martin Cepek, Peter J. Müller, and Carsten  
Rühlemann

*FB Geowissenschaften, Universität Bremen, Postfach 330 440, D-28334 Bremen, Germany*

### Abstract:

We investigated coccolithophore assemblages and alkenone concentrations in three sediment cores of the western equatorial Atlantic and eastern subtropical South Atlantic. We calculated the numbers of coccosphere units and compared them to the alkenone concentrations. A prominent feature, that occurs in all three cores, is a decrease in alkenone concentrations in sediments younger than 65.000 years. Coeval a decrease in numbers of coccospheres/g sediment of the alkenone producing species *Emiliana huxleyi* and *Gephyrocapsa* spp. occurred. According to our calculations *E. huxleyi* became the dominant species not before about 40 kyrs in the western equatorial Atlantic and not before the Holocene in the cores from the South East Atlantic, which is significantly later than the decrease in alkenone concentrations. Moreover it became evident, that during times when *Gephyrocapsa* spp. were the dominant species, numbers of coccospheres are significantly higher than at times when *E. huxleyi* dominated the assemblages. The combined records of these alkenone producing species reveal a general trend towards lower values in younger sediments, comparable to the decrease in alkenone concentrations. The absence of a highly significant correlation between the alkenone concentrations and the absolute numbers of *E. huxleyi* and *Gephyrocapsa* spp. may be explained by the contrary diagenetic behavior of the organic (alkenones) and inorganic compounds (calcite) produced by those coccolithophores.

Introduction:

Coccolithophores reveal the most thoroughly sedimentary record among all other phytoplankton groups, as their calcite scales are relatively well preserved compared to organic walled or siliceous microfossils in sediments not significantly influenced by carbonate dissolution. Their distribution patterns in surface sediments is not only linked to the general biogeographical zonation of the oceans (McIntyre and Bé, 1967; Geitzenauer et al., 1977; Roth, 1994) , but also reflect small scale variability in changing surface water conditions such as temperature, nutrients or surface water stratification (Giraudeau and Bailey, 1995; Samtleben et al., 1995). Consequently, coccoliths are used as proxies, for interpreting paleoceanographic changes (Baumann et al., in press; Kinkel et al., in press). The rapid evolutionary development within the coccolithophores yielded numerous valuable biostratigraphic events (Thierstein et al., 1977; Backman and Shackleton, 1983; Wei, 1993) , but limited their use for reconstructing sea surface temperatures or salinities by transfer functions (Molfino et al., 1982; Giraudeau, 1992; Pujos, 1992), since there are no modern analogs for fossil assemblages older than the last glacial interval.

In most parts of the modern oceans and their recent sediments, *Emiliana huxleyi* is the dominant coccolithophore species (Westbroek et al., 1993). One of the most fascinating features of this species are the large blooms, which cover thousands of square kilometers (Holligan et al., 1993; Brown and Yoder, 1994). It is assumed, that a considerable part of the calcium carbonate in pelagic oceans is formed by this species (Westbroek et al., 1993). Moreover, the production of dimethylsulfide (DMS), the influence of the coccoliths on the albedo of surface waters and the production of organic carbon are thought to influence the global climate and carbon cycle (Holligan et al., 1993; Westbroek et al., 1993). Specific organic compounds of coccolithophores, namely long-chain alkenones, became more and more intensely studied since they were detected in marine sediments two decades ago (Boon et al., 1978). The ratio between di- and triunsaturated C<sub>37</sub> alkenones, the U<sub>37</sub><sup>k</sup> index (Prahl and Wakeham, 1987), is highly correlated with sea surface temperature (SST) (e.g., (Rosell-Melé et al., 1995; Müller et al., 1998)) and is consequently used in paleo-SST reconstructions ((Kennedy and Brassell, 1992; Rostek et al., 1993; Schneider et al., 1996)).

Therefore *E. huxleyi* has been extensively studied in the field and laboratory, but it is not clear if we can transfer the results of these studies directly to the closely related species of the genus *Gephyrocapsa*, the most likely ancestor of *E. huxleyi*. There are few studies on the global dominance intervals of *Gephyrocapsa* during the Mid- and Late –Pleistocene, which appears to be different from the *E. huxleyi* dominance interval of the Holocene (Gartner, 1988; Bollmann et al., 1998).

Investigations including both, coccolithophore counts and geochemical analysis of alkenones are still very scarce (Summerhayes et al., 1995; Jordan et al., 1996; Sawada et al., 1996; Müller et al., 1997, Herbert et al. 1998) and are generally based on relative abundances of coccolith counts. Usually, analysis of fossil coccolithophore assemblages deals with counts and calculations of coccoliths instead of coccospheres. Thus reconstruction by coccoliths may be biased, since all coccolithophores consist of a large and varying number of coccoliths per coccosphere. The fact that coccolith counts refer only to a part of the individual coccosphere makes a comparison to other micropaleontological data difficult. Accordingly, a recalculation of coccoliths to coccospheres would be reasonable to reconstruct surface water history above the studied sediments. Up to now, only few authors addressed to this problem (Giraudeau and Pujos, 1990; Giraudeau, 1992; Pujos, 1992), because the number of coccoliths per coccosphere is not always known, especially not for those which are extinct. In addition, it is necessary to differentiate between relative abundances of coccoliths (as well as coccospheres) and their absolute numbers, as the first is more likely to reveal ecological information, while the latter one should be related to productivity of coccolithophores ( Flores, 1997; Kinkel et al., in press).

We compare three South Atlantic sediment records of coccosphere numbers and carbon-normalized alkenone concentrations for the time interval that includes the dominance change between *Gephyrocapsa* and *E. huxleyi*. We find significantly higher numbers of coccospheres and carbon-normalized alkenone concentrations in sediments that are dominated by species of the genus *Gephyrocapsa*, which we relate to an enhanced production or sedimentation pattern of coccolithophores during the dominance interval of *Gephyrocapsa* compared to the *E. huxleyi* dominance in the Holocene.

#### Oceanographic settings

The southeastern Atlantic is mainly influenced by the Benguela Current system. The Benguela Current (BC) originates as a northward flow off the Cape of Good Hope and splits into two branches, the colder Benguela Coastal Current (BCC), that continues to flow northward along the coast of Namibia and Angola, and the warmer Benguela Oceanic Current (BOC) which turns northwestward into the central South Atlantic. Wind induced coastal upwelling occurs throughout the year in the Northern Benguela region and likely influences the site at the Namibia margin (GeoB 1710-3), whereas the Walvis ridge site (GeoB 1028-5), is situated beneath the BOC and is episodically influenced by filaments from the upwelling area

(Lutjeharms and Meeuwis, 1987). A comprehensive description on the Benguela Current system is given by Shannon and Nelson (1996).

The western tropical Atlantic site (GeoB 1523-1) is located about 1000 km northeast of the Amazon River mouth and is influenced by the seasonal (June - January) retroflexion of the North Brazil Current (NBC), which forms the western limb of the North Equatorial Counter Current (NECC) (Müller-Karger et al., 1995). Interpretations of satellite-derived phytoplankton pigment concentrations suggested that eddies along the NBC retroflexion might trigger enhanced productivity (Longhurst, 1993).

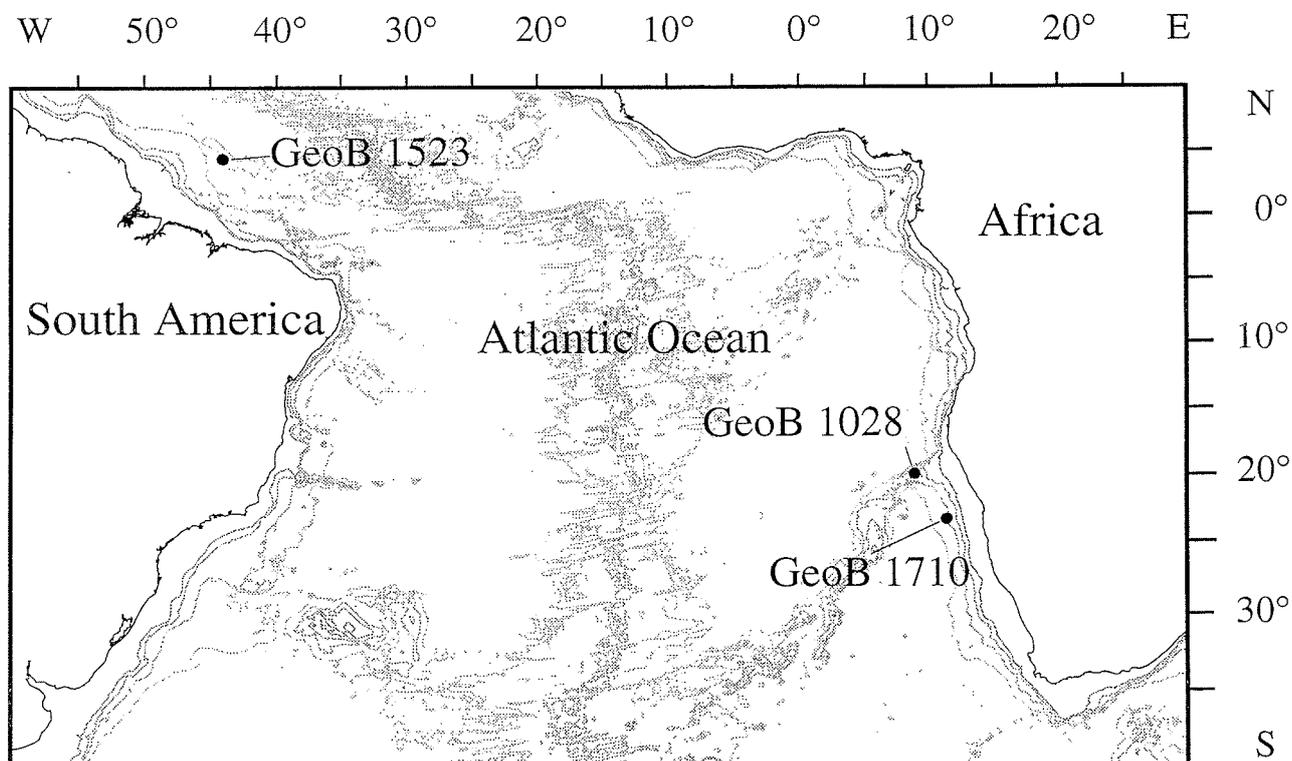


Fig. 1: Gravity core locations

### Material and Methods

The gravity cores of this study were recovered during RV *Meteor* cruises to the South Atlantic from the continental slope of Namibia, the eastern crest of the Walvis Ridge and western flank of the Ceara Rise M 6/6 (GeoB 1028-5 Wefer et al., 1988), M 16/2 (GeoB 1523-1, Schulz et al., 1991) and M 20/2 (GeoB 1710-3 Schulz et al., 1992). (see Fig. 1).

