J. Nannoplankton Res. **30** (1), 2008, pp.9-21 © 2008 International Nannoplankton Association, Inc.
ISSN 1210-8049 Printed by Cambridge University Press, UK

Spatial distribution of living coccolithophores along an east-west transect in the subtropical South Atlantic

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Manuscript received 29th November, 2007; revised manuscript accepted 8th February, 2008

Abstract The upper-water-column distribution of living coccolithophores in the subtropical South Atlantic and Benguela Upwelling regime was examined along an E-W transect of 11 phytoplankton stations. Coccolithophore standing crops ranged from less than 10 000 cells/l in the nutrient-depleted, shallow-water stations of the western Subtropical Gyre to 396 300 cells/l in the medium-depth stations of the nutrient-enriched Benguela Current. *Emiliania huxleyi* was the most abundant species, with concentrations of up to 200 000 individuals/l. The present study reveals hydrographic controls on the distribution of some of the major taxa. Assemblages in the Benguela Current were characterised by at least five species (*E. huxleyi*, *Gephyrocapsa ericsonii*, *Rhabdosphaera xiphos*, *Umbellosphaera irregularis*, *Syracosphaera halldalii*), which exhibit their highest cell numbers at the easternmost stations, reflecting higher nutrient levels. The upper photic zone (0-80m water-depth) of the Subtropical Gyre generally contained holococcolithophores and the species *Discosphaera tubifera*, *Umbellosphaera tenuis*, *Calciosolenia brasiliensis* and *Syracosphaera pulchra*, which exhibit an affinity for lower nutrient-levels. The flora in the lower photic zone (>80m-100m water-depth) was characterised by abundant *Florisphaera profunda* in the nutrient-depleted Subtropical Gyre, whereas *Calcidiscus leptoporus*, *Oolithotus fragilis* and *Umbilicosphaera sibogae* occurred in the deep boundary-zone from the Benguela Current to the Subtropical Gyre waters. Thus, the vertical distribution of all coccolithophore taxa, except the three placolith-bearing species *Gephyrocapsa oceanica*, *G. ericsonii* and *E. huxleyi*, was probably controlled by upper-photic-zone water-temperature and stratification of the water-column.

Keywords South Atlantic, living, ecology, plankton

1. Introduction

Phytoplankton, at the base of the marine food-chain, serve as a key to understanding both marine ecology and biogeochemistry. However, to integrate palaeobiology and modelling of climatic changes into this study requires a detailed understanding of the ecology of these organisms. Critical to such an understanding is knowledge on the extent of, and controls on, species-level biodiversity. Coccolithophores are the predominant group of calcifying marine phytoplankton, have the best fossil record of all phytoplankton, and play a unique role in the global carbon cycle. They are characterised by calcareous scales (coccoliths), which surround the living cell to form an extracellular covering called a coccosphere (*e.g.* Winter & Siesser, 1994; Young, 1994). Classification of both living and fossil coccolithophores is based exclusively on coccolith morphology and, at species level, on fine variations in size and shape (Jordan & Green, 1994; Young *et al.*, 2003).

General aspects of coccolithophore biogeography and habitat are known from taxonomic surveys of the plankton and of bottom-sediments (*e.g.* Knappertsbusch, 1990; Samtleben & Schröder, 1992; Kleijne, 1993; Winter *et al.*, 1994; Samtleben *et al.*, 1995; Baumann *et al.*, 2000; Hagino *et al.*, 2000; Cros, 2001; Triantaphyllou *et al.*, 2002). Individual species are mostly cosmopolitan, but with more or less limited latitudinal distributions. Thus, broad biogeographic coccolithophore zones are recognised (McIntyre & Bé, 1967; Okada & Honjo, 1973; Winter *et al.*, 1994). In part, these latitudinal zones reflect temperature tolerance but, even at this level, it is apparent that other factors are of major significance. For instance, the presence of nannofloral zones associated with equatorial upwelling and the subtropical oligotrophic gyres suggest control by nutrients/trophic level, rather than temperature alone. However, although much information is available on the oceanic scale (*e.g.* McIntyre & Bé, 1967; Okada & Honjo, 1973; Honjo & Okada, 1974; Kleijne, 1991, 1992, 1993; Hagino *et al.*, 2000), as well as of smaller areas (*e.g.* Winter *et al.*, 1979; Reid, 1980; Winter, 1985; Mitchell-Innes & Winter, 1987; Samtleben & Schröder, 1992; Ziveri *et al.*, 1995a, b; Baumann *et al.*, 1999, 2000; Cros, 2001; Triantaphyllou *et al.*, 2002, 2004), the environmental parameters that control coccolithophore distribution are still poorly understood. This reflects, in part, a shortage of suitable studies on natural populations. Much of the available data deal with relative abundances in coccolithophore assemblages, which are likely biased. Little work has been done so far on absolute numbers or on absolute abundances of single species relative to ecological parameters in modern communities (*e.g.* Venrick, 1982). In addition, in many studies, only surface-water samples (*e.g.* from 5m or 10m water-depth) have been investigated.

