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The significance of extant coccolithophores as indicators of ocean water masses, surface water temperature, and paleoproductivity: a review

KARL-HEINZ BAUMANN, Bremen; HARALD ANDRULEIT, Hannover; BABETTE BÖCKEL, Bremen; MARKUS GEISEN, Bremerhaven & HANNO KINKEL, Kiel

with 13 figures

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Abstract: Coccolithophores are one of the main groups of marine phytoplankton playing key roles in the marine ecosystem as primary producers and in marine biogeochemistry. These organisms have gained considerable attention as they play a unique role in the global carbon cycle because of their combined effects on both the organic carbon and the carbonate pump. Although steady advances in research on coccoliths as biogeochemical agents and palaeontological proxies were obtained knowledge of the biology of these organisms has only progressed considerably in recent years. It has been confirmed that holococcolithophores are not autonomous but stages in the life cycle of heterococcolithophores. A general introduction to the taxonomy and biology of extant coccolithophores is followed by a brief overview of the environmental parameters affecting these phytoplanktonic organisms and their biogeography. Another chapter summarizes the investigations on coccolithophores in the Arabian Sea which have been conducted during the past years to produce a synthesis of the production of living coccolithophores in the photic zone, their transformation to settling assemblages, their accumulation on the seafloor, and their final burial in the sediments. In the following, applications of coccolithophores to palaeoenvironmental analyses are provided as case studies. In particular, the usage of both ecologically restricted species, such as *Florisphaera profunda*, for palaeoproductivity studies and of a new coccolithophore-based palaeothermometry for surface-water reconstructions are presented. In addition, haptophyte-specific biomarkers (long-chain alkenones) are reviewed and their applicability for palaeoceanographical reconstructions is demonstrated.

Keywords: coccolithopores • phytoplankton • Recent • Quaternary • biology • ecology • paleoproxy • alkenones • carbonate producer

Kurzfassung: Coccolithophoriden, einzelliges marines Phytoplankton, stellen eine der Hauptprimärproduzenten in den Ozeanen dar. Diesen haptophyten Algen kommt als Karbonatproduzenten und photoautotrophe Organismen eine bedeutende Rolle im Kohlenstoffkreislauf zu, den sie sowohl über die Karbonat- als auch über die biologische Pumpe beeinflussen. Trotz der intensiven Fortschritte in der Bearbeitung als Träger biogeochemischer Informationen und ihrer steigenden Bedeutung als Paläoumweltindikatoren ist der Kenntnisstand über die Biologie von Coccolithophoriden erst in jüngster Zeit wesentlich erweitert worden. Es hat sich gezeigt, dass Holococcolithophoriden keine autonomen Organismen, sondern Phasen im Lebenszyklus von Heterococcolithophoriden sind. Nach einer Einführung in die Taxonomie und Biologie von Coccolithophoriden werden die Umweltparameter, die diese Phytoplanktongruppe beeinflussen, vorgestellt und ihr Vorkommen sowohl geographisch als auch ökologisch beschrieben. Das folgende Kapitel stellt beispielhaft die Bildung des geologischen Signals von Coccolithophoriden dar. Hierzu wurden Planktongemeinschaften aus dem Oberflächenwasser mit Sinkgemeinschaften aus Partikelfallen sowie den unterlagernden Oberflächensedimentgemeinschaften verglichen und bewertet. In den folgenden Fallstudien wird auf die Bedeutung von Coccolithophoriden als Paläoumweltindikatoren eingegangen. Insbesondere werden die Anwendung einzelner, ökologisch relevanter Arten, wie die in der tieferen photischen Zone lebende *Florisphaera profunda*, für Paläoproduktivitätsrekonstruktionen sowie eine neue, auf Coccolithophoridenarten basierende Rekonstruktion von Oberflächenwassertemperaturen dargestellt. In vielen paläozeanographischen Arbeiten werden Haptophyten-spezifische Biomarker (langkettige Alkenone) intensiv für Temperaturrekonstruktionen genutzt. Im Vergleich zu anderen planktischen Karbonatproduzenten zeigt sich, dass Coccolithophoriden heute und im Pleistozän einen wesentlichen Anteil am Eintrag von (anorganischen) Kohlenstoff in das geologische Archiv ausmachen.

Schlüsselwörter: Coccolithoporiden • Phytoplankton • rezent • Quartär • Biologie • Ökologie • Paläoproxy • Alkenone • Karbonatproduzenten

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Addresses of the authors: KARL-HEINZ BAUMANN and BABETTE BÖCKEL, FB Geowissenschaften, Univ. Bremen, Postfach 330440, D-28334 Bremen. – HARALD ANDRULEIT, Federal Institute for Geosciences and Natural Resources, Postfach 510153, D-30631 Hannover. – MARKUS GEISEN, Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, D-27570 Bremerhaven. – HANNO KINKEL, Institute for Geosciences, Univ. Kiel, Olshausenstr.40, D-24118 Kiel.

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Introduction

The living coccolithophores are marine, unicellular phytoplankton, belonging to the phylum Haptophyta and the division Prymnesiophyceae (JORDAN & CHAMBERLAIN 1997). Their morphology is characterised by an exoskeleton composed of numerous minute calcite platelets – the coccoliths – that are readily preserved in the sedimentary record.

Coccolithophores are one of the main groups of marine phytoplankton playing key roles in the marine ecosystem as primary producers and in marine biogeochemistry, owing to their great abundance, fast turnover rates, and their capability to carry out photosynthesis and calcification (WINTER & SIESSER 1994; BOWN 1998). They are, from a quantitative point of view, among the most important pelagic calcifying organisms in the modern ocean (BAUMANN et al. 2004; HAY 2004). The evolution of calcareous nannoplankton resulted in a major shift in the locus of global calcification from the continental shelves towards deep oceans, which fundamentally changed ocean chemistry and global sedimentation patterns. Recently, coccolithophores have gained increased attention as they play a unique role in the global carbon cycle and are peculiar because of their combined effects on both, the biological carbon and the carbonate pump. Because of their biochemical effects (dimethylsulfide – which act as a source molecule for cloud nucleation) they are likely to produce additional feedback to climate change (WESTBROEK et al. 1993).

In addition, coccoliths are phenomenally abundant in sea-floor sediments, and preserve the composition of the overlying photic-zone communities due to protected and accelerated sedimentation in faecal pellets or in marine snow. Therefore, they are valuable indicators of palaeoceanographical change. Coccolithophores have one of the most abundant fossil records of any phylum and this fossil record is continuous from their first occurrence in the Late Triassic to the present day (e.g. BOWN et al. 2004). These diverse properties have prompted intensive research on extant coccolithophores over the past decades. Within the present paper we provide a review of the state of the art of knowledge on extant coccolithophores and on their utility for palaeoenvironmental and palaeoceanographical reconstructions. An overview is presented on their biology, ecology and biogeography, of the transformation of living communities to fossil assemblages, and examples are given on their application in geological studies. In particular, the usage of species for palaeoproductivity studies and a new coccolithophore-based palaeothermometry for surface-water reconstructions are presented. In addition, haptophyte-specific biomarkers (long-chain alkenones) are reviewed and their applicability for palaeoceanographical reconstructions is demonstrated.

Biology of coccolithophores

Their long evolutionary record, high evolutionary turnover and enormous abundance in sediments have made them ideal biostratigraphical marker fossils and hence they have been widely used for dating of sediments and classical palaecological work. It was however only in the beginning of the 20th century that researchers (e.g. KAMPTNER 1927; LOHMANN 1902; MURRAY & BLACKMAN 1898) started observing and exploring the biology of the organisms. Although steady advances in research on coccoliths as biogeochemical agents and palaeontological proxies were obtained, these have not been paralleled by information in the biology of the species. Knowledge of the biology of coccolithophores has, however, progressed considerably in recent years due to increased numbers of culture studies and meticulous observations in plankton samples and are most recently reviewed and summarized by BILLARD & INOUYE (2004).

Coccolithophores include all haptophyte algae possessing calcified scales (coccoliths) at some stage in their life cycle. Following the taxonomic revision of the division Haptophyta recently proposed by EDVARDSEN et al. (2000), coccolithophores belong to the class Prymnesiophyceae, which also features non-calcifying organisms. Coccolithophores generally occur as single cells and their typical features have been previously compiled in earlier reviews (PIENAAR 1994; INOUYE 1997; BILLARD & INOUYE 2004; summarized in Fig. 1).

The taxonomy of coccolithophores is based on the morphology of the coccoliths that cover their cell. Two major groups exist, the holo- and heterococcoliths (Fig. 2), of which the heterococcolithophore stage is more common. Whereas holococcoliths are formed out of numerous, minute euhedral calcite crystallites the heterococcoliths are formed of a radial array of variably shaped crystal units (see e.g. YOUNG et al. 1992, 1997). Formation of the heterococcoliths takes place intracellularly (PIENAAR 1994; WESTBROEK et al. 1989). In contrast, biomineralization of holococcoliths appears to occur outside the cell (ROWSON et al. 1986, YOUNG et al. 1999). Within these basic categories, various terms are used by workers on living coccolithophores and based on morphological characteristics of certain taxa: cricoliths, helicoliths, etc. for heterococcoliths; calyptroliths, crystalloliths, etc. for holococcoliths (for terminology see YOUNG et al. 1997; Fig. 2). The abundance of such terms reflects the high diversity of coccolith morphology. In addition, two families of extant coccolithophores produce so-called nannoliths (Ceratolithaceae, Braarudosphaeraceae) which are anomalous calcareous structures lacking the typical features of hetero- or holococcoliths. Today the extant coccolithophore biodiversity based on the dominant diploid stage is estimated to be in the order of 200 species (YOUNG et al. 2003).