The age models for the sediment cores are based on graphic correlation of stable isotope  $\delta^{18}\text{O}$  records to the SPECMAP standard record (Imbrie et al., 1984) and were adopted from previous studies (GeoB 1523-1 in Rühlemann et al., 1996; GeoB 1028-5 in Schneider et al., 1996; GeoB 1710-3 in Schmiedel and Mackensen, 1997).

### *Coccolithophore analysis and counting:*

For preparation of sediment samples we used a filtering technique as described by Andrulleit (1996). A small amount of sediment (0.04 to 0.1 g) was weighed and brought into suspension. After dilution with a rotary splitter the suspension was filtered through polycarbonate membrane filters (Schleicher & Schuell<sup>TM</sup>, 50 mm diameter, 0.4  $\mu\text{m}$  pore size). A piece of the filter was cut out and mounted on an aluminum stub, which was gold coated for Scanning Electron Microscope (SEM) investigations. Coccoliths were counted along a transect at a magnification of  $\times 3000$  and  $\times 5000$ , respectively, until a total of at least 300 coccoliths was reached. Taxonomic classification of *Gephyrocapsa* was carried out according to Samtleben (1980) and Bollmann (1997). Taking into account overall length and bridge angle we distinguished three different species, *G. ericsonii*, *G. muellerae*, and *G. oceanica*, which dominate the assemblages during the investigated interval. *G. ericsonii* has the smallest coccoliths with overall length less than 2.7  $\mu\text{m}$  and a small bridge angle ( $< 45^\circ$ ), while *G. muellerae* produces coccoliths of larger than 2.7  $\mu\text{m}$  (in general between 3 and 4  $\mu\text{m}$ ) also having a small bridge angle ( $< 45^\circ$ ). We included *G. aperta*, which was separately listed in core GeoB 1028-5 (Müller et al., 1997) into *G. ericsonii*, since a clear separation of these small forms is rather tentative and can not be justified by morphometric measurements (Samtleben, 1980; Bollmann, 1997). The largest coccoliths are produced by *G. oceanica*, which are on an average larger than 4  $\mu\text{m}$  and which have a large bridge angle of  $> 60^\circ$ . In core GeoB 1028-5, a miscellaneous group of *Gephyrocapsa* sp.  $> 3\mu\text{m}$  is distinguished, which includes coccoliths larger than 3  $\mu\text{m}$ , where no further specification was carried out. However, due to the size of the coccoliths, we suggest, that in general this group consist of *G. muellerae*. For simplification, we also included *Gephyrocapsa* sp.  $< 3\mu\text{m}$  from core GeoB 1028-5 into *G. ericsonii*, although this miscellaneous group may contain some forms that are larger than generally expected in *G. ericsonii*. However, since we discuss no intraspecific variations within the genus *Gephyrocapsa*, this is of no further significance.

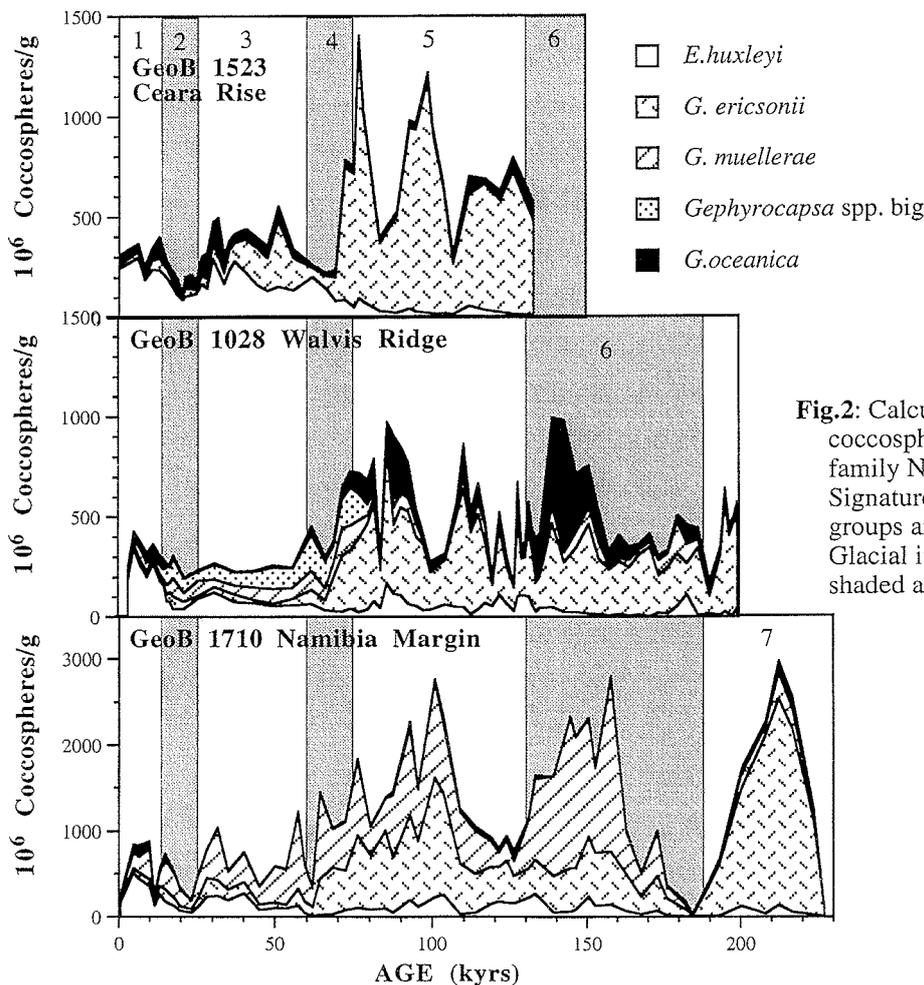
Coccolith numbers were then converted to coccosphere units, assuming that coccospheres of *E. huxleyi* are covered by 24 coccoliths and coccospheres of the genus *Gephyrocapsa* bear 14 coccoliths. These data are based on own observations on living coccolithophores from the South Atlantic as well as various other sources (see Table 2). Although it is known that numbers of coccoliths per coccosphere are not constant, and that especially *E. huxleyi* produces multiple layers of coccoliths and even shed coccoliths during its life cycle (Balch et al., 1993), these values seem to be a reasonable average.

*Geochemical analysis:*

The calcium carbonate and total organic carbon (TOC) contents of the sediments were determined by combustion of acid-treated and -untreated samples using a Hereaus CHN-O-Rapid elemental analyzer, as described by Müller et al. (1994).

Depending on the alkenone content of the sediments, 0.5 to 5 g of freeze-dried and homogenized material were extracted using successively less polar mixtures of methanol and methylen chloride (MeOH, MeOH/CH<sub>2</sub>Cl<sub>2</sub> 1:1, CH<sub>2</sub>Cl<sub>2</sub>). Originally, we used a modified flow-blending technique (Ultra Turrax T25 at 24,000 rpm) for extraction. Later, we switched over to ultrasonication for 3 minutes, and an UP 200H Sonic disruptor probe (200W, amplitude 0.5, pulse 0.5) inserted into the centrifuge tube, without changing the solvent mixtures.

Full details of the analytical method are given by Müller et al. (1994, 1998). Alkenone concentrations were normalized to organic carbon, expressed as carbon-normalized alkenone concentrations (K37), to minimize the influence of carbonate dissolution and diagenetic effects, that enhance both TOC contents and alkenone concentrations.



**Fig.2:** Calculated numbers of coccospheres / g sediment of the family Noerhabdaceae vs. age. Signatures for single species or groups are shown in the legend. Glacial intervals marked by shaded areas.

Results:

*Coccospheres*

Highest coccosphere numbers are observed in core GeoB 1710-3, with values ranging from 23 to 3022 x 10<sup>6</sup> coccospheres/g sediment. Pronounced minima occur in MIS 6.6 (coeval to the prominent TOC spike and carbonate minima) and early MIS 5 (Fig. 2). On an average, values are highest in MIS 5, 6 and 7, drop to lower values in MIS 4 and remain low up to the MIS 1. Similar trends are observed in the two other cores, whereas the absolute numbers are significantly lower, with values ranging between 155 to 994 x 10<sup>6</sup> in core GeoB 1028-5 and 126 to 1399 x 10<sup>6</sup> in core GeoB1523-1 (Fig. 2).

Species composition within the family Noelrhabdaceae display significant dissimilarities between the three cores. The most abundant species in the MIS 1 sections of all cores is *E. huxleyi*.

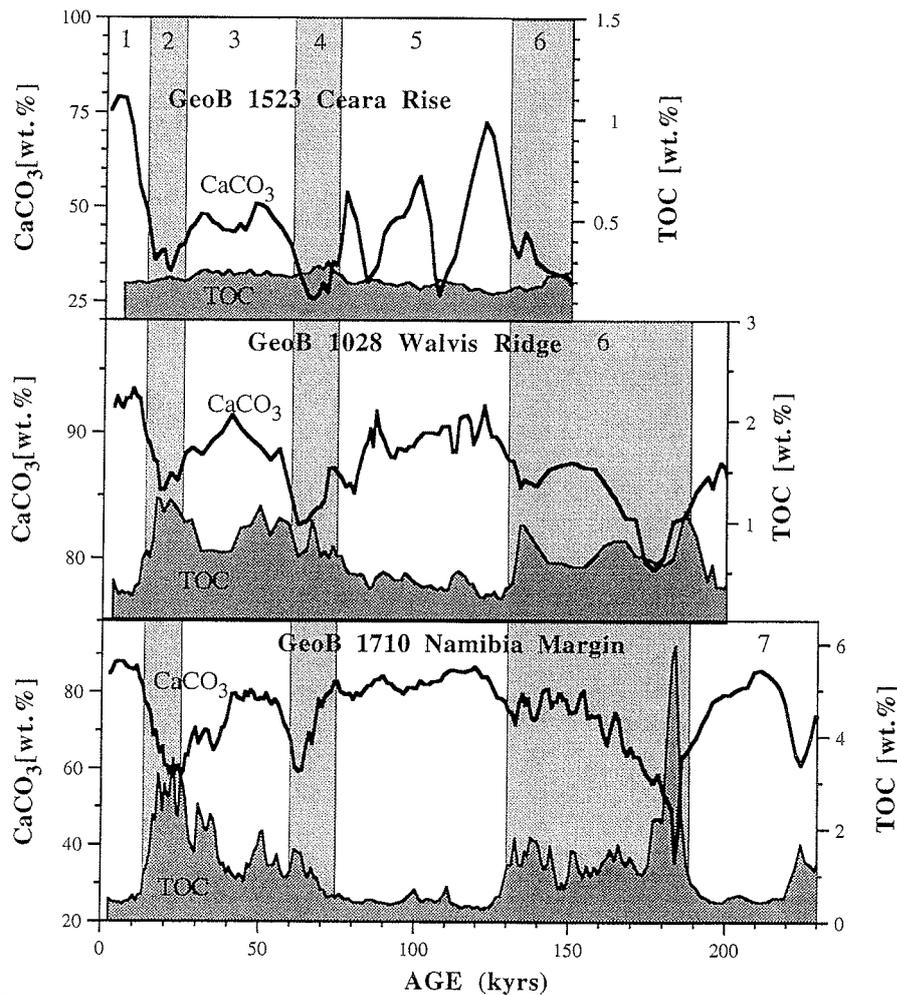


Fig. 3: Calcium carbonate (solid line) and total organic carbon (shaded area) contents (wt.-%) vs. age.