Nevertheless, the eastern part of the study area is one of the few regions where quite a number of coccolithophore studies have been conducted during the last 15 years. Most of these studies dealt with the Benguela Upwelling regime off SW Africa. Distinct species assemblages have been shown to be strictly associated with the various surface and subsurface water-masses and related hydrological fronts

generated by the upwelling processes (*e.g.* Friedinger & Winter, 1987; Giraudeau *et al.*, 1993; Giraudeau & Bailey, 1995). The temporal variations in coccolithophore populations also mirror the seasonal changes of the main hydrographic conditions off SW Africa (Giraudeau *et al.*, 2000; Romero *et al.*, 2002). In turn, the highest coccolith fluxes are inversely correlated with fluctuations in sea-surface temperature and, thus, with the seasonal dynamics of coastal upwelling occurrence. Results obtained from surface-sediment studies also indicate that the coccolith distribution seems to be temperature- and nutrient-controlled, covarying with the seaward extension of the upwelling filament zone in the Benguela region (Giraudeau, 1992; Baumann *et al.*, 1999; Boeckel & Baumann, 2004). In contrast, coccolithophores have been very scarcely investigated in the oligotrophic South Atlantic since McIntyre & Bé (1967), and data on living coccolithophores in this area are extremely limited (Boeckel & Baumann, 2008). The nannoplankton distribution to the south of Africa has been studied (Verbeek *et al.*, 1989), but beyond that, only the occurrence and distribution of the species in surface-sediments has been investigated (Mostajo, 1984; Boeckel *et al.*, 2006).

Therefore, the aims of this study were: 1) to investigate the coccolithophore species composition in an E-W transect, from the nutrient-enriched waters of the Benguela Current towards the nutrient-depleted waters of the Subtropical Gyre; (2) to examine and correlate the species occurrences to the means of phosphate and nitrate content, as well as temperature, in order to add some precision to the habitat preferences of the species; and finally (3) to study the depth-distribution of the species in each of the oceanic regimes.

2. Modern oceanography of the study area

The oceanic upper-layer circulation of the eastern South Atlantic has been summarised in a number of comprehensive reviews (Lutjeharms & Meeuwis, 1987; Peterson & Stramma, 1991; Reid, 1996; Shannon & Nelson, 1996), so only a brief summary is given here.

An important feature of the South Atlantic circulation system (Figure 1) is the cross-equatorial transport of warm surface-waters from the Indian Ocean and from the anticyclonic South Atlantic Gyre into the North Atlantic Ocean, by means of the South Equatorial Current. In the eastern South Atlantic off SW Africa, the surface-water circulation is dominated by the northward-directed Benguela Coastal Current, the coastal tongue of the Benguela Current (BC), and the warmer, southward-flowing Angola Current (Figure 1). The Benguela Coastal Current and Angola Current converge between 14˚ and 16˚S, forming a marked front on the shelf (Angola-Benguela Front), which is well-defined in terms of both temperature and salinity (Shannon & Nelson, 1996). In addition, the prevailing winds in this region in turn drive an offshore surface drift and cause coastal upwelling of cold, nutrient-rich water, especially

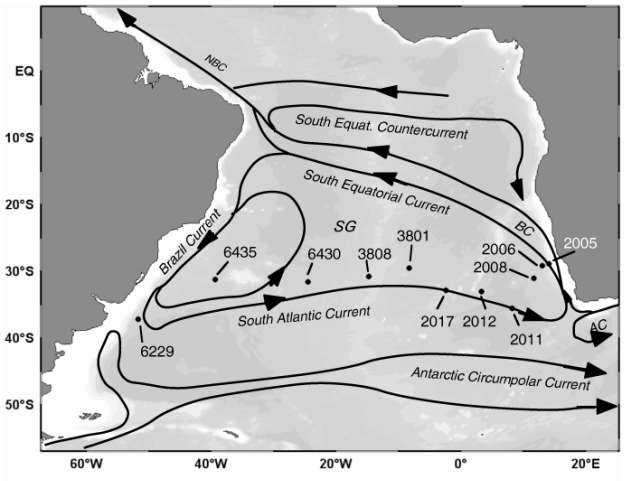

Figure 1: Schematic map of the main circulation in the upper level of the South Atlantic Ocean (redrawn mainly from Peterson & Stramma, 1991). Locations of the water-stations are indicated as black dots. AC – Agulhas Current, BC – Benguela Current, SG – Subtropical Gyre

during austral winter. Upwelling occurs in a number of upwelling cells, south of about 18˚S, with a major, semi-permanent cell at 27˚S (Shannon & Nelson, 1996). This upwelling leads to enhanced biological productivity off Namibia. The typical westward extent of the upwelling is between 150 and 250km off the coast.

Further offshore, the north-westward-flowing Benguela Oceanic Current, which is the oceanic portion of the BC, is characteristic of the upper-layer waters. This flow feeds into a broad, north-westward-flowing South Equatorial Current, forming the eastern limb of the Subtropical Gyre (SG). The South Equatorial Current itself consists of two branches, a main stream flowing south of 10˚S and a trade-wind-forced smaller, faster-flowing branch, between 2˚ and 4˚S (Peterson & Stramma, 1991). At about 10˚S, off Brazil, the South Equatorial Current splits into two branches, the southward-flowing Brazil Current and the northward-flowing North Brazil Current (Figure 1; Peterson & Stramma, 1991). The Brazil Current transports relatively warm surface-water southwards, until it encounters the cold, northward-moving Malvinas Current. This generates the highly dynamic Brazil-Malvinas Confluence that causes the eastward deflection of the Brazil Current into the South Atlantic Current. At the southern border of the Subtropical Front, the warmer South Atlantic Current waters parallel the cold and nutrient-rich Antarctic Circumpolar Current in the south. The boundary between subtropical and subantarctic waters might extend regionally over a large area between 30˚ and 45˚S (Smythe-Wright *et al.*, 1998). Off the south-western tip of Africa, the SAC meets the westward-directed Agulhas Current, which