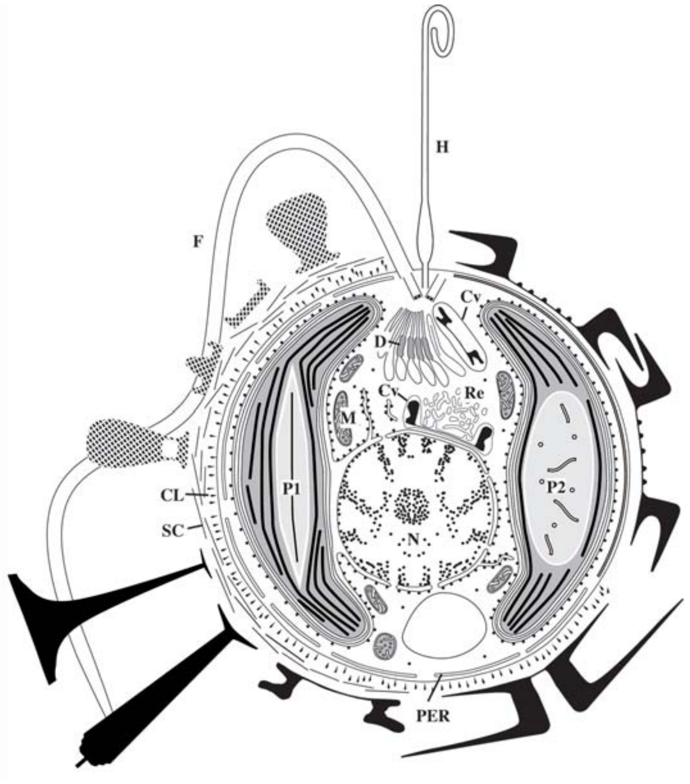
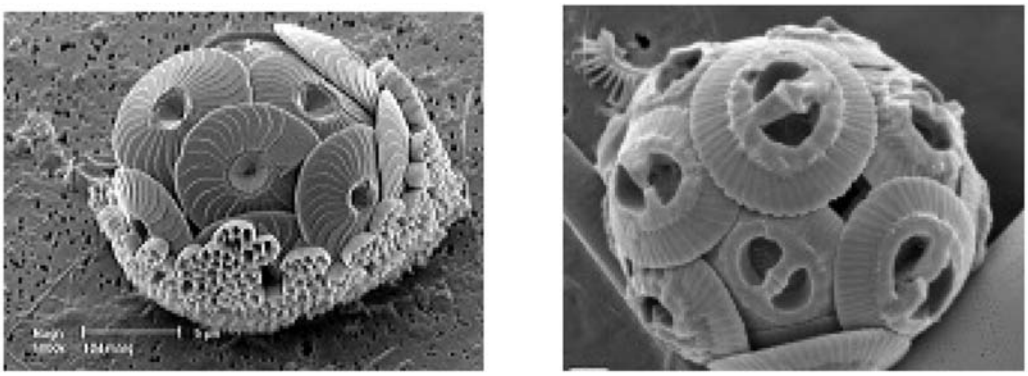
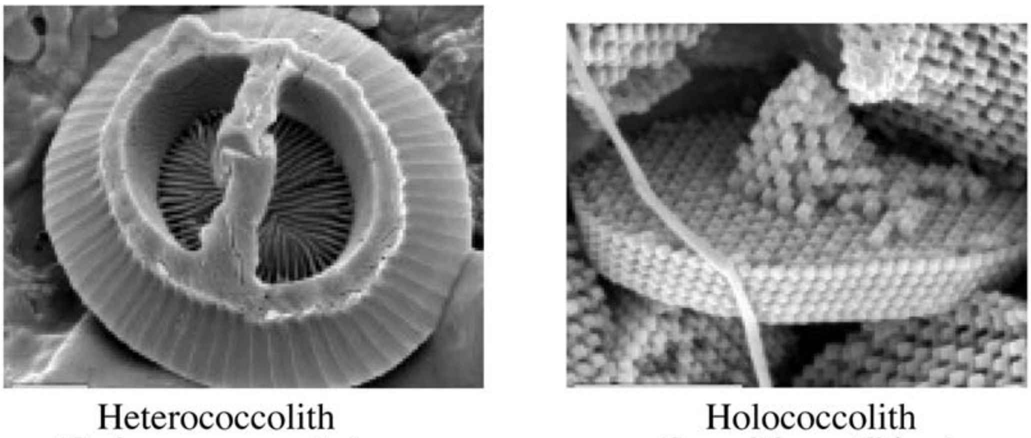


Fig. 1. Schematic representation of the cell structures of coccolithophores. Morphological features and different types of coccoliths seen in various species are combined in this figure. Two types of coccolith-forming vesicles found in *Pleurochrysis* (top) and *Emiliania* (bottom) are illustrated. Pyrenoid (P1) is typical in the coccolithophores and pyrenoid (P2) is seen in *Emiliania* and *Gephyrocapsa*. Heterococcoliths are plotted black and holococcoliths are blotted by a lattice pattern. – CL: columnar deposit, Cv: coccolith forming vesicle, D: peculiar dilation of Golgi body, F: flagellum, H: haptonema, M: mitochondrial profiles, N: nucleus, P1: pyrenoid traversed by thylakoids, P2: pyrenoid traversed by tubular structures, PER: peripheral endoplasmic reticulum, Re: reticular body, SC: unmineralized organic scales (modified from BILLARD & INNOUYE 2004).



Combination coccosphere
(*Calcidiscus leptoporus* with holococcoliths previously assigned to *Syracolithus quadriperforatus*)

Coccosphere
(*Gephyrocapsa oceanica*)



Heterococcolith
(*Gephyrocapsa oceanica*)

Holococcolith
(*Syracolithus catilliferus*)

Fig. 2. Examples for the general terminology used in coccolithophorid algae.

Coccolithophore life cycles

The dominant reproductive mode of coccolithophores is asexually by mitotic division and, generally following miotic division, the coccoliths are redistributed on the daughter cell. In many haptophytes however a complex life cycle has also been demonstrated, which involves two or more morphologically distinct phases. The typical coccolithophore life cycle consists of a diploid stage, which is covered with heterococcoliths and a motile, haploid stage usually covered by holococcoliths (Fig. 3). Thus, it has been confirmed that holococcolithophores and probably other anomalous coccolithophores as well are not autonomous, as previously been thought, but stages in the life cycle of heterococcolithophores. For a more comprehensive review on life cycles in haptophytes, the reader is referred to BILLARD (1994), BILLARD & INUOYE (2004) and HOUDAN et al. (2003).

Although this alternating life cycle has been demonstrated in culture (PARKE & ADAMS 1960; GEISEN et al. 2002; HOUDAN et al. 2003) and by combination cells from field samples (CORTÉS 2000; CROS et al. 2000; GEISEN et al. 2002) little is known for about the causative factors that trigger phase changes. There are, however, hints that holococcolithophores thrive in more oligotrophic waters such as the eastern Mediterranean. Summarizing available data it can be speculated that the ability to rapidly undergo phase transitions is an important tool for the genetic recombination and hence evolution for marine planktonic biota which are being challenged by constantly changing environments.

Culture studies

Coccolithophores can be maintained in clonal culture and where such cultures are available physiological experiments can be conducted (BRAND 1994). Until recently most such experiments were conducted on *Emiliania huxleyi* (BRAND 1981, 1982), but recently data have become available from different species, e. g. *Calcidiscus leptoporus* (QUINN et al. 2003), *Syracosphaera pulchra*, *Helicosphaera carteri* and *Umbilicosphaera* spp. (GEISEN et al. 2004). These tests have provided evidence that coccolith morphology is stable if tested under different ecological parameters and hence under strong genetic control and not ecophenotypic in nature (GEISEN et al. 2004). Conducting experiments using different environmental parameters and testing the stability of the morphology and size (biometrics) of the coccoliths allows for a better understanding of the constraints of a species concept which is – in the case of the fossil record – entirely based on the morphology of the coccoliths. In addition biological experiments can be

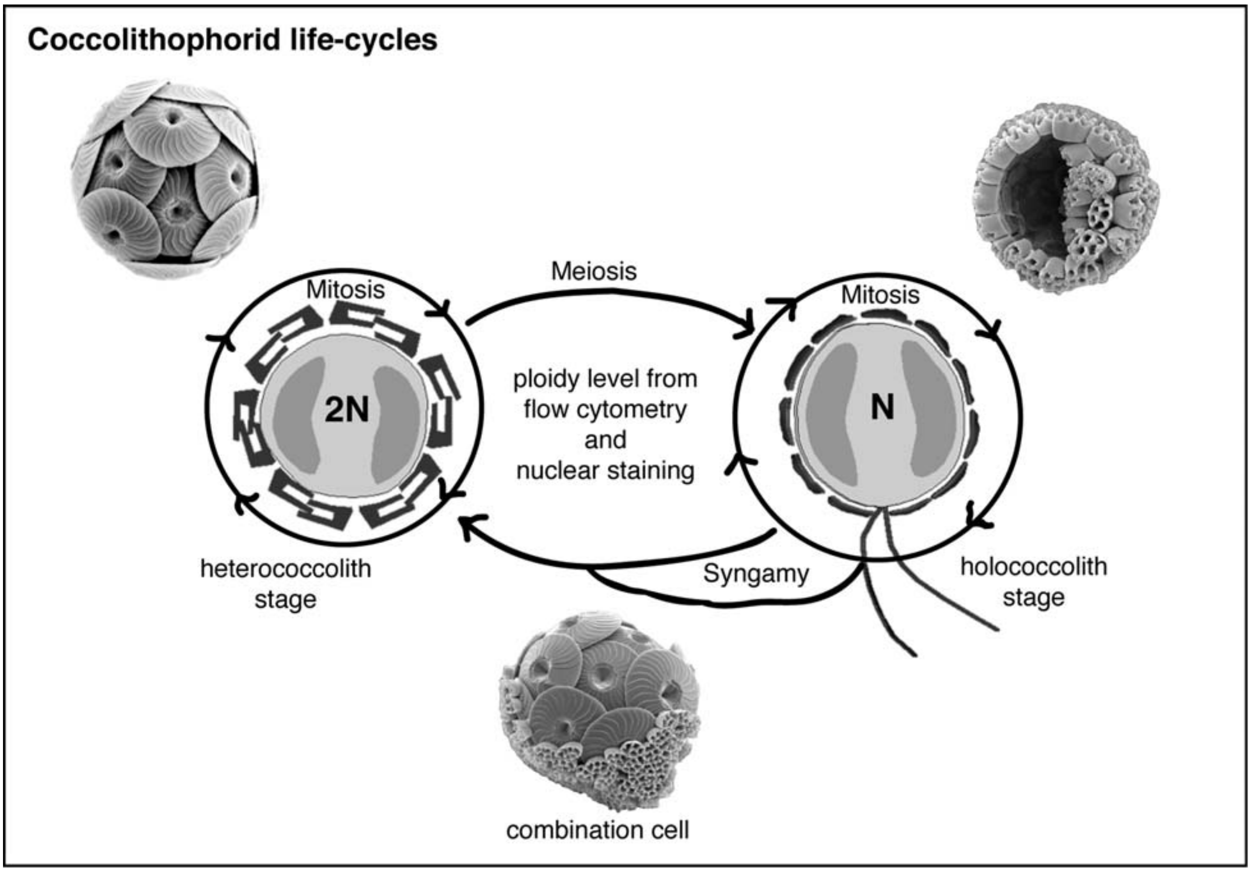


Fig. 3. Schematic illustration of coccolithophorid life cycles (from GEISEN et al. 2002).

used to model changes to global biogeochemical cycles, e. g. the carbon cycle (Riebesell et al. 2000), but also to deliver basic parameters for ecosystem models (e. g. Riegman et al. 1998).