In the western tropical Atlantic (GeoB 1523-1) *G. ericsonii* is dominant in sediments older than MIS 4 and *G. oceanica* occurs in low but relatively constant numbers through the entire core. *G. muelleriae* and other *Gephyrocapsa spp.* big are almost absent.

At the Walvis Ridge (GeoB 1028-5) *G. muelleriae* and *Gephyrocapsa spp.* big are dominant from MIS 2 to mid MIS 4, with subordinate numbers in *G. oceanica* and *G. ericsonii*. In sediments older than mid MIS 4 *G. ericsonii* dominate the assemblage and numbers of *G. oceanica* are higher as well, while *G. muelleriae* becomes a subordinate species (Fig. 2).

At the Namibia Margin site (GeoB 1710-3) *G. muelleriae* is the most abundant species from the early MIS 1 to late MIS 5 and during most of MIS 6. *G. ericsonii* dominate the assemblage in MIS 7 and most of MIS 5. Numbers of *G. oceanica* are very low compared to all the other species, with highest abundance in the MIS 1, early MIS 5 and MIS 7.

The dominance reversal between *E. huxleyi* and *Gephyrocapsa spp.* was not synchronous, it occurred first in the tropical Atlantic (GeoB 1523-1) in late MIS 4 (around 65 ka), then in late MIS 2 (15 ka) at the Walvis Ridge (GeoB 1028-5) and at last in the mid MIS 1 on the Namibia Margin (GeoB 1710-3) (Fig. 2).

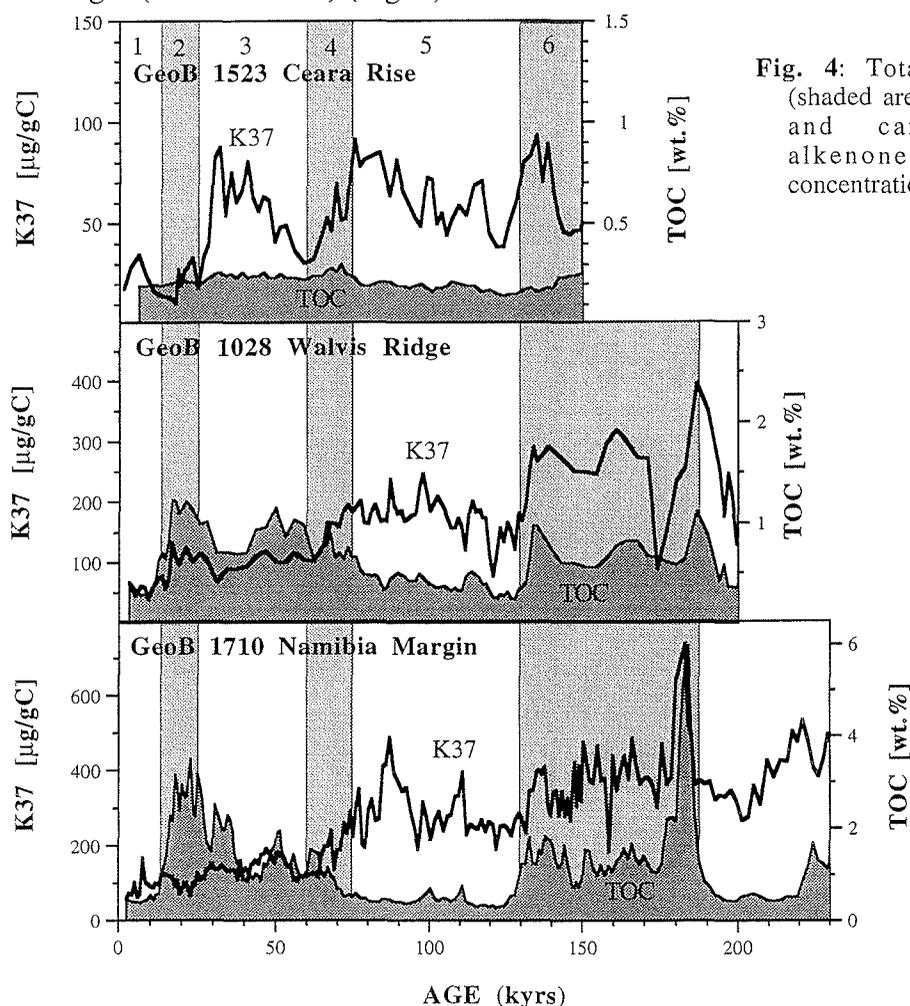


Fig. 4: Total organic carbon (shaded area) contents (wt.-%) and carbon-normalized alkenone (solid line) concentrations vs. age

### *CaCO<sub>3</sub>- and TOC- contents*

Calcium carbonate contents are highest in core GeoB 1028-5 from the Walvis Ridge with values ranging from 79 to 94 wt.-%. Highest values occur during the Marine Oxygen Isotope Stage (MIS) 1 and MIS 5.5, whereas lowest values are observed in MIS 2, 4 and substage 6.6 (Fig. 3). TOC contents of the same core range between 0.2 and 1.2 wt.-% and is, in general, higher in the glacial intervals. The TOC record of the entire core (400 kyrs) shows a periodicity of 23 kyr, which is attributed to wind-induced upwelling and productivity changes (Schneider et al., 1996). A similar pattern for both carbonate and TOC is observed in GeoB 1710-3. Here, carbonate values range from 36 to 88 wt.-%, with minima occurring in MIS 2, 4 and 6.6. TOC values are significantly higher than in core GeoB 1028-5 ranging from 0.3 to 6 wt.-%, with a prominent spike in substage 6.6 (Fig. 3).

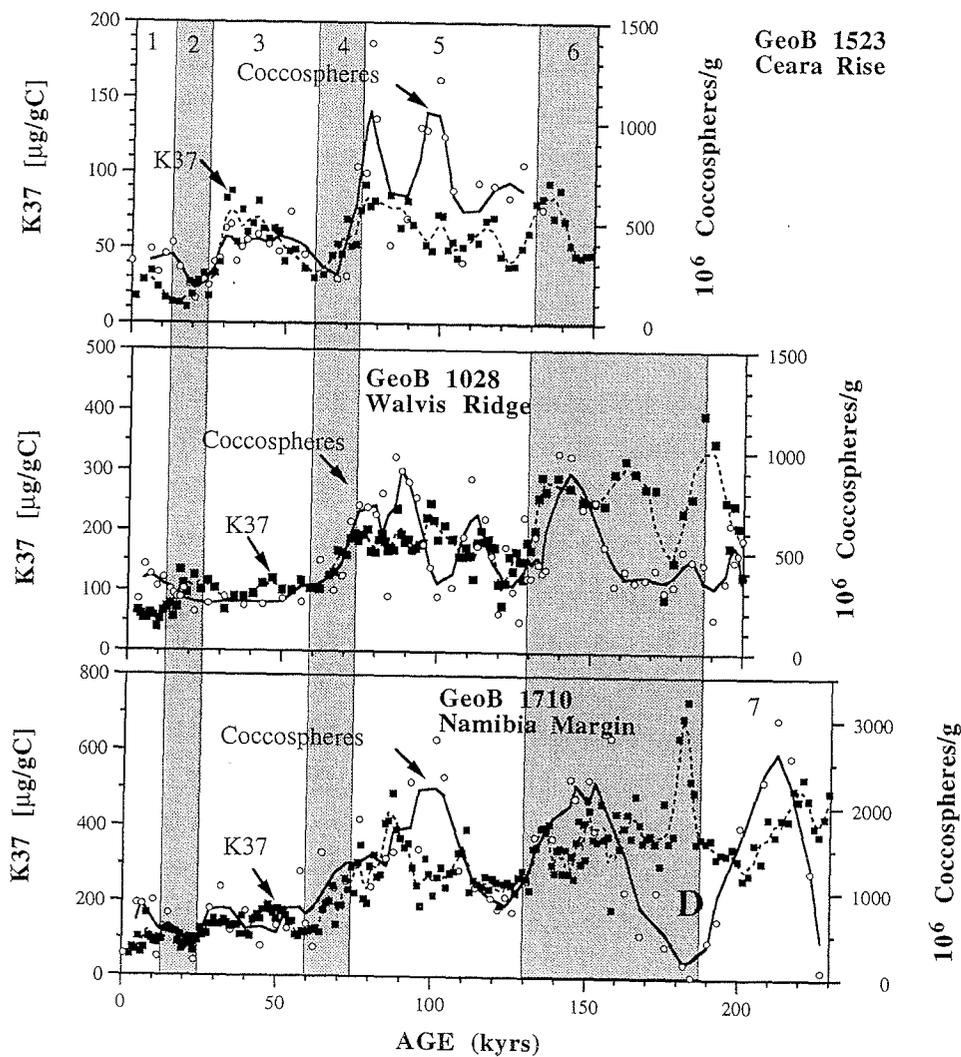
Carbonate- and TOC-contents are significantly lower in core GeoB 1523-1 from the Ceara Rise (25.7 to 79.1 wt.-% and 0.1 to 0.3 wt.-%, respectively) than in the two other cores. Here, carbonate contents again show distinct minima during MIS 2, 4 and 6, with additional minima in substages 5.2 and 5.4. The TOC values remain fairly constant with an average TOC content of 0.21 wt.-% (Fig. 3).