Cultures have furthermore been available to test, if the morphological variability relates to true genetic change. Results from this research have broadly supported the higher level taxonomy of coccolithophores (generic, familial and ordinal groupings) (Edvardsen et al. 2000; Fujiwara et al. 2001; Medlin et al. 1997; Saez et al. 2004), but have challenged species concepts with the discovery of pseudo-cryptic speciation in coccolithophores – which may provide insight into the process of speciation (Sáez et al. 2003; Geisen et al. 2004).

Coccolithophore ecology and biogeography

Factors affecting living coccolithophores

Coccolithophores rely on photosynthesis as their prime nutritional mode restricting them to the photic zone of the oceans. Within the uppermost water column, there are a number of environmental parameters that are known to affect plankton communities in general, on both spatial and temporal scales.

Water temperature has often been thought of as one of the most important factors. This may be due to the fact that during many investigations only temperature and salinity measurements were taken. McIntyre & Bé (1967) showed that most common species had relatively narrow temperature ranges, although subsequent workers extended these ranges. Thus, temperature seems to play a role in controlling the largest scale distribution of species, largely defining broad latitudinally arranged biogeographical zones. However, on smaller scales temperature ranges are less informative and important, as no water-body has annual temperature fluctuations covering an extremely large range. For subtropical populations temperature change is perhaps unimportant, whereas for subpolar communities, temperature plays a more prominent role due to the formation and breakdown of the seasonal thermocline (Andruleit et al. 2003).

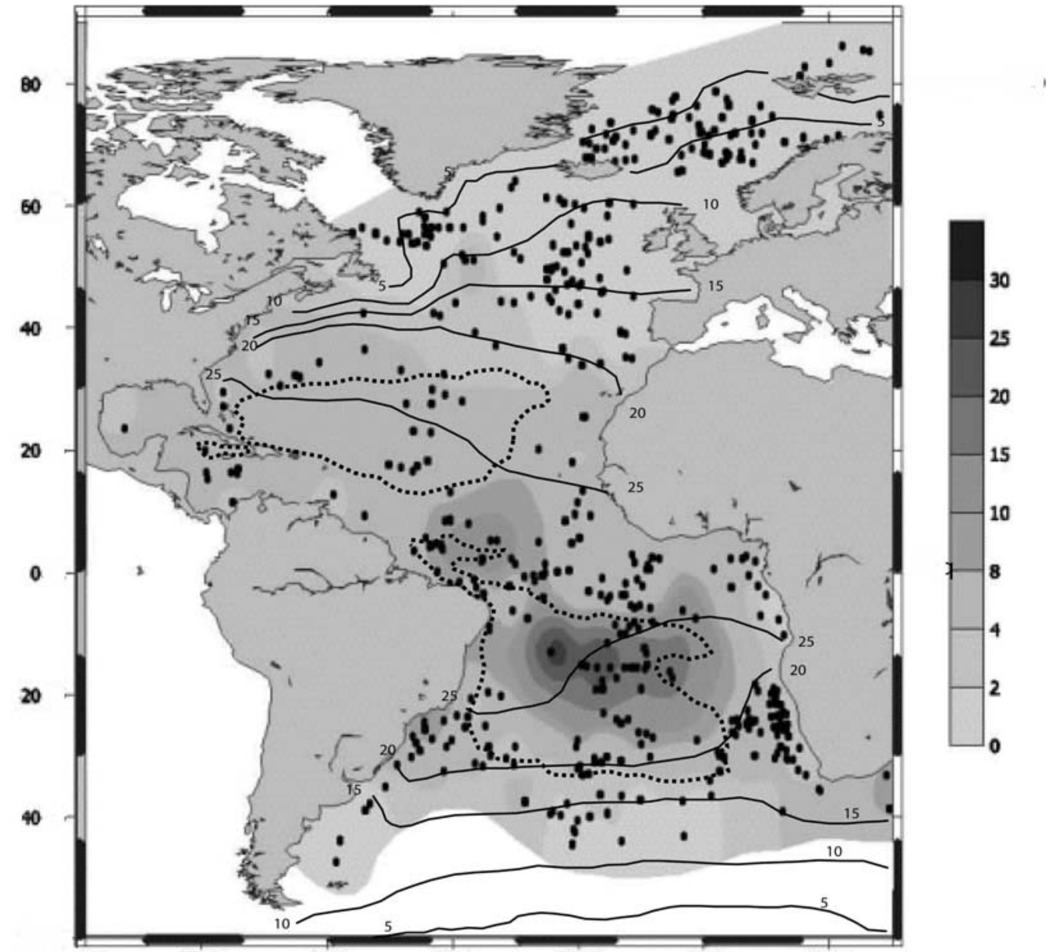


Fig. 4. Relative abundances of *Umbilicosphaera sibogae* (excluding the deep-dwelling species *Florisphaera profunda*) in Atlantic Ocean surface sediments (modified from Ziveri et al. 2004). Solid line = annual mean sea-surface temperature. Dotted line = centre of oligotrophic gyre.

Most coccolithophores live in the open ocean and so are adapted to salinities of 32–37 ppt. However several species have a wider salinity tolerance (BRAND 1994) and are known from low salinity environments, such as fjords. Coccolithophorid species diversity is highest in stratified, warm oligotrophic environments, where salinity values are relatively high. The rather euryhaline characteristic of the coccolithophores is indicated by the occurrence of 52 species in the Gulf of Elat (Aqaba), where the mean salinity is 41 ppt (WINTER et al. 1979). In contrast, in areas characterised by lower salinities, such as the coastal areas, coccolithophorid diversity is relatively low, and the species may be specialised (i.e. benthic or partly calcified). Sediments of the North Sea only contain a sparse, low diverse nannoflora mainly restricted to *Emiliania huxleyi* (HOUGHTON 1988, 1991). At present, only one coccolithophorid species, *Hymenonas roseola*, is known to inhabit freshwater environments.

All phytoplankton require certain nutrients for their growth and biochemical reactions. The most important nutrients are considered to be nitrate and phosphate. In particular, in coccolithophores, nitrate is essential for growth and calcification; however, at unnatural high nutrient concentrations calcification is inhibited. Phosphate seems to act as a controlling agent for calcification. It has been shown that phosphate concentrations were lower in waters where coccolithophores, mainly *E. huxleyi*, bloomed (TOWNSED et al. 1994; VAN DER WAL et al. 1995). Thus, at least *E. huxleyi* seems to have high phosphate uptake kinetics and so can compete in low phosphate environments. In eutrophic (nutrient-rich) environments coccolithophores are often outcompeted by diatoms forming relatively minor components of the total communities. Nonetheless, certain coccolithophorid species (notably many placolith-bearing species) are adapted to such conditions. Since productivity is much greater in eutrophic conditions, a very large proportion of total coccolith production occurs under such conditions. Nonetheless, many coccolithophores are K-selected, i.e. adapted to oligotrophic conditions. Coccolithophores as a group achieve their highest relative abundances within phytoplankton communities in such oligotrophic environments. The effect of tropic levels on coccolithophorid ecology is discussed in WINTER & SIESSER (1994), and detailed case studies are given by, e.g. KINKEL et al. (2000).

As coccolithophores are photosynthetic organisms, they require light for carbon fixation. Most species therefore live in the upper photic waters (<50–80 m), but may become photo-inhibited close to the surface. *Emiliania huxleyi* is unusual in this respect in that it appears to be uninhibited by high light levels (TYRELL & MERICO 2004). This may account for its success at outcompeting other species when it forms gigantic blooms. In contrast, some species, such as *Florisphaera profunda*, inhabit the lower photic zone (= LPZ), which is characterised by low light levels (<1% to 4% of the surface irradiance!). The LPZ is usually a permanent feature of the subtropical gyres, but may develop in well-stratified waters in equatorial and temperate regions during summer months. Thus, it is not surprising that the LPZ flora is rare or absent in turbulent waters, i.e. in coastal or upwelling areas.

Coccolithophore biogeography

Individual species typically occur in all the world's oceans but with more or less limited latitudinal distribution. Three to four broad coccolithophorid floral zones are previously recognised (MCINTYRE & BÉ 1967; GEITZENAUER 1977; WINTER & SIESSER 1994): Subarctic, Temperate, Subtropical, Tropical and Subantarctic. These floral zones are consistently recognisable especially in oceanic plankton samples, and have been associated with major water masses. However, this is a simplistic distribution that does not take into account coastal currents, gyres, eddies, upwelling and rather obscures species-specific biogeography. In addition, it does not show any difference between North and South Atlantic distribution. In the classical present coccolithophorid biogeography the species assemblages are rather similar to their counterparts in the opposing hemisphere.

This has recently been revised for a few particular species in the Atlantic Ocean (ZIVERI et al. 2004). In especially, *Calcidiscus leptoporus* and *Umbilicosphaera sibogae* surprisingly show much higher abundances in the South Atlantic than in the North Atlantic, whereas the absence of *Coccolithus pelagicus* in the sub-Antarctic is already well-known. The biogeographical distribution of *C. pelagicus* primarily reflects the well-documented smaller sub-Arctic species (BAUMANN 1995) with clear abundance maxima in the northern Atlantic, corresponding rather closely to areas with mean temperatures below 10°C. However, the *Umbilicosphaera* pattern is more ambiguous, since the North and South Atlantic show broadly similar habitats in terms of temperature, salinity, productivity and macronutrients. Other species also show preferences for habitats not seen before. In particular, *Syracosphaera pulchra* shows a warm water low productivity preference whilst *Helicosphaera carteri* shows a warm water higher productivity distribution. This is a clearer distribution than might have been expected since f.e. *S. pulchra* has not been regarded as one of the typical oligotrophic specialists.