### *Carbon-normalized alkenone concentrations*

The carbon-normalized alkenone concentrations (K37) show similar trends for all three cores, although we notice large differences in absolute values between the sites (Fig. 4). Generally, concentrations are low in sediments younger than mid MIS 4 (about 65 kyrs) and, increase in sediments older than MIS 4. Carbon-normalized alkenone concentrations are significantly lower in core GeoB 1523-1 compared to the sediment cores (GeoB 1028-5 and 1710-3) from the southeastern Atlantic. At the Namibia Margin (GeoB 1710-3) values range from 56 to 738  $\mu\text{g/g}$  TOC. Concentrations are low (between 60 and 200  $\mu\text{g/g}$  TOC) in sediments younger than 65 ka and rise to values between 200 and 500  $\mu\text{g/g}$  TOC in sediments older than 65 ka. A prominent spike with values as high as 740  $\mu\text{g/g}$  TOC occurs in substage 6.6 coinciding with the prominent TOC peak (Fig. 4). At the Walvis Ridge (GeoB 1028-5) carbon-normalized alkenone concentrations vary from 40 to 400  $\mu\text{g/g}$  TOC, with lowest concentrations in MIS 1. Values at the Ceara Rise vary between 10 and 90  $\mu\text{g/g}$  TOC.

*Discussion*

A major problem in comparing organic and inorganic carbon compounds in pelagic sediments is the influence of carbonate dissolution due to the oxidation of organic matter at the sediment water interface, which can lead to supralysoclinal dissolution of calcareous sediment components (Dittert et al., in press). This effect is especially evident at sites with high organic carbon production and fluxes, like continental margins and may therefore explain the strong discrepancy between the alkenone and coccosphere record in MIS 6 at the Namibia Margin (indicated with **D** in Fig. 5). The marked increase in the TOC contents during early MIS 6, which are caused by intensified upwelling (Kirst et al., in press), favored the preservation of alkenones and lead to an obvious dissolution of coccoliths.



**Fig.5:** Carbon-normalized alkenone concentration (black squares) and calculated numbers of coccospheres (*Emiliania huxleyi* + *Gephyrocapsa* spp.)  $\times 10^6$  / g sediment vs. age. The dashed (alkenones) and solid (coccospheres) lines indicate the 3point moving average of the data points.

The sites investigated in this study vary not only in terms of productivity in the overlying watermasses, but also in their potential in preserving organic matter. The tropical western Atlantic site is the one with the lowest productivity today, and paleoproductivity estimations ranging between 40 and 50 g C m<sup>-2</sup>a<sup>-1</sup> (Rühlemann et al., 1996) indicate that productivity did not change considerably in the Late Quaternary. This is also reflected by the coccolithophore assemblage composition at this site, which is in general dominated by high abundances of *Florisphaera profunda*, an indicator for reduced surface water productivity (Kinkel et al. in press.). In contrast, the sites in the southeastern Atlantic show substantial higher modern productivity (e.g. Berger, 1989) and paleoproductivity values were substantially increased due to orbital forced variations in upwelling intensity (Schneider et al., 1996, Kirst et al. in press.), as documented in highest TOC values (see Fig. 2). However, there are obvious differences in the coccolithophore-, alkenone- and TOC- record between the two cores from this area. All three parameters in core GeoB 1028-5 at the Walvis Ridge show lower values, compared to core GeoB 1710-3 at the Namibia Continental Margin, which can be explained by the more offshore position and the diminishing effect of coastal upwelling. In comparison, the western tropical Atlantic site has similar coccosphere numbers as the site at the Walvis Ridge, but much lower TOC values and alkenone concentrations. The typical enhanced TOC values during the last glacial in the southeastern Atlantic are not reflected by the alkenone concentrations, which remain low during most of MIS 2-4. Moreover the decline in alkenone concentrations in cores GeoB 1028 and 1710 from the last interglacial (MIS 5) to the last glacial (MIS 2-4) is opposite to the trend of increasing TOC values in the same period. Elevated alkenone concentrations are found in MIS 5 and 6, although TOC values are low in all sites during MIS 5 and a covariation between carbon-normalized alkenone concentrations and TOC can only be observed in MIS 6.

There is strong evidence that alkenone concentrations are severely influenced by postdepositional degradation (Prahl et al., 1989; Flügge, 1997; Villanueva et al., 1997; Hoefs et al., 1998), depending on the flux of TOC to the seafloor, oxic respiration of TOC at the sediment water interface, and early diagenesis. The investigated cores were retrieved from totally different depositional regimes. At the tropical Atlantic site (GeoB 1523-1) TOC fluxes are low (Rühlemann et al., 1996) and reddish sediment colors due to Fe-hydroxides (Schulz et al., 1992) indicate full oxic conditions throughout the entire core, leading to a readily degradation of TOC. Nevertheless there is significant variation in the alkenone concentrations with time at this site, indicating a change in the production rate of alkenones. At the Namibia Margin TOC fluxes are significantly higher due to wind induced upwelling and enhanced primary productivity. Preservation of TOC in sediments of continental margins is generally improved not only due to higher fluxes, but also by higher sedimentation rates (Müller and Suess, 1979), which reduce the residence time of organic carbon at the sediment-water

interface, where the remineralization of organic matter is most intense. At the Walvis Ridge we presumably encounter an intermediate position between the two other sites with respect to TOC flux and preservation.

Nevertheless we assume, that general patterns related to coccolithophore productivity should be detected in both the organic geochemical as well as the micropaleontological record and only become biased by vast changes in calcium carbonate and organic carbon sedimentation. Despite the great differences regarding TOC fluxes and preservation, all sites show similar trends in alkenone concentrations over the past 250 kyrs, which most likely can be explained with similar changes in coccosphere numbers of *E. huxleyi* and *Gephyrocapsa* spp. in the same period.

The synchronous increase of alkenone concentrations in sediments older than MIS 4 is an obvious, but not well understood phenomena that occurs also in other sediment cores from the South Atlantic, so far investigated (Schneider et al., 1996; Müller et al., 1997). Similar distribution patterns of alkenones were reported for the upwelling area off northwest Africa (Martinez et al. 1996). Up to now, the typical procedure of counting and calculating coccoliths and comparing them with the alkenone record (Summerhayes et al., 1995; Jordan et al., 1996; Baumann et al., in press) provided results that can only be interpreted in terms of changing coccolithophore ecology due to SST variations, as revealed by alkenone-derived SST's. The only comparison between coccolith counts and alkenone concentrations carried out so far by (Müller et al., 1997) lead to the conclusion that coccolithophores of the genus *Gephyrocapsa* are the predominant alkenone contributors to Late Quaternary sediments on the Walvis Ridge. This is in general based on the positive correlation between the carbon-normalized alkenone concentration and the relative abundance of *Gephyrocapsa* spp. coccoliths. A weaker, but still significant, correlation between the carbon-normalized alkenone concentration and the numbers/g dry sediment of *Gephyrocapsa* spp. was reported as well. We extended the approach of Müller et al. (1997) by investigating two additional cores from totally different environments. We focused on the absolute abundance of coccospheres/g dry sediment of the alkenone producing species, since it is obvious, that the relative abundance of coccoliths is influenced by various other factors not related to alkenone production. Sediments from tropical oceans for example, are often characterized by high relative abundances (more than 50%) of the deep living coccolithophore species *F. profunda*. Moreover, the relative abundance of a species is not necessarily coupled to its absolute number, but rather reflects the ecology of coccolithophores.

However, there seems to be a change in the sedimentation of both organic and inorganic compounds of coccolithophores, during the Late Quaternary. We conclude that coccolithophores contribute much less to the organic carbon flux today and during the Holocene, than in sediments predating the MIS stage 4/5 boundary, which is in good

agreement with our coccosphere counts. It is not clear, whether this is due to higher coccolithophore productivity or different sedimentation mechanisms. Higher productivity of coccolithophores suggest that there has been a change in the contribution of this group to gross overall phytoplankton productivity. The only places where living *Gephyrocapsa* are reported to occur in high numbers today, are coastal and open ocean upwelling regions ( e.g. Mitchel-Innes and Winter, 1987, Kleijne et al. 1989), indicating that this species can react to higher nutrient supply with higher production rates, even outcompeting *E. huxleyi*, which is also present in the same water masses, but seems to have a somewhat lower affinity to higher nutrient levels (Kinkel et al., in press). We therefore suggest that during times, when species of the genus *Gephyrocapsa* dominated the coccolithophore assemblages, they were more productive compared to modern, *E. huxleyi* dominated, assemblages, which is reflected in both coccosphere numbers and alkenone concentrations.

### Conclusions

A significant change in numbers of coccosphere units of the long-chain alkenone producing species *Emiliana huxleyi* and *Gephyrocapsa* spp. and long-chain alkenone concentrations was observed in three sediment cores from the South Atlantic was observed to occur around 70 ka.

We relate the observed pattern to a change in coccolithophore production or sedimentation pattern, which is more or less related to the dominance of certain coccolithophore species, although the faunal turnover pattern occurs much later. The observation of higher productivity of *Gephyrocapsa* is in accordance to previous studies, and is improved here by quantitative determination of coccolith counts and their transformation to coccosphere units.

Although we do not know which of the above-mentioned processes caused the observed long term pattern in the Late Quaternary, an increase in coccolithophore production and or sedimentation would have strong implications on biogeochemical cycles and the interpretation of past productivity or sedimentation records (e.g. Villanueva et al., 1997; Schubert et al., 1998).

Since there is a lot of information about the production, and sedimentation of coccoliths and biomarkers in *Emiliana huxleyi*, future studies should focus on species of the *Gephyrocapsa*, since they have dominated the fossil coccolithophore record for most of the past 1.3 Ma (Gartner, 1988; Bollmann et al., 1998).

*Acknowledgements:*

We thank the crew and scientists on board the "R.V. Meteor" for their help during coring and sampling operations, Claudia Wienberg for preparing coccolith samples and Hella Buschhoff and Ralph Kreutz for careful gaschromatographic analyses. Alkenone data for cores GeoB 1028-5 and GeoB 1710-3 were kindly provided by Götz Ruhland and Isabel von Storch.

This research was funded by the Deutsche Forschungsgemeinschaft (Sonderforschungsbereich 261 at Bremen University, SFB Contribution No.XXX).

References:

- Backman, J. and Shackleton, N. J., 1983. Quantitative Biochronology of Pliocene and Early Pleistocene calcareous nannofossils from the Atlantic, Indian and Pacific Ocean. *Mar. Micropaleontol.* 8, 141-170.
- Baumann, K.-H., Cepek, M. and Kinkel, H., in press. Coccolithophores as indicators of ocean water masses, surface water temperature, and paleoproductivity. In: G. Fischer and G. Wefer (Eds), *Use of Proxies in Paleoceanography - Examples from the South Atlantic*. Springer, Berlin, Heidelberg, pp
- Bollmann, J., Baumann, K.-H. and Thierstein, H. R., 1998. Global dominance of *Gephyrocapsa* coccoliths in the late Pleistocene: Selective dissolution, evolution, or global environmental change? *Paleoceanography* 13, 517-529.
- Boon, J. J., van der Meer, F. W., Schuyl, P. J. W., de Leeuw, J. W., Schenk, P. A. and Burlingame, A. L., 1978. Organic geochemical analysis of core samples from site 362, Walvis Ridge, DSDP Leg 40 In: (Eds), *Initial Reports of the Deep Sea Drilling Project*, Washington, D.C., pp 627-637.
- Brown, C. W. and Yoder, J. A., 1994. Coccolithophorid blooms in the global ocean. *J. Geophys. Res.* 99, 7467-7482.
- Dittert, N., Baumann, K.-H., Bickert, T., Henrich, R., Huber, R., Kinkel, H. and Meggers, H., in press. Carbonate dissolution in the deep sea: Methods, Quantification and Paleoceanographic Application In: G. Fischer and G. Wefer (Eds), *Use of Proxies in Paleoceanography: Examples from the South Atlantic*. Springer, Berlin, Heidelberg, pp
- Gartner, S., 1988. Paleoceanography of the Mid-Pleistocene. *Mar. Micropaleontol.* 13, 23-46.
- Geitzenauer, K. R., Roche, M. B. and McIntyre, A., 1977. Coccolith Biogeography from North Atlantic and Pacific Surface Sediments In: A. T. S. Ramsay (Eds), *Oceanic Micropalaeontology*. Academic Press, London, pp 973-1008.

- Giraudeau, J., 1992. Coccolith paleotemperature and paleosalinity estimates in the Caribbean Sea for the Middle -Late Pleistocene (DSDP leg 68 - Hole 502B). *Memorie di Scienze Geologiche* 43, 375 - 387.
- Giraudeau, J. and Bailey, G. W., 1995. Spatial dynamics of coccolithophore communities during an upwelling event in the Southern Benguela system. *Cont. Shelf Res.* 15, 1825-1852.
- Holligan, P. M., Fernández, E., Aiken, J., Balch, W. M., Boyd, P., Burkill, P. H., Finch, M., Groom, S. B., Malin, G., Muller, K., Purdie, D. A., Robinson, C., Trees, C. C., Turner, S. M. and van der Waal, P., 1993. A biogeochemical study of the coccolithophore *Emiliana huxleyi* in the North Atlantic. *Global Biogeochem. Cycles* 7, 879 - 900.
- Kennedy, J. A. and Brassell, S. C., 1992. Molecular records of the Santa Barbara basin: comparison with historical records of annual climate change. *Org. Geochem.* 19, 235-244.
- Kinkel, H., Baumann, K.-H. and Cepek, M., in press. Living and Late Quaternary coccolithophores from the equatorial Atlantic: response to surface water productivity. *Mar. Micropaleontol.*
- Kirst, G. J., Müller, P. J., Schneider, R. R., von Storch, I. and Wefer, G. R. s., in press. Late Quaternary temperature variability in the Benguela Current system derived from alkenones. *Quat. Res.*
- McIntyre, A. and Bé, A., 1967. Modern Coccolithophoridae in the Atlantic Ocean. I. Placoliths and cyrtholiths. *Deep-Sea-Res.* 14, 561-597.
- Molfino, B., Kipp, N. G. and Morley, J. J., 1982. Comparison of Foraminiferal, Coccolithophorid and Radiolarian Paleotemperature Equations: Assemblage Coherency and Estimate Concordancy. *Quat. Res.* 17, 279 -313.
- Müller, P. M., Kirst, G., Ruhland, G., von Storch, I. and Rosell-Melé, A., 1998. Calibration of the alkenone paleotemperature index UK<sub>37</sub> based on core-tops from the eastern South Atlantic the global ocean (60°N-60°S). *Geochim. Cosmochim. Acta* 62, 1757-1772.
- Prahl, F. G. and Wakeham, S. G., 1987. Calibration of unsaturation patterns in long-chain ketone compositions for paleotemperature assessment. *Nature* 330, 367-369.
- Pujos, A., 1992. Calcareous nannofossils of Plio-Pleistocene sediments from the northwestern margin of tropical Africa In: C. P. Summerhayes, W. L. Prell and K. C. Emeis (Eds), *Upwelling Systems: Evolution since the Early Miocene*. 64. Geological Society, Avon, pp 343-358.
- Rosell-Melé, A., Eglinton, G., Pflaumann, U. and Sarnthein, M., 1995. Atlantic core-top calibration of the U<sup>K</sup><sub>37</sub> index as a sea-surface palaeotemperature indicator. *Geochim. Cosmochim. Acta* 59, 3099-3107.
- Rostek, F., Ruhland, G., Bassinot, F. C., Müller, P. J., Labeyrie, L. D., Lancelot., Y. and Bard, E., 1993. Reconstructing Indian Ocean sea surface temperatures and salinity using  $\delta^{18}\text{O}$  and alkenone records. *Nature* 364, 319-321.
- Roth, P., 1994. Distribution of coccoliths in oceanic sediments. In: A. Winter and W. G. Siesser (Eds), *Coccolithophores*. Cambridge University Press, Cambridge, pp 199-218.

- Samtleben, C., Schaefer, P., Andrulleit, H., Baumann, A., Baumann, K.-H., Kohly, A., Matthiessen, J. and Schroeder-Ritzrau, A., 1995. Plankton in the Norwegian-Greenland Sea: From Living communities to Sediment Assemblages - an actualistic approach. *Geol. Rundsch.* 84, 108 - 136.
- Schneider, R. R., Müller, P. J., Ruhland, G., Meinecke, G., Schmidt, H. and Wefer, G., 1996. Late Quaternary surface temperatures and productivity in the east-equatorial South Atlantic: response to changes in Trade / Monsoon wind forcing and surface water advection. In: G. Wefer, W. H. Berger, G. Siedler and D. Webb (Eds), *The South Atlantic: Present and Past Circulation..* Springer, Berlin, pp 527-551.
- Schubert, C. J., Villanueva, J., Calvert, S. E., Cowie, G. L., von Rad, U., Schulz, H., Berner, U. and Erlenkeuser, H., 1998. Stable phytoplankton community structure in the Arabian Sea over the past 200,000 years. *Nature* 394, 563-566.
- Thierstein, H. R., Geitzenauer, K. R., Molino, B. and Shackleton, N. J., 1977. Global synchronicity of late Quaternary coccolith datum levels: Validation by oxygen isotopes. *Geology* 5, 400-404.
- Villanueva, J., Grimalt, J. O., Cortijo, E., Vidal, L. and Labeyrie, L., 1997. A biomarker approach to the organic matter deposited in the North Atlantic during the last climatic cycle. *Geochim. Cosmochim. Acta* 61, 4633-4646.
- Wei, W., 1993. Calibration of Upper Pliocene - Lower Pleistocene nannofossil events with oxygen isotope stratigraphy. *Paleoceanography* 8, 85-99.
- Westbroek, P., Brown, C. W., van Bleijswijk, J., Brownlee, C., Brummer, G. J., Conte, M., Egge, J., Fernández, E., Jordan, R., Knappertsbusch, M., Stefels, J., Veldhuis, M., van der Waal, P. and Young, J. R., 1993. A model system approach to biological climate forcing. The example of *Emiliana huxleyi*. *Global and Planetary Change* 8, 27-46.

## Conclusions and Perspective

The results of this study showed, that the major oceanographic features in the equatorial Atlantic influence the living coccolithophore communities and these signals are documented in fossil coccolith sediment assemblages. Although coccolithophores are a major component in the phytoplankton assemblages in surface waters of the equatorial Atlantic, there is surprisingly little quantitative information is available from this region.

Coccolithophores are often misinterpreted, since most textbooks state that “coccolithophores dominate the low productive tropical areas of the oceans”, and thus they are often considered as indicators for low productivity. Indeed some coccolithophore species are adapted to low nutrient conditions of the oligotrophic areas where they constitute a large part of the phytoplankton assemblages. However it is evident, and has been shown in this study, that a number of coccolithophores react well to increased nutrient levels by enhanced growth rates. Once nutrient level exceed a certain threshold value these species do not only dominate the assemblages, but they are produced in such large amounts, that the fossil assemblages underlying these areas show increased accumulation rates of this species as well.

### Living assemblages

The distribution of living assemblages clearly reflects the changing nutrient regimes that are associated with the atmospheric and oceanic current regimes of the equatorial region. Higher nutrient concentrations, in equatorial Atlantic almost exclusively associated with upwelling during boreal summer, are indicated in a sharp rise in the total standing stock of coccolithophores the upper photic zone and a change in the living assemblage composition from a dominance oligotrophic species *Umbellosphaera tenuis* and *Umbellosphaera irregularis*, to a dominance of *Emiliania huxleyi*. The lower photic zone is always dominated by the deep dwelling species *Florisphaera profunda* and *Gladiolithus flabellatus*, which appear to be adapted to high nutrient and low light environments.

Future studies should focus on the exact environmental conditions that determine coccolithophore growth in the equatorial region, e.g. nutrient conditions. Furthermore sediment traps studies should be carried out to monitor the duration of enhanced coccolithophore production and the magnitude of the associated carbonate and organic carbon fluxes.