From the amount of information available on the oceanic scale distribution of nannoplankton, three groups of species could be separated with distinct morphologies and biogeographies (YOUNG 1994). Therefore, particular environments are dominated by characteristic assemblages, which can be distinguished by their coccolith types and coccosphere morphology (Fig. 5). Placolith-bearing species have been recorded to be characteristic for meso- to eutrophic environments such as upwelling areas (equatorial divergence and coastal up-

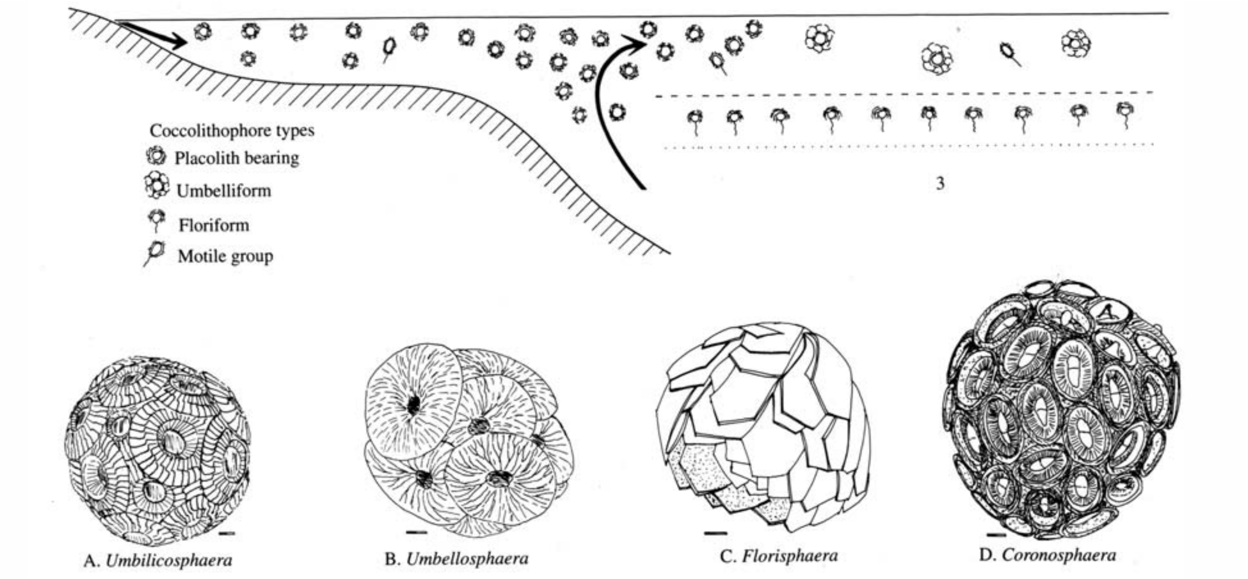


Fig. 5. Characteristic assemblages distinguished by their coccolith types and coccosphere morphology (modified from Young 1994).

welling) and shelf seas, where they often reach bloom proportions. They mainly include *Emiliania huxleyi*, *Gephyrocapsa* spp., *Umbilicosphaera* spp. and a few other species. Their coccoliths are composed of a proximal and distal shield joined by a central column. Umbelliform assemblages, composed of *Umbellosphaera* spp. and *Discosphaera tubifera*, bear coccoliths with large processes, which flare distally to produce a double-layered coccosphere. They dominate oligotrophic mid-ocean environments. The floriform species form coccospheres with a dense asymmetrical mass of coccoliths surrounding a much smaller cell. They mainly characterise the deep photic zone assemblage in a stable water column of low- to mid-latitudes deep photic zone assemblage in a stable water column of low- to mid-latitudes.

Transformation of living communities to fossil assemblages: a case study from the northern Arabian Sea

Assessment of the quality and accuracy of the information preserved in the sedimentary record is a basic prerequisite for the development of comprehensive palaeoreconstructions. This chapter summarizes the investigations on coccolithophores in the Arabian Sea which have been conducted during the past years to produce a synthesis of the production of living coccolithophores in the photic zone, their transformation to settling assemblages, their accumulation on the seafloor, and their final burial in the sediments (Fig. 6).

The hydrography of the Arabian Sea is controlled by the SW-monsoon in summer (June to September) and the NE-monsoon (December to February) in winter. In

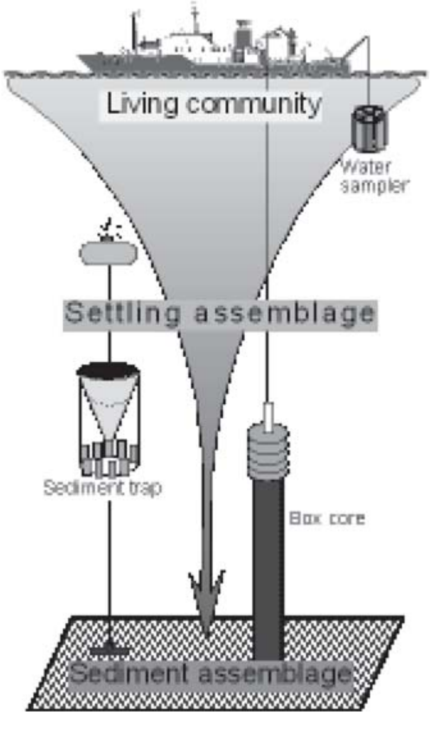


Fig. 6. llustration of the different realms of the used datasets. Water samples help to investigate extant coccolithophores but only give a snapshot of the persistently changing communities. Sediment traps collect already altered settling assemblages over a longer period up to years. The preserved fossil record is thus strongly altered and impoverished.

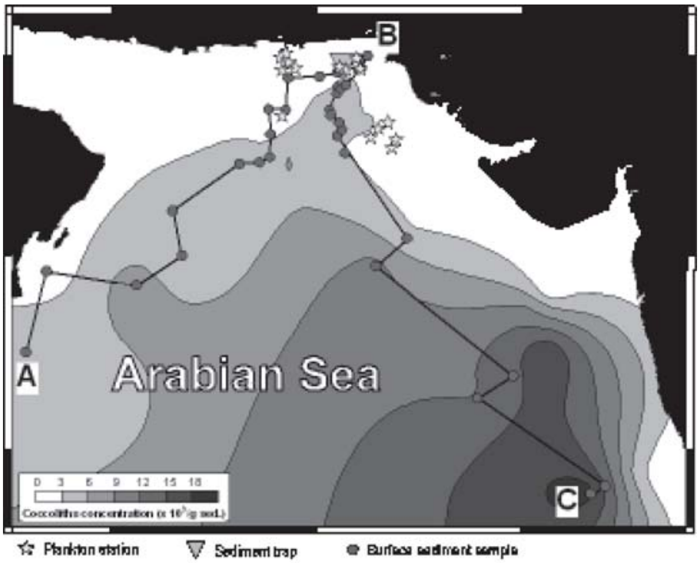


Fig. 7. Map of the Arabian Sea with isolines of absolute coccolith concentrations in surface sediments. Locations of 16 plankton stations, the trap mooring, and surface sediment samples are shown.

addition to monsoonal upwelling during the SW-monsoon along the western boundary of the Arabian Sea due to Ekman transport, wind-induced deep mixing is responsible for high productivity and increased particle fluxes during both monsoon seasons (Banse & McClain 1986). A large number of samples from different realms were used for the present study (Figs. 6, 7) and identical or corresponding approaches were followed to provide a basis for the comparison and discussion of the different datasets.

A plankton study on samples retrieved during September 1993 at the end of the SW-monsoon in the northeastern Arabian Sea (Fig. 8) yielded a rather heterogeneous pattern with regard to species composition in surface waters, apparently as a result of short-term local variability in ecological conditions (Andruleit et al. 2003). Therefore, a “mean plankton community” was calculated from 71 plankton samples of 16 stations by taking the average abundance of each species (for further details see Andruleit et al. in press). Obviously, this mean community exhibits a species composition, which hardly ever occurs in natural living communities (Fig. 8). For example the co-occurrence of *Florisphaera profunda, Umbellosphaera* spp., and *Calciosolenia murrayi* should never been found since the three taxa inhabit rather different ecological niches. This mean community was taken as a basis for a qualitative comparison of the export out of the plankton realm with the settling assemblages retrieved from sediment traps at 590 m depth (Andruleit et al. in press; Fig. 8).

When comparing the plankton with the sediment traps, striking differences but also high similarities become obvious. Only a few species with significant relative abundances in the plankton, such as *Algirosphaera robusta* and *Calciopappus rigidus*, were not important contributors to the settling assemblages. This may be interpreted as a hint to the processes, which alter the living communities during their transformation to settling assemblages. Only the coccolithophores, which were incorporated without total destruction into fast sinking faecal pellets or marine snow aggregates are likely to be preserved (Honjo 1976, 1980). Biological breakage and dissolution due to grazing is probably a major alteration factor for the coccolithophore communities (Harris 1994). Delicate forms are preferentially destroyed, whereas heavily calcified or blooming species probably have a higher preservation potential (Andruleit, 1997). However, without further grazing of the zooplankton or incorporation into aggregates (marine snow), many coccolithophores would possibly not be transformed into settling and sediment assemblages, but could disintegrate and eventually be dissolved in the upper water column (Young 1994; Milliman et al. 1999).

Nevertheless, much of the plankton communities are preserved in the traps, despite the fact that all settling assemblages were naturally subject to severe alteration processes. Taking the different ecological tolerances and niches of the entrapped taxa into account it becomes obvious that several communities contributed to the settling assemblage. Thereby, altered and mixed seasonal species assemblages are produced which still reflect information of the former living communities but their record has to be unravelled carefully. The annual trap record of the northeastern Arabian Sea is, therefore, well suited to give a representative annual pattern of the coccolithophorid succession in that region. Absolute as well as relative abundances exhibit changes in the assemblage, which can be correlated to the monsoon seasons (Andruleit et al. 2000). High fluxes were recorded at the beginning of the SW (summer) and the NE (winter) monsoons, with highest fluxes during the latter (December to February). However, the great variety of species compositions seen in the plankton samples is not preserved in the annual cycle (Fig. 8). Instead a rather