## Surface sediments:

The seasonal pattern observed in the water column is transformed whilst settling through the water column and by early diagenetic processes, both in the water column and at the water sediment interface. The strong decrease in the relative abundance of the oligotrophic species *Umbellosphaera tenuis* and *Umbellosphaera irregularis* in the surface sediment compared to their dominant role in the living assemblages in the oligotrophic areas, is obvious. However, the main features observed in the water column were still recognizable in the surface sediments. This was possible due to the presence of the lower photic zone assemblage (*Florisphaera profunda* and *Gladiolithus flabellatus*), which is well preserved in the sediments and dominates the sediment in the oligotrophic regions. In contrast, areas beneath increased productivity are in general characterised by higher abundance of *Emiliania huxleyi* and *Calcidiscus leptoporus*.

It would be desirable if absolute accumulation rates for surface sediments, e.g. by using radionuclide techniques, were accessible, in order to determine the fate of calcium carbonate and organic matter production by coccolithophores. This could improve qualitative carbonate dissolution proxies as presented in Part II.4 (Dittert et al. 1999) and contribute to the efforts in calculating the carbonate budget of the ocean and its temporal changes.

The above summarized observations enabled us to use fossil coccolithophore assemblages to study the upper photic zone dynamics and resulting productivity changes in the equatorial Atlantic during the Late Quaternary. The most striking feature in the paleorecord of coccolithophores the Equatorial Atlantic are the huge fluctuations in coccolith accumulation rates in the southequatorial site (GeoB 1117-2). The increase in coccolith accumulation rates can be attributed to a shoaling of the thermocline and nutricline, indicated by a decrease in the relative abundance of *Florisphaera profunda*, which goes along with an intensification and extension of the upwelling area. This is corroborated by the relative abundance of tropical planktonic foraminifera assemblage which shows the same cyclic pattern as the abundance of *Florisphaera profunda*. The underlying mechanisms in the cyclic patterns observed in the warm tropical foraminifera assemblage and the abundance of *Florisphaera profunda* is the interaction between the monsoon and trade wind intensity in the equatorial Atlantic, with stronger monsoon leading to a deeper thermocline and nutricline and stronger trade winds to the exact opposite scenario. Therefore the covariation of the *Florisphaera profunda* signal with the insolation at 15° north, that is almost exclusively forced by the precessional cycle of the earth orbital parameters, is not surprising. The use of coccolith accumulation rates has improved previous ecological concepts of thermocline and nutricline dynamics, that were solely based on coccolith census counts (e.g. Molino and McIntyre, 1990, Beaufort et al. 1997). Although surface water current variability was more pronounced in the equatorial Atlantic, even small changes, as they are characteristic for

---

the oligotrophic western tropical Atlantic site (GeoB 1523) could be recognized in both, coccolith accumulation rates and floral composition. Both Late Quaternary records could be embedded in a number of other proxy parameters (planktic foraminiferas, carbonate and organic carbon mass accumulation rates), that confirm the trend observed in the coccolithophore record.

It appears likely, that changes in the paleoproductivity of the equatorial Atlantic significantly contributed to the draw down of atmospheric  $p\text{CO}_2$ , which is recorded in air bubbles of ice cores from Antarctica (e.g. Birch et al. 1999). The use of coccolith accumulation rates indicates that indeed the primary productivity was largely increased during most of marine isotope stage 3 and 2. However further studies need to verify the timing of enhanced upwelling intensity as well as the spatial spreading of the upwelling area. In addition one has to keep in mind, that coccolithophores are not the only organism group, that contributes to primary productivity. Indeed, the accumulation record of diatoms from a sediment core in the eastern equatorial Atlantic shows prominent peaks in diatom accumulation rates during oxygen isotope stage 4 (Abrantes et al. 1994), when coccolith accumulation rates were low in the southern Equatorial Atlantic. A similar picture as the diatom accumulation has been shown for organic dinoflagellate cysts with prominent peak during oxygen isotope stages 2, 4 and 6 (Höll et al., 1998). Thus it is likely, that changes in the phytoplankton species succession, as observed on a seasonal basis in the modern ocean can although occur on longer time scales, during the build up and decline of a productivity cycle in the equatorial Atlantic.

In contrast to the coccolithophore accumulation rates, other main calcareous plankton groups, foraminifera and calcareous dinoflagellates, show a accumulation pattern with enhanced accumulation during low production phases (see Chapter II and Höll et al. 1998). Thus one has to be cautious, using carbonate accumulation rates as a proxy for productivity in this region.

A growing number of paleoceanographic studies use the alkenone unsaturation index ( $U_{37}^k$ ) for sea surface temperature (SST) reconstructions and the carbon isotopic composition of this coccolithophore derived biomarker to calculate paleo –  $p\text{CO}_2$  values. This clearly emphasizes, that more integrated studies, like the one presented in Chapter II.5, combining micropaleontological and organic geochemical approaches to coccolithophores, are needed.

The use of the  $U_{37}^k$  does not seem to be influenced by changing species composition e.g. Müller et al. 1998), however for the paleo  $p\text{CO}_2$  reconstructions which are influenced by cell geometry, calcification rates and growth rates, knowledge of the coccolithophore assemblages composition may be essential.

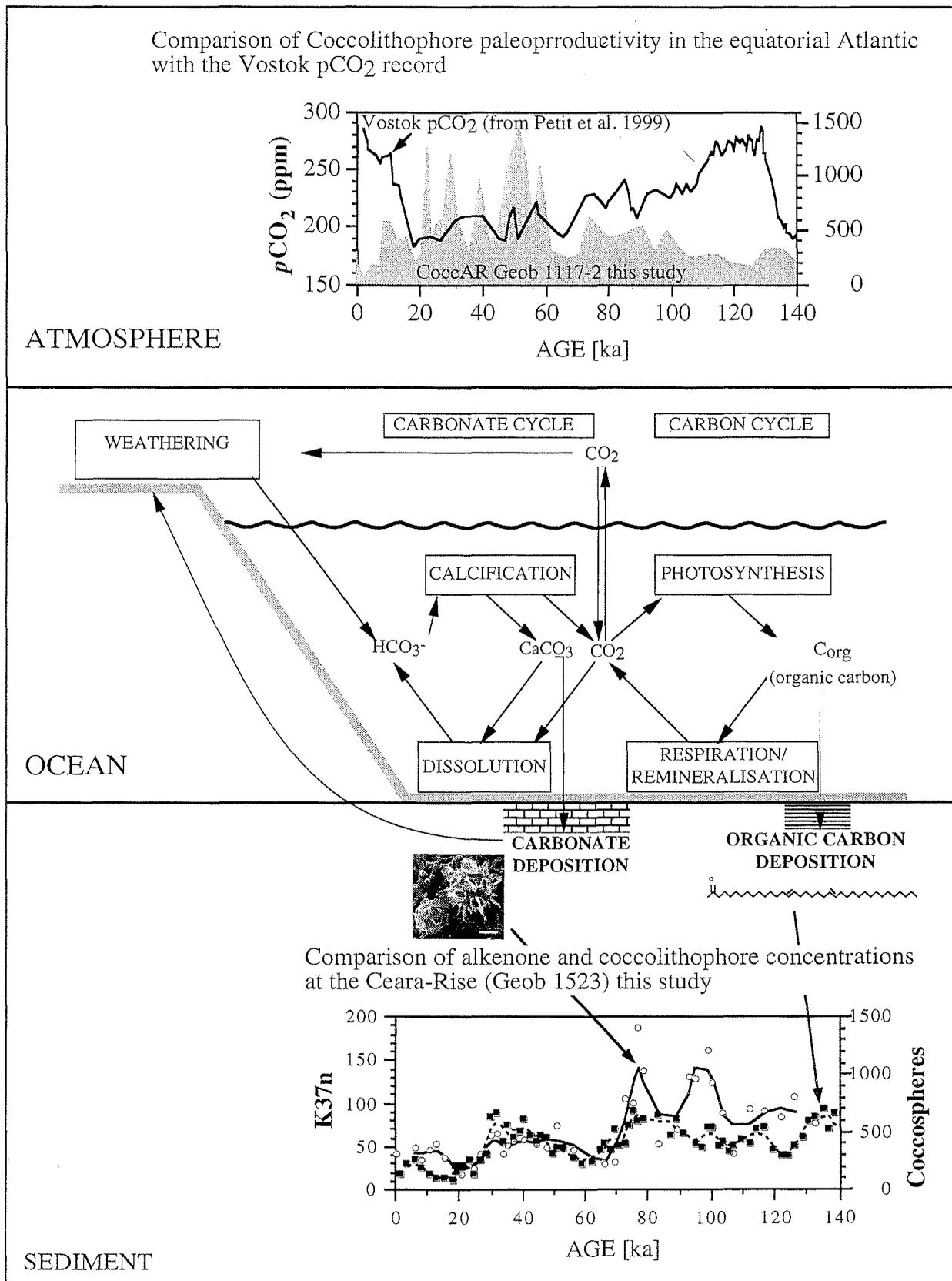


Figure III.1 Summary of the possible role that coccolithophores in the global carbonate and carbon cycling.

In figure III.1 I have summarized the possible effects of coccolithophore on the biogeochemical carbonate and carbonate cycles in the atmosphere, ocean and in sediments. In the future we must make stronger efforts to quantify these processes, by improving existing proxy parameter, and development of new methods. These would include the stable carbon and oxygen isotope and trace metal composition of coccolithophore carbonate, the biometric investigation of coccoliths as well as more detailed organic biomarker studies.

In summary it can be stated, that the use of coccolithophores for tracing present and past changes in the equatorial Atlantic surface water circulation, has been a successful approach, especially since it provides insight into the productivity changes in one of the major phytoplankton groups in the ocean.

### References

- Abrantes, F., Winn, K., Sarnthein, M., 1994. Late Quaternary paleoproductivity variations in the NE and equatorial Atlantic: diatom and Corg evidence. In: Zahn, R., Pedersen, T.F., Kaminski, M.A., Labeyrie, L. (Eds.). *Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Change*. NATO ASI Series, Springer, Berlin, pp. 425-441
- Beaufort, L., Lancelot, Y., Camberlin, P., Cayre, O., Vincent, E., Bassinot, F. and Labeyrie, L., 1997. Insolation cycles as a major control of equatorial Indian Ocean primary production. *Science* 278, 1451-1454.
- Dittert, N., Baumann, K.-H., Bickert, T., Henrich, R., Huber, R., Kinkel, and H., Meggers, 1999. Carbonate dissolution in the deep sea: methods, quantification and paleoceanographic application. In G. Fischer & G. Wefer (Eds.), *Proxies in paleoceanography*; Berlin Heidelberg: Springer. pp 255-284.
- Molffino, B. and McIntyre, A., 1990a. Precessional Forcing of Nutricline Dynamics in the Equatorial Atlantic. *Science* 249, 766-769.
- Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola J-M, Basile I, Bender M, Chappellaz J, Davis M, Delaygue G, Delmotte M, Kotlyakov VM, Legrand M, Lipenkov VY, Lorius C, Pepin L, Ritz C, Saltzman E, Stievenard M. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399:429-36

**Taxonomy:**

In general the classification scheme of Jordan and Kleijne (1994) was applied. Since this study did not focus on taxonomy or diversity among coccolithophorids, only the species that were mentioned within the text will be listed. It has to be mentioned, that the coccolithophore flora in the tropical Atlantic is extremely diverse and a vast number of species were observed in both, water and sediment samples. However it is obvious, that most samples are dominated by those few species listed below and the majority of species have a random occurrence or are present in such low numbers and abundance, that they were useless for ecological or paleoceanographic interpretation.

Kingdom: Protista Haeckel (1866)

Class: Prymnesiophyceae Hibberd (1976)

Family: **Noelrhabdaceae** Jerkovic (1970)

Genus: *Emiliana* Hay et Mohler in Hay et al. (1967)

*Emiliana huxleyi* (Lohmann, 1902) Hay & Mohler (1967).

(Plate I, 1 and 2)

Genus: *Gephyrocapsa* Kamptner (1943)

*Gephyrocapsa ericsonii* McIntyre & Bé (1967)

(Plate I, 3 and 4)

*Gephyrocapsa muellerae* Bréhéret (1978)

*Gephyrocapsa oceanica* Kamptner (1943)

(Plate I, 5 and 6)

Family: **COCCOLITHACEAE** Poche (1913)

Genus: *Calcidiscus* Kamptner, 1950

*Calcidiscus leptoporus* (Murray & Blackman, 1898) Loeblich & Tappan (1978)

(Plate II, 1 and 2)

Genus: **Umbilicosphaera** Lohmann, 1902

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

(Plate II, 3, 4, 5 and 6)

**Genera Incertae Sedis**

Genus: *Umbellosphaera* Paasche, in Markali and Paasche (1955)

*Umbellosphaera irregularis* Paasche, in Markali and Paasche (1955)

*Umbellosphaera tenuis* (Kamptner, 1937) Paasche, in Markali and Paasche (1955)

(Plate III, 5 and 6)

---

Genus: *Florisphaera* Okada & Honjo (1973)

*Florisphaera profunda* Okada and Honjo (1973)

(Plate III, 1 and 2)

Genus: *Gladiolithus* Jordan and Chamberlain (1993)

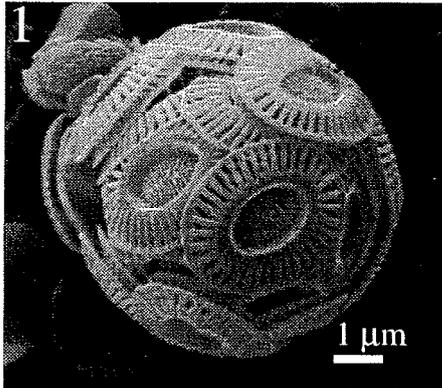
*Gladiolithus flabellatus* (Halldal and Markali) Jordan and Chamberlain (1993)

(Plate III, 3 and 4)

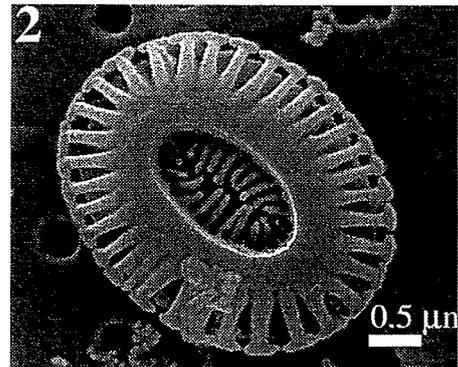
#### References:

- Bréhéret, J., 1978. Formes nouvelles quaternaires et actuelles de la famille Gephyrocapsaceae (Coccolithophorides). C.r. hebdomadaire de l'Académie des Sciences, Paris 287, 447-449.
- Gaarder, K. R., 1970. Three new taxa of Coccolithinae. Nytt. Mag. Bot 17, 113-126.
- Halldal, P. and Markali, J., 1954. Observations on coccoliths of *Syracosphaera mediterranea* Lohm. and *S. molischii* Schill. in the electron microscope. J. Cons. perm. Internat. Expl. Mer. 19, 329-336.
- Hibberd, D. J., 1976. Prymnesiophytes (=Haptophytes) In: E. R. Cox (Eds), Phytoflagellates. Elsevier, Amsterdam, pp 273-318.
- Jerkovic, L., 1970. Noelaerhabdus nov. gen. type d'une nouvelle famille de Coccolithophoridés fossiles: Noelaerhabdaceae du Miocène supérieur de Yougoslavie. C.r. hebdomadaire de l'Académie des Sciences, Paris 270, 468-470.
- Jordan, R. W. and Green, J. C., 1994. A checklist of the extant Haptophyta of the world. J. mar. biol. Ass. UK. 74, 149-174.
- Jordan, R. W. and Kleijne, A., 1994. A classification system for living coccolithophores In: A. a. S. Winter W.G. (Eds), Coccolithophores. Cambridge University Press, Cambridge, pp 83-106.
- Loeblich, A. R. J. and Tappan, H., 1978. The coccolithophorid genus *Calcidiscus* Kamptner and its synonyms. J. Paleontol. 52, 1390-1392.
- Lohmann, H., 1902. Die Coccolithophoridae. Arch. Protistenk. 1, 89-165.
- Markali, J. and Paasche, E., 1955. On two species of *Umbellosphaera*, a new marine coccolithophorid genus. Nytt. Mag. Bot. 4, 95-100.
- McIntyre, A. and Bé, A., 1967. Modern Coccolithophoridae in the Atlantic Ocean. I. Placoliths and cyrtholiths. Deep-Sea-Res. 14, 561-597.
- Okada, H. and Honjo, S., 1973. The distribution of oceanic coccolithophorids in the Pacific. Deep-Sea-Res. 20, 355-374.
- Poche, F., 1913. Das System der Proterozoa. Arch. Protistenk. 30, 136-160.
- Weber - Van Bosse, A., 1901. Études sur les algues de l'Archipel Malaisien III: Note préliminaire sur les résultats algologiques de l'expédition du Siboga. Jard. Bot. Buitenz., Ann. 17, 126-141.

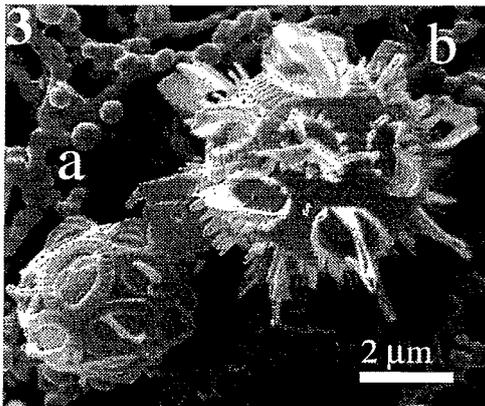
Plate I



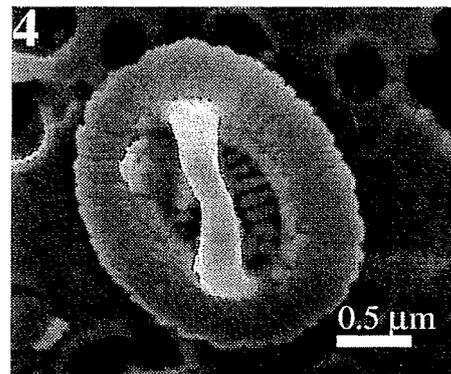
*Emiliana huxleyi*  
coccosphere



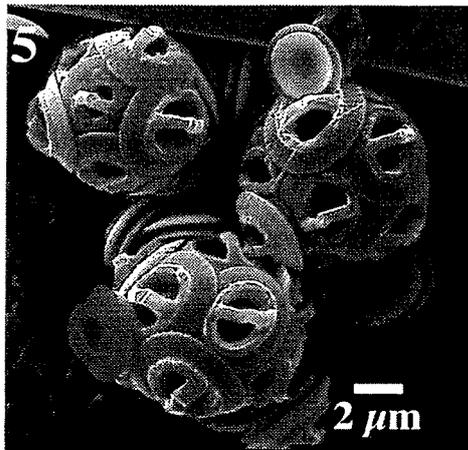
*Emiliana huxleyi*  
coccolith, distal view



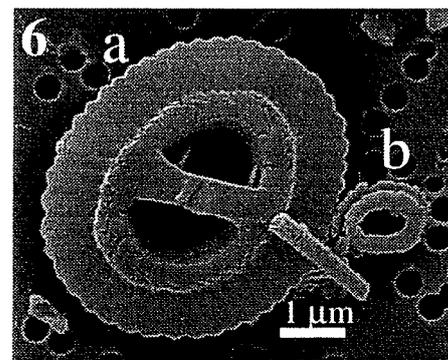
*Gephyrocapsa ericsonii* (a) and  
*Gephyrocapsa ornata* (b), coccospheres



*Gephyrocapsa ericsonii*  
coccolith distal view

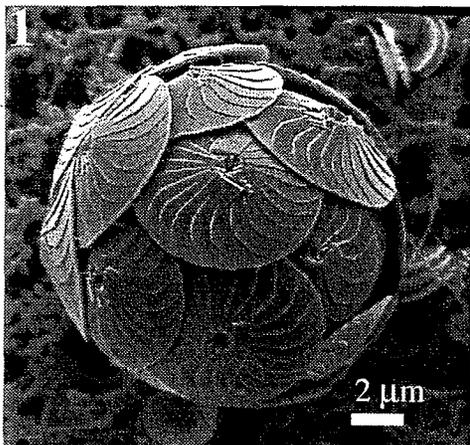


*Gephyrocapsa oceanica* coccospheres

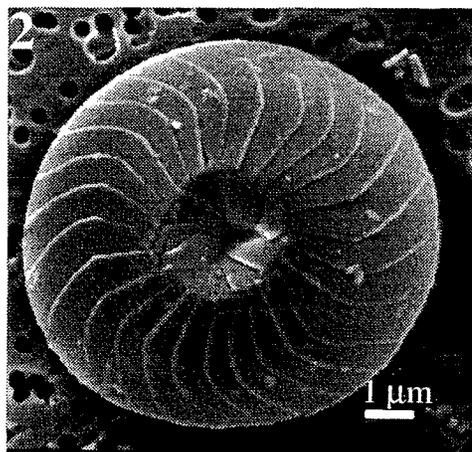


*Gephyrocapsa oceanica* (a) coccolith  
distal view, *Gephyrocapsa* spp. small (b)  
coccolith proximal view