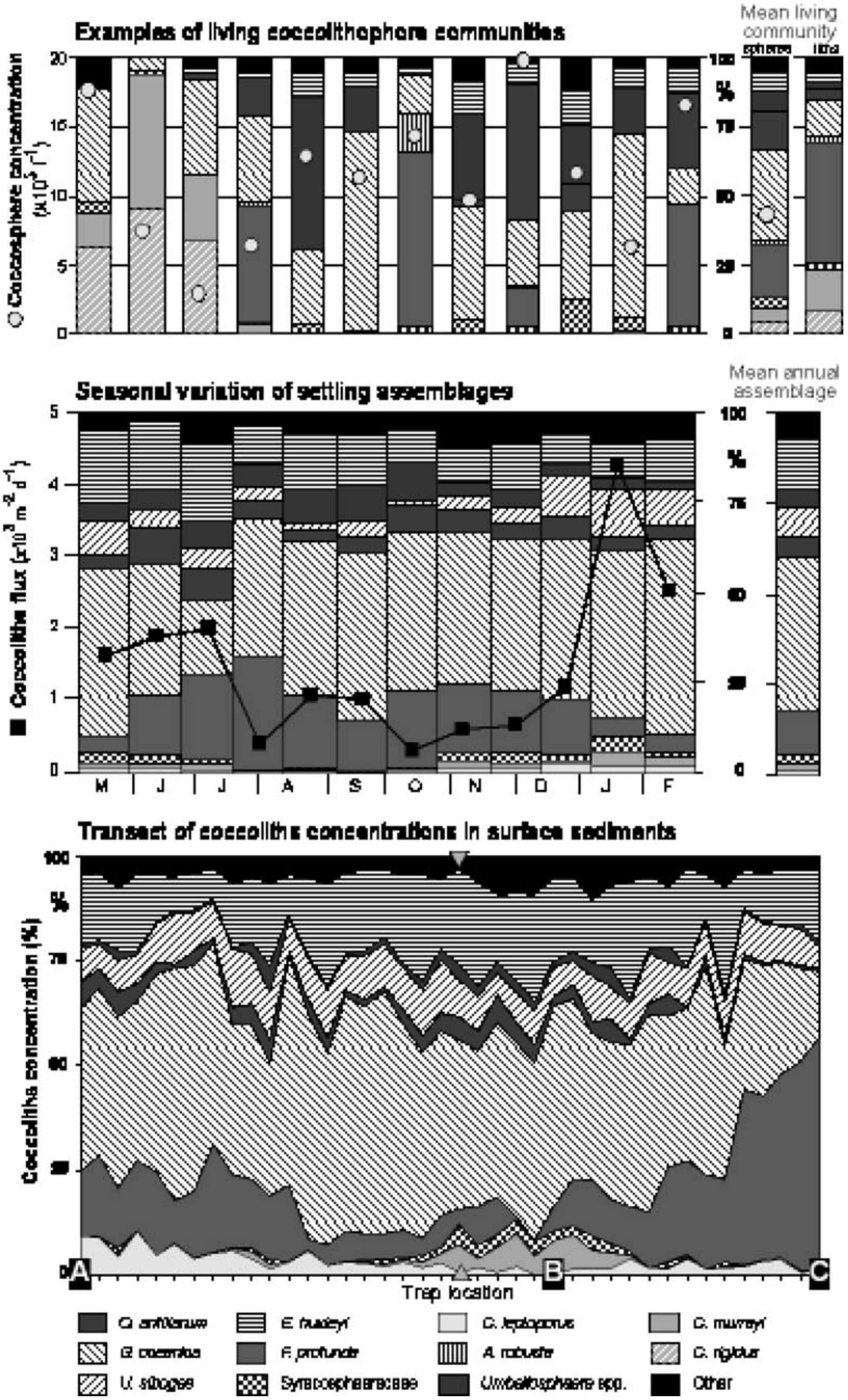


Fig. 8. Comparison of living coccolithophore communities with settling assemblages and coccolith assemblages from surface sediments. Despite the great variety of living communities only a smoothed record characterizes the trap assemblages. The mean living community of September is shown for comparison with the trap assemblage of October (regarding a time lag of approximately 14 days to the trap depth of 590 m). The annual mean of the trap assemblages is shown for comparison with the spatial distribution of coccoliths in surface sediment samples across the northern Arabian Sea (ANDRULEIT et al. in press).

smoothed signal consisting of similar species compositions with only gradual intra-annual changes characterize the settling assemblages.

The sediment trap was located in the northeastern region and should therefore display an annual averaged assemblage, which is similar to the underlying surface sediment assemblage (ANDRULEIT & ROGALLA 2002). Indeed, when comparing the mean trap record with the sedimentary record a remarkable high match can be seen (Fig. 8). There is a high agreement in the species composition (disregarding rare species grouped as "other"), and even the proportions are almost the same. This means that the information record of the traps is transformed into the sediment almost without biases in the relative species abundances. The intra-annual species succession in the trap reflects the changing environmental conditions while the annual mean closely resembles the sedimentary record where only a mixed signal of the two monsoon seasons is preserved.

As shown in previous studies (BAUMANN et al. 1999, 2000) and above it is possible to trace the record of coccolithophores from living communities to sediment assemblages on the basis of relative species abundances. A full quantitative approach, however, is much more difficult. Additionally, resuspension and lateral advection, which affect the surface sediment assemblages as well as the settling assemblages found in the traps, overprint and increase the downward fluxes. This phenomenon seems to be quite common and affects most sediment traps in the catchment area of continental shelves and slopes (ANDRULEIT 1997; BEAUFORT & HEUSSNER 1999; ANDRULEIT et al. 2000; SPRENGEL et al. 2000). Strongly calcified resistant forms (e.g. *C. leptoporus*) have a high preservation potential and, thus, become more prominent during the alteration process, whereas other species such as *E. huxleyi* are abundant due to seasonal high productivity. Therefore, either a robust structure or high cell densities in surface waters are basic prerequisites to become preserved in the fossil record.

Palaeoenvironmental significance of coccolithophores

Coccolithophores have been relatively little used for Pleistocene palaeoclimatic and palaeoceanographic reconstruction by comparison with other plankton groups. This is primarily due to their high rate of evolutionary divergence, compounded by a succession of assemblages dominated by a few, relatively cosmopolitan species that are tolerant to a wide range of conditions. However, recent advances that have come from intensive study of fine-scale variations in particular species have made some single species/species groups a particularly useful tool for palaeoenvironmental reconstructions (e.g. GEISEN et al. 2004). Case studies briefly presented in the following include the response of the total coccolithophore assemblages as well as single species such as *Gephyrocapsa oceanica* to palaeoproductivity changes in the equatorial Atlantic during the last 140,000 years together with palaeoproductivity estimates based on the deep-dwelling *Florisphaera profunda*. A recently developed *Gephyrocapsa*-based SST transfer function is presented. In addition, their significance as carbonate producers is reviewed followed by an introduction into biomarker studies on coccolithophores.

Coccolithophores in the equatorial Atlantic Ocean: response to palaeoproductivity changes during the last 140,000 years

Biogeographic distribution patterns of coccoliths in surface sediments are commonly used to infer temperature conditions and circulation patterns (e.g. MCINTYRE 1967; ROTH & COULBOURN 1982; HOUGHTON 1988; BAUMANN et al. 1999, 2000), as well as productivity gradients (MOLFINO & MCINTYRE 1990; BEAUFORT et al. 1997). In surface sediments underlying the oligotrophic water masses of the equatorial Atlantic, deep-dwelling species such as *Florisphaera profunda* and *Gladiolithus flabellatus* (the so-called Lower Photic Zone = LPZ flora) are most abundant and variations within their occurrences were explained in terms of changes in nutricline depth (MOLFINO & MCINTYRE 1990). Accordingly, high abundances of the LPZ flora are associated with a deep nutricline and deep thermocline, whereas low abundances are characteristic for 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 & MCINTYRE 1990; MCINTYRE & MOLFINO 1996; BASSINOT et al. 1997), but also for the northwestern Pacific (AHAGON et al. 1993) and the Indian Ocean (OKADA & MATSUOKA 1996; BEAUFORT et al. 1997). In particular, BEAUFORT et al. (1997) indicated that the %-abundance of *F. profunda* in surface sediments seems to be a function of the primary productivity and, thus, providing a robust transfer function for paleoproductivity estimates; this has successfully been applied to Late Quaternary sediments from the Atlantic, Indian, and Pacific Oceans (BEAUFORT et al. 1997; HENRIKSON 2000).

A good example of the use of fossil distribution patterns of coccolithophores in reconstructing surface waters is that of KINKEL et al. (2000). They used species composition, coccolith numbers /g sediment, and coccolith accumulation rates for interpretation of changes in the surface water productivity. During the past 140.000 years the surface water circulation of the equatorial Atlantic changed drastically, mainly due to changing wind stress and advection of cool and nutrient rich waters from the south-eastern Atlantic, which caused an intensification and lateral expansion of the equatorial upwelling area. This is monitored in the coccolithophore assemblages of two sediment cores from the southern and western equatorial Atlantic (Fig. 9).