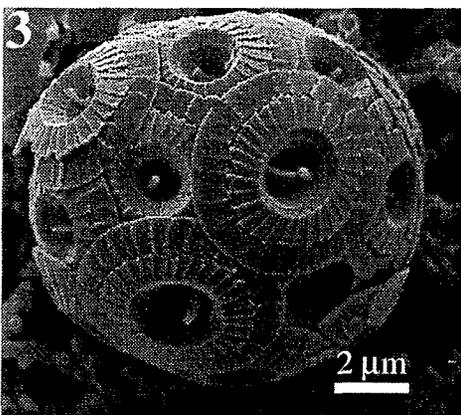
Plate II



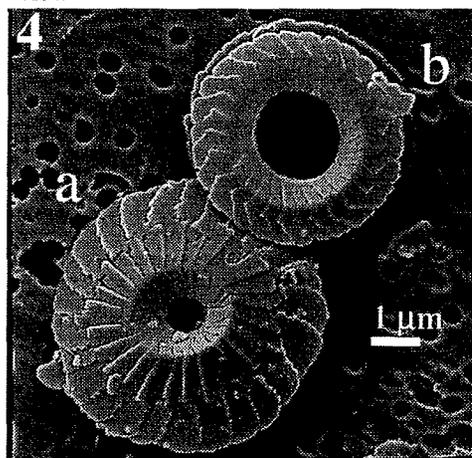
*Calcidiscus leptoporus*, coccosphere



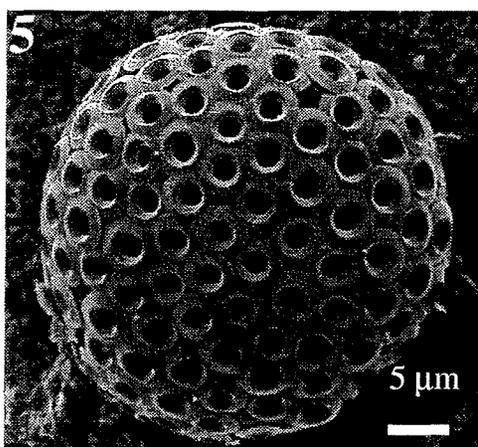
*Calcidiscus leptoporus*, coccolith distal view



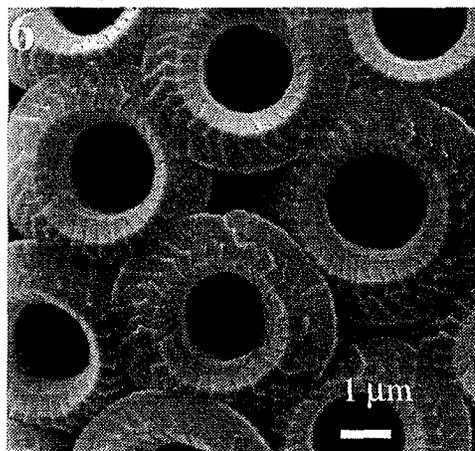
*Umbilicosphaera sibogae* var. *foliosa*, coccosphere



*Umbilicosphaera sibogae* var. *foliosa* (a), *U. sibogae* (b), coccoliths distal view

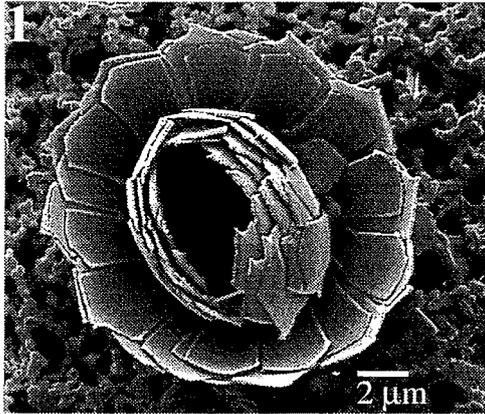


*Umbilicosphaera sibogae* var. *sibogae*, coccosphere

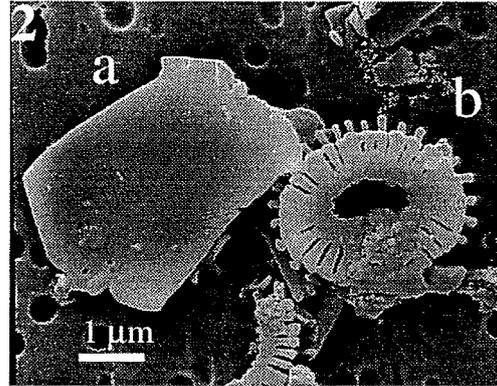


*Umbilicosphaera sibogae* var. *foliosa*, detail from 5

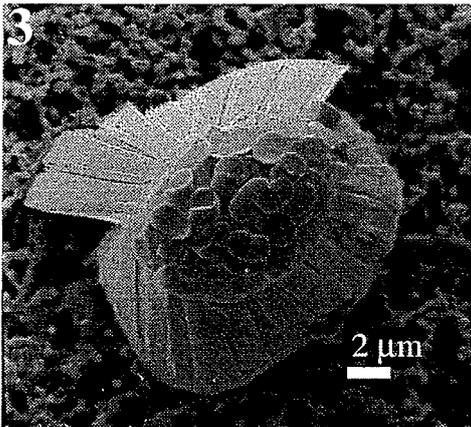
Plate III



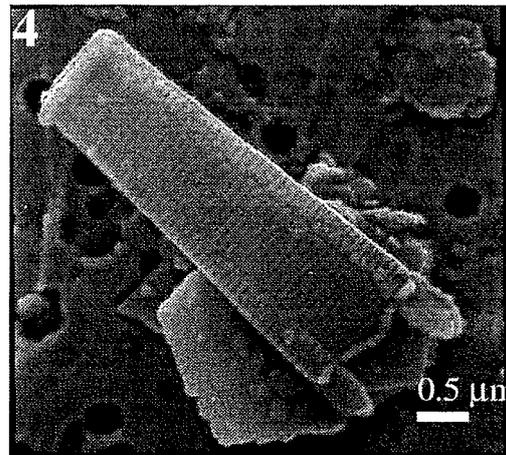
*Florisphaera profunda*, coccosphere



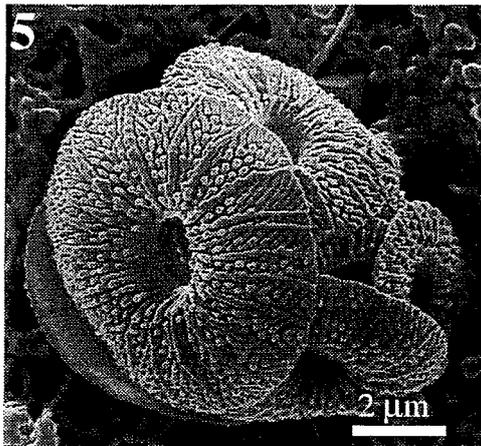
*Florisphaera profunda* (a) coccolith, *Emiliana huxleyi* (b) coccolith proximal view



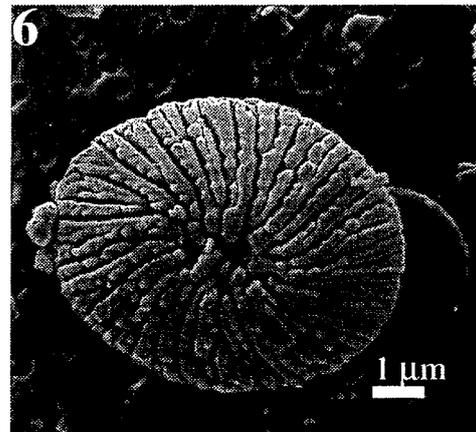
*Gladiolithus flabellatus*, coccosphere



*Gladiolithus flabellatus*, coccolith



*Umbellosphaera tenuis*, coccosphere



*Umbellosphaera tenuis*, coccolith distal view

---

## Danksagung

Bei Herrn Prof. Dr. Rüdiger Henrich möchte ich mich für die Vergabe and Betreuung dieser Arbeit bedanken. Herrn Prof. Dr. Helmut Willems sei für die freundliche Übernahme des Zweit - Gutachtens gedankt.

Nicolas Dittert gilt mein ganz spezieller Dank für all die Jahre die wir im Büro, auf See und an manchen anderen, nicht näher definierten Orten, gemeinsam zugebracht haben. Es ist viel mehr geworden als nur eine gemeinsame Doktorarbeit und ich werde die Zeit immer in guter Erinnerung halten, pass auf die Finger auf, wer weiss wozu Du sie gebrauchen kannst.

Allen Kollegen der Arbeitsgruppe Sedimentologie - Paläozeanographie moechte ich fuer die angenehme Arbeitsatmosphäre der letzten Jahre danken. Gleiches gilt für alle Kollegen im SFB 261, die durch ihre Diskussionsbereitschaft und die freundliche Überlassung von Daten und Probenmaterial zum Gelingen dieser Arbeit beigetragen haben.

Der "Cocco - Mafia" an der Uni-Bremen, Karl-Heinz Baumann, Martin Cepek und Claudia Sprengel sei gedankt, daß sie mich nicht alleine mit den kleinen Dingen gelassen hat und unsere Zusammenarbeit und Diskussionen unkompliziert und oft genug auch lustig waren. Karl - Heinz sei besonders gedankt für endlose Geduld beim Lesen halbgarer Manuskripte, vor abfahrenden Zügen und verschlossenen Metroschranken. Bei Martin muss ich mich entschuldigen, daß ich immer noch kein korrektes "C" Schreiben kann, ich hoffe eine Krokette beruhigt Dich.

Diese ganze Arbeit wäre nicht möglich gewesen, ohne meine wunderbare Frau Petra, die während der ganzen Zeit hinter mir stand. Mit unseren Töchtern Ann-Kathrin und Jule warst und bist Du das Beste was einem bei so einer Arbeit aufmuntern kann, und ich schwöre hoch und heilig: ich schreibe nicht noch eine.

Meine Eltern möchte ich für ihre Unterstützung meines Studiums und der Ermutigung zu dieser Dissertation danken.