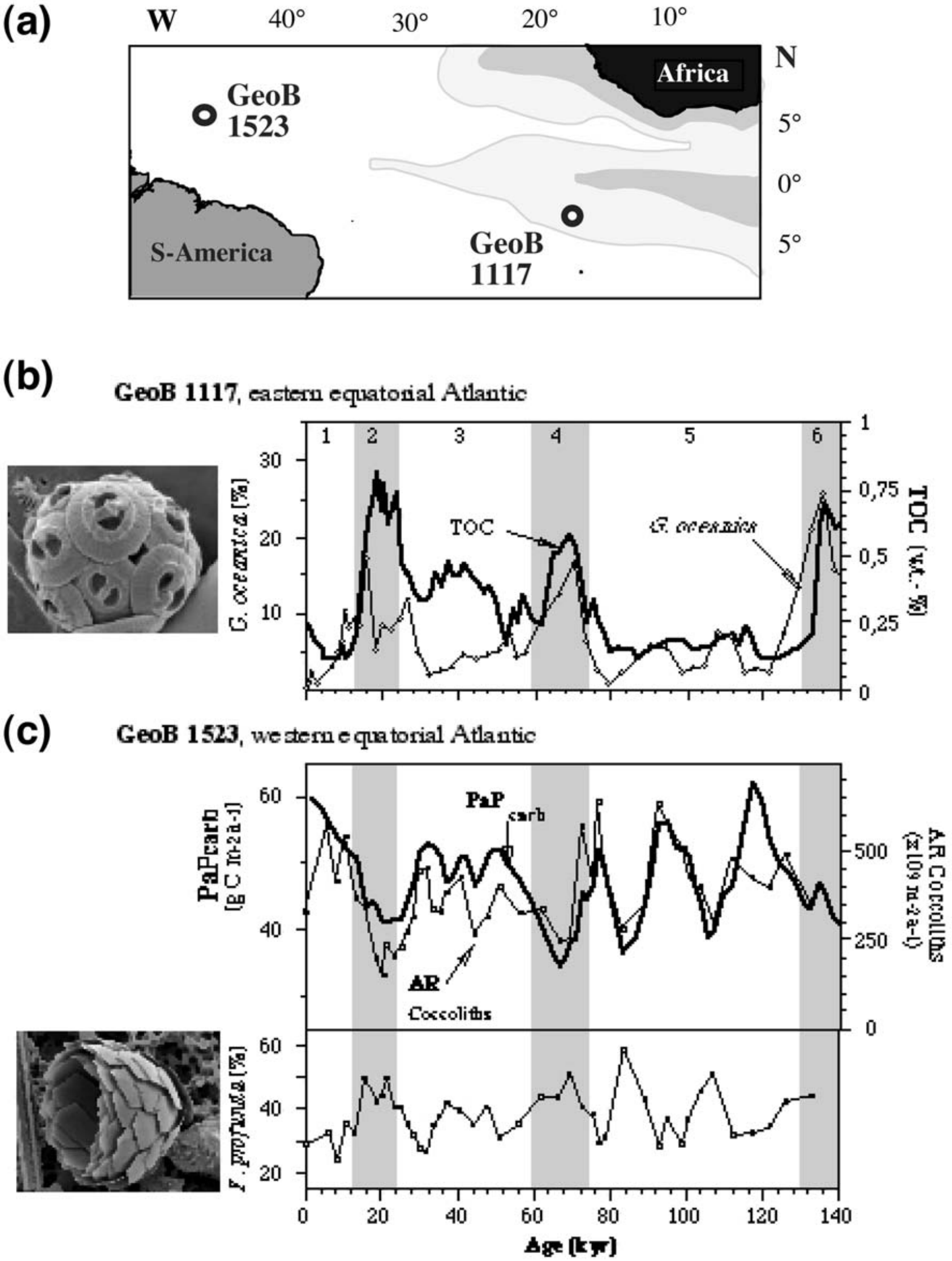


Fig. 9. – **(a)** Location of sediment cores GeoB 1117 and GeoB 1523. The grey shadings indicate higher phytoplankton pigment concentrations (> 0.4 mg/m^3) recorded by the Coastal Zone Color Scanner (CZCS) from 1979–1986. Comparison of **(b)** the total organic carbon contents (TOC) and the relative abundance of *G. oceanica* in sediment core GeoB 1117, and **(c)** between the paleoproductivity estimations (PaPcarb), the coccolith accumulation rate, as well as the relative abundance of the deep-dwelling species *F. profunda* in sediment core GeoB 1523 (modified from KINKEL et al. 2000).

A striking increase in coccolith numbers and coccolith accumulation rates has been observed in sediment core GeoB 1117 from the southern equatorial Atlantic during the last glacial (KINKEL et al. 2000). This increase was attributed 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 also supported by the floral composition of the coccolithophore assemblages. In particular, the relative abundances of *Gephyrocapsa oceanica* corroborate the organic carbon contents, with maxima in isotope stages 2, 4 and 6 (Fig. 9b). Higher abundances of *G. oceanica* were previously described from upwelling areas of the Indian Ocean, the Benguella Upwelling, and the Gulf of California (e.g. KLEIJNE et al. 1989; GIRAUDEAU 1992; ZIVERI & THUNNELL 2000).

In the western equatorial Atlantic (GeoB 1523) an opposite trend was observed during glacial periods, which probably was caused by a deepening of the thermocline and its seasonal coverage is limited to the westernmost parts. Highest coccolith numbers and accumulation rates 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. 9c). Further indication for decreased surface water productivity is given by high abundances of *Florisphaera profunda*, as proposed in several studies (MOLFINO & MCINTYRE 1990; OKADA & MATSUOKA 1996; BEAUFORT et al. 1997). In GeoB 1523, *F. profunda* is the most abundant species, making up between 24 and 58% of the assemblage. The records of the coccolith accumulation rate together with the palaeoproductivity estimates (Fig. 9c) and the relative abundance of *F. profunda* show contrasting cyclic variations throughout the entire core, with peaks in *F. profunda* abundance rather consistently corresponding to minima of coccolith accumulation rate. This contrast is probably 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*. Together with *G. flabellatus* this is the only common species that is restricted to the lower euphotic zone (~60 to ~180 m water depth) of the tropical and subtropical oceans (OKADA & 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. An increase in the relative abundance of this species thus can be attributed to a weakened upwelling intensity with a deep thermocline and nutricline.

Coccolithophore-derived palaeotemperature estimates

Various methods have already been established to reconstruct late Quaternary sea surface temperatures (SSTs) from oceanic sediments: statistical estimates based on microfossil assemblage compositions, trace elements and oxygen isotopes in foraminiferal carbonate, as well as alkenone unsaturation ratios (summary by MIX et al. 2001; and see below). Qualitative SST changes have been derived previously from the relative abundances of certain *Gephyrocapsa* species (WEAVER & PUJOL 1988; TAKAHASHI & OKADA 2000). Observed down-core patterns were consistent with the expected glacial-interglacial temperature variability, reflecting decreased temperatures during glacial periods.

Recently, BOLLMANN et al. (2002) introduced a global sea surface temperature calibration based on the relative abundance of different morphotypes within the coccolithophore genus *Gephyrocapsa*. The authors showed that this temperature transfer function has potential for the reconstruction of paleotemperatures in the temperature range from 14.0°C to 29.4°C. The standard error of 1.78°C is comparable to that of foraminifera transfer functions. The use of this temperature transfer function as an additional palaeo-thermometer for the late Pleistocene and Holocene was most recently been applied and validated in sediments off NW Africa (HENDERICKS & BOLLMANN 2004; Fig. 10). A good correspondence was found between the *Gephyrocapsa*-based and alkenone-derived palaeotemperatures. Both data sets indicate a glacial drop in SST of about 3 °C compared to Holocene values. Similar results come from the Mg/Ca palaeotemperature record, although consistently cooler temperatures were inferred from this proxy. Largest discrepancies, both in terms of down-core amplitude changes and same-age temperature estimates, were found with available planktic foraminiferal data (Fig. 10). This was mainly attributed to differences in the season of production, ecologic preferences and habitats, and/or preservation.

In addition to the down-core record, sediment samples corresponding to the Last Glacial Maximum (LGM) were analysed in order to derive palaeo-SST maps off Northwest Africa. The authors found lowest glacial temperatures (14–15.5°C) offshore Morocco and south of the volcanic Canary Islands, likely due to intensified upwelling related to stronger trade winds. Smallest glacial-interglacial temperature fluctuations were found off Cape Blanc (2.5–4°C), and larger fluctuations (up to 6°C) occurred in the remaining region. Thus, *Gephyrocapsa*-derived temperature estimates provide support that the main activity of coastal upwelling must have migrated to the north during the LGM, away from today's perennial upwelling centre offshore Cape Blanc (21°N). Previous authors have postulated a change in direction and/or seasonality of the NE trade winds in this area.

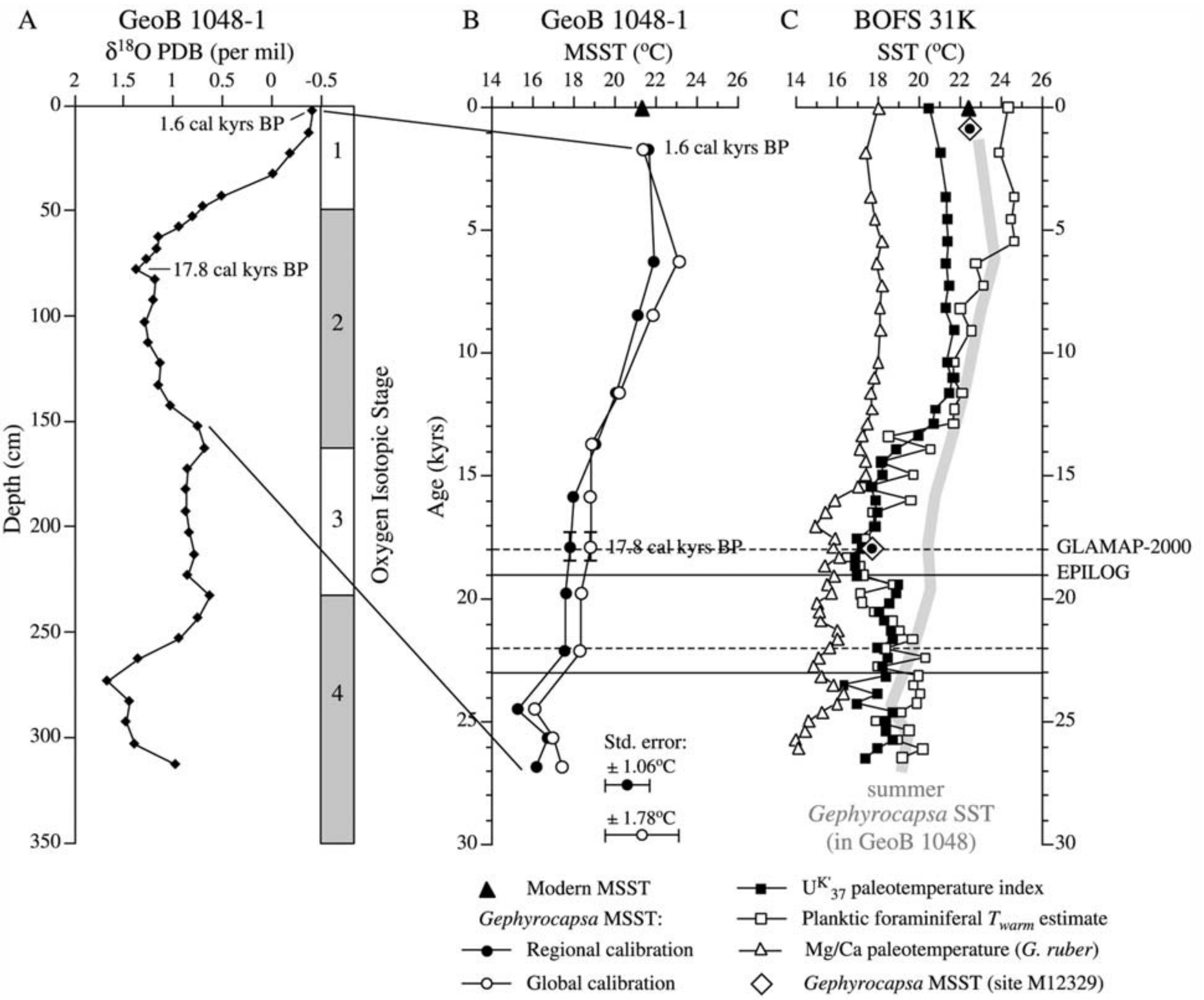


Fig. 10. – **A**: Fine fraction carbonate oxygen isotope stratigraphy of sediment core GeoB1048 off Cape Blanc. – **B**: Downcore palaeotemperature records in core GeoB 1048. Mean SST estimates based on regional and global Gephyrocapsa transfer functions. – **C**: SST estimates based on alkenones and planktic foraminifera, as well as the Mg/Ca ratio in foraminiferal calcite (shallow-dwelling species *G. ruber*) in BOFS core 31K (modified from HENDERICKS & BOLLMANN 2004).

The importance of coccolithophores as carbonate producers

Coccolithophores influence biogeochemical cycles and the global climate system by contributing significantly to the oceanic pumps of organic carbon (via photosynthesis) and carbonate (via calcification) and hence affect the surface ocean CO_2 balance (BRAND 1994; WESTBROEK et al. 1993; WINTER & SIESSER 1994). However, there is relatively little data on the contribution of different planktic calcifying organisms (e.g. coccolithophores, foraminifera, pteropods) to the global calcium carbonate production, but it is estimated that about 20–60% of the pelagic marine carbonate production is provided by coccoliths (e.g. MILLIMAN 1993; ZIVERI et al. 1999).

For estimation of coccolithophore carbonate a new methodology allows the conversion of coccolith flux rates into mass fluxes (BEAUFORT & HEUSSNER 1999; YOUNG & ZIVERI 2000). Thereby, the carbonate mass estimate includes a given shape factor of coccolith types, the density of calcite, and the average length of a species.

Calculation of the global ocean carbonate budget includes carbonate production, accumulation, and dissolution, but published estimations of the carbonate budget vary widely. The quantity of biogenic carbonate produced annually in the surface ocean broadly is in the order of 1.0–1.3 gigatons (WESTBROEK et al. 1993), from which about 85% dissolves in the water column or at the sediment-water interface. Other authors assume that about 60% of the carbonate accumulates in sediments, whereas the remaining 40% are dissolved (MILLIMAN 1993). Information on the ocean-floor distribution of carbonate, which is the main component of deep-sea sediments above the lysocline, is already available (ARCHER 1996). Reliable estimates as to the relative proportions of the various pelagic carbonate producers,

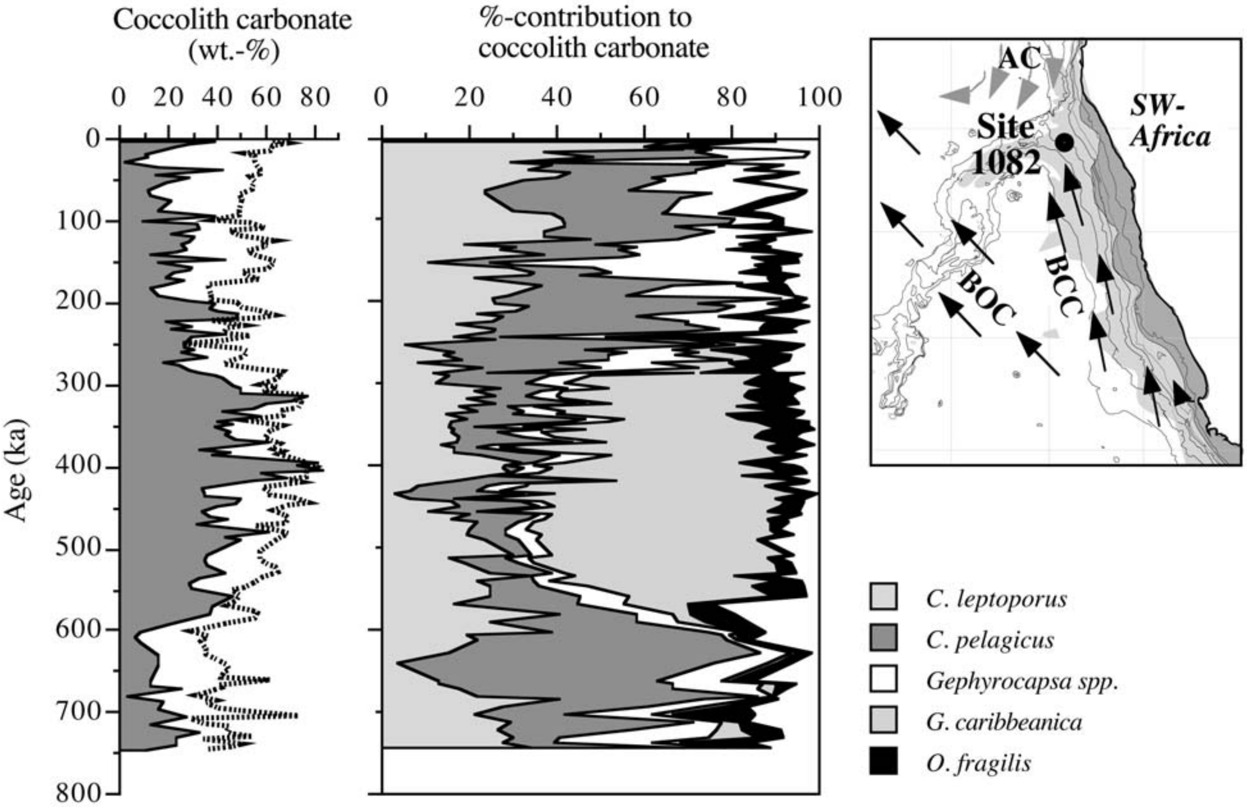


Fig. 11. Absolute coccolith carbonate content (wt-%; dotted line – total carbonate content) and %-contribution of the dominant coccolith carbonate producing species (modified from Baumann & Freitag 2004). Besides a few rather massive species such as *C. leptoporus* and *C. pelagicus*, the numerically important gephyrocapsids, i. e. *G. caribbeanica*, likely produce a relatively high proportion of the coccolith carbonate.

however, are still sparse (e. g. Giraudeau et al. 2000; Schiebel et al. 2002; Baumann et al. 2004a, b). Recent studies on South Atlantic surface sediments clearly reveal a variable pattern of carbonate sedimentation and accumulation for planktic foraminifera and coccolithophores, respectively (Baumann et al. 2004a). Whilst coccoliths carbonate dominates the oligotrophic gyres of the South Atlantic, carbonate produced by planktic foraminifera is more important in more fertile, mesotrophic to eutrophic areas, such as the equatorial divergence zone. Mass estimates of coccolith carbonate burial in surface sediments of the South Atlantic document coccoliths to be major carbonate contributors in most mid-Atlantic Ridge sediments, exceeding up to 70 wt-%. In contrast to these oligotrophic areas, they are of minor importance in sediments accumulating on the continental margins, here accounting for only a fifth of the carbonate fraction.

Moreover, based on estimates of mean coccolith masses, species-specific coccolith carbonate was calculated for the South Atlantic Ocean (Baumann et al. 2004b). Even though absolute numbers of most species, particularly of *Oolithotus fragilis*, *Rhabdosphaera clavigera*, *Coccolithus pelagicus*, and *Helicosphaera carteri*, are many times lower than total numbers of *Emiliania huxleyi*, these subordinate massively calcifying species contribute most to coccolith carbonate. Despite the large cell numbers generated by *E. huxleyi* and *F. profunda*, as single species they are of minor importance to coccolithophore carbonate production. Although absolute accumulation of coccolith carbonate in upwelling regions is estimated to be about three times higher than in the oligotrophic gyres, the latter areas are about 5 to 10 times larger. This means that total accumulation of coccolith-carbonate in oligotrophic areas exceeds by far that of the upwelling regimes, and is therefore important with respect to the geological archive.

Coccoliths also build up the dominant part of the total carbonate in the Pleistocene as shown for Site 1082 off SW-Africa (Baumann & Freitag 2004) where they constitute a significant fraction of the carbonate content during most of the last 680ka (Fig. 11). Only few species significantly contribute to the coccolith carbonate. The relatively massive species *C. leptoporus* and *C. pelagicus* as well as the numerically dominant gephyrocapsids are the most important contributors. The calculated coccolith carbonate content is obviously linked to the bulk carbonate record and, therefore, is indicative for the development of the productivity regime of this area.

The dominance of coccolith carbonate of up to >80 wt-% (>95% of the total carbonate) during the mid-Brunhes time (580 to 280 ka) indicate that a change in the productivity of the northern Benguela upwelling system have occurred. This time interval is characterised by a significant increase in carbonate (total as well as in coccolith derived $CaCO_3$) that is associated with the appearance of *Gephyrocapsa caribbeanica* (Fig. 11). Before and after this event the carbonate is clearly more diluted by other components such as biogenic opal, organic carbon, and terrigenous matter. For Site 1082, these bulk proxies indicate a decline in absolute rates of productivity for the past 580 ka (BAUMANN & FREITAG 2004). However, from the present data it is obvious that fluctuations and total amount of productivity remained on a very low level only during the *G. caribbeanica* interval whereas it slightly increased after about 280 ka. *G. caribbeanica* seems to be a good equivalent to the modern cosmopolitan species *E. huxleyi*, an assumption mainly based on its dominance and global distribution. Therefore it can be concluded, that the distribution of this species seems to be relatively independent both of water temperature and nutrient level, although its extremely high numbers also point to at least seasonally nutrient-enriched subpolar to subtropical waters, and to the fact that they most probably are bloom-forming coccolithophores. Nevertheless, its significance for carbonate burial during the mid-Brunhes time interval is conspicuous.

Sea surface temperature reconstructions by alkenones

In addition to work on floristic analysis, geochemical palaeo-proxies based on coccolithophorid-derived material have become increasingly important, notably alkenone palaeothermometry. The history of coccolithophore biomarker research is not as straight forward as one might think, but started with the detection of a series of novel long chain ketones in sediments from the Walvis Ridge, commonly referred to as long chain alkenones (LCA) (BOON et al. 1978). Two years later their structure was confirmed and the biosynthesis of this molecules was detected in cultures of the extant coccolithophore species *Emiliania huxleyi* (VOLKMAN et al. 1980). Further studies of Prymnesiophyceae showed, that LCAs are common among several species of the order Isochrysidales, and that the unsaturation pattern observed among them is related to growth temperature (MARLOWE et al. 1984; Fig. 12).

In a subsequent study (BRASSELL et al. 1986) demonstrated that the unsaturation index of LCAs, the so called $U_{37}^{K'}$ index co-varied with stable oxygen isotope values ($\delta^{18}O$) of planktic foraminifera in a Quaternary sediment core, indicating, that this might be a new proxy for reconstructing past sea surface temperatures (SST). The original unsaturation index included the di-, tri-, and tetraunsaturated C37-Methylketones:

$$U_{37}^{k} = \frac{(C_{37:2} - C_{37:4})}{(C_{37:2} + C_{37:3} + C_{37:4})} .$$

Since tetra-unsaturated methylketones are relatively rare in most oceanic sediments, only occur in high latitudes and areas of reduced salinities, this unsaturation index was simplified to the so called

$$U_{37}^{K'} = \frac{(C_{37:2})}{(C_{37:2} + C_{37:3})} .$$

The calibration of $U_{37}^{K'}$ against temperature on particulate organic matter from the Pacific and Atlantic Ocean as well as in laboratory cultures of *E. huyleyi* provided the first paleo-SST transfer function based on these new biomarkers (Fig. 12). Since then, this method has been widely applied in Late Quaternary paleoceanographic research.

This approach was further validated by a core-top calibration using a large globally distributed dataset (MÜLLER et al. 1998; Fig. 12). Within this study the highest correlation between $U_{37}^{K'}$ and annual mean sea-surface temperature was found and the linear regression yielded an equation, that was almost identical to the one found by (PRAHL & WAKEHAM 1987). The fact, that $U_{37}^{K'}$ is used as a proxy for annual mean temperature, might be a little surprising, given the strong seasonality in coccolithophore production (BIJMA et al. 2001). Therefore shifts in seasonality have to be taken into account, especially in comparison with other SST-proxies (NÜRNBERG et al. 2000). Coccolithophore production is highest during colder seasons in tropical and subtropical environments, and during warmer seasons in high latitudes (BIJMA et al. 2001). However, this is not reflected

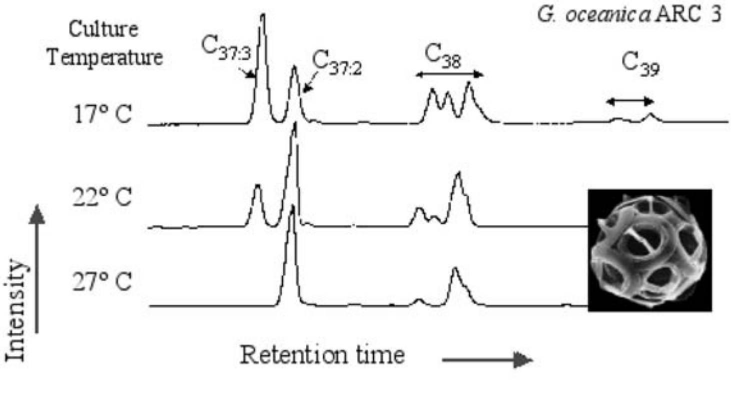


Fig. 12. Partial gas chromatograms of the long-chain, unsaturated alkenone compositions measured in cultures of *G. oceanica* (strain ARC 3) grown isothermally in batch cultures at three different temperatures (KINKEL unpubl. data).

in the global core-top calibration of $U^{K'}_{37}$ and SST. Moreover, the comparison between $U^{K'}_{37}$ and production weighted SST, which takes into account primary productivity seasons (Müller et al. 1998), does not provide a better fit than annual SST.

The calibration of core-top sediments is assumed to be valid between 60°N and 60°S, since data from higher latitudes do not fit the linear trend. Several studies have tried to improve the method in higher latitudes (Sikes & Volkman 1993; Rosell-Melé et al. 1995), but it appears, that factors other than temperature might influence the $U^{K'}_{37}$ index in cold waters. The application of the method to Late Quaternary sediments in the northern North Atlantic clearly demonstrated, that other mechanisms than temperature must be acting on the unsaturation degree of LCAs, and it was speculated that salinity might be one influencing component (Rosell-Melé et al. 2002). Besides the cold end of the calibration, there is no linear response of $U^{K'}_{37}$ to SST at temperatures above 27°C (Pelejero & Grimalt 1997; Sonzogni et al. 1997), which has been taken into account for studies in tropical regions (Pelejero et al. 1999). In addition, several regional calibrations were set up which provided different $U^{K'}_{37}$-SST equations, especially along the California margin and in the Mediterranean (Herbert et al. 1998; Ternois et al. 1997).

Besides the apparent robust calibrations of core-tops (Fig. 13), serious doubts arose from various culture studies and investigations of particulate organic matter in the water column, that yielded $U^{K'}_{37}$-temperature relationships, that were not in line with the original equation of Prahl & Wakeham (1987) and the global core-top data of Müller et al. (1998). Laboratory culture experiments with *Gephyrocapsa oceanica* pointed towards species specific $U^{K'}_{37}$-temperature relationships as the cause for deviations from the original calibration (Volkman et al. 1995). However, similar results were found in cultures of both *E. huxleyi* and *G. oceanica*, with no consistent pattern arising, that could be attributed to one of them (Conte et al. 1995; Sawada et al. 1996; Conte et al. 1998). In particular, the comparison of $U^{K'}_{37}$ values and the species composition of Late Quaternary nannofossil assemblages show no influence of species composition on the climatic signal that is incorporated in the biomarkers (Müller et al. 1997; Villanueva et al. 2002).

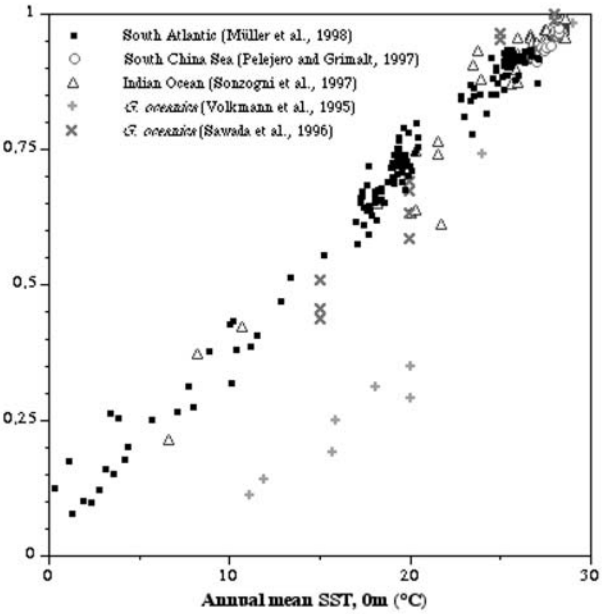


Fig. 13. Relationships between $U^{K'}_{37}$ and annual mean SST (0 m) for surface sediments from the global ocean (own compilation). The obtained global core-top calibration ($U^{K'}_{37}$' = 0.033 T + 0.044) of Müller et al. (1998) is absolutely identical to the *E. huxleyi* equation of Prahl & Wakeham (1987).

Although there is some evidence for a diagenetic alteration of the $U^{K'}_{37}$ signal depending on the degradation rate of organic matter during early sedimentary burial (e.g. Hoefs et al. 1998), this process might only be taken into account in environments where redox parameters fluctuate strongly over time, which is not likely in open marine sediments. Recently it has been shown, that LCAs might be suspect to re-sedimentation and lateral advection (Benthien & Müller 2000) which could distort the temperature reconstruction locally, and even more lead to temporal offsets between planktic foraminifera (or other microfossils) and biomarkers of several thousand years within the same sample (Ohkouchi et al. 2002).

LCAs have a fossil record that date back to the early Cretaceous. However, it is not known, which group of coccolithophores can be assigned to LCA biosynthesis in the Cretaceous. For younger time intervals alkenones in the open marine environment are most likely produced by members of the order *Isochrydales*, with the genera *Reticulofenestra*, *Gephyrocapsa* and *Emiliania* being the dominating coccolithophores in most nannoplankton assemblages since the Eocene. The rise of the genus *Reticulofenestra* in the Eocene coincides with a general change in the unsaturation pattern of LCAs, similar to those observed in the modern ocean. Thus it is likely, that the $U^{K'}_{37}$ paleotemperature approach can be applied for the last 50 Ma. To date the longest time series of $U^{K'}_{37}$ temperatures extends back into the Pliocene (Marlow et al. 2000), but failed in older sediments, most likely due to strong diagenesis in open marine settings (Pagani et al. 1999).

Future perspectives

In recent years, the information on coccolithophore biology has increased considerably. Culture tests have provided evidence that coccolith morphology is rather stable if tested under different ecological parameters and hence under strong genetic control (for details see Geisen et al. 2004). Nevertheless, many ecological questions to newly evolved species remain unsolved. In addition, ecophenotypic variability cannot be excluded in nature. Consequently, the details of palaeoenvironmental and -oceanographical reconstructions have not really been extended.

An increasing need therefore is the determination of present-day biogeographical distribution patterns as well as their comparison 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 and to add to the palaeoecological meaning of some of the coccolithophorid species. In addition, more information from sediment trap studies are needed to better understand the transformation of a living coccolithophorid community in the plankton into a coccolith assemblage of the underlying deep-sea sediments.

Analysis of coccoliths in sediment cores give useful information about the location of different water masses in the past and consequently about the palaeoecology and palaeoceanography in this area. However, there still is a lack in understanding the controls 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.

For paleoceanographical reconstructions in general, the calcium carbonate shells produced by foraminifera have been widely used, whereas knowledge of the potential of coccolith calcite as a recorder of geochemical proxies is poor. Yet, within the last years a number of studies have taken up promising approaches that try to explore geochemical composition and isotope studies in coccoliths (Ziveri et al. 2003; Stoll & Ziveri 2004). The huge potential of coccoliths in stable oxygen and carbon isotopes was already demonstrated twenty years ago, when it was shown, that fractionation affects in coccoliths are much larger than those in planktonic foraminifera (Dudley et al. 1986). However, the difficulty to separate coccoliths from bulk sediments and process monospecific samples, have hampered the geochemical proxy evaluation and application of coccoliths. With a modified settling method Stoll & Ziveri (2002) partly overcame this problem and provided a feasible method to measure geochemical and stable istope composition of near monospecific coccolith assemblages. Already this approach was applied to Late Quaternary and Paleogene sediments, with promising results from Sr/Ca ratios in coccoliths, which should provide a growth rate proxy for coccolithophores (Stoll et al. 2002).

In addition to the methods mentioned above, compound specific carbon isotopes of coccolithophorid-derived alkenones can be used to reconstruct the p CO_2 conditions of surface waters in which they grew. Although this method has been applied to Miocene sediment sequences (Pagani et al. 1999), serious problems result from the fact, that carbon isotope fractionation are not only a function of p CO_2, but are influenced by other parameters like cell geometry and growth rate, which are difficult to asses from the fossil record (e.g. Benthien et al. 2002). Therefore, we need to combine geochemical assessments of coccolithophorid growth rates, stable carbon isotopes in coccolith calcite and morphometry to narrow the large uncertainties that still prohibit exact p CO_2 reconstructions.

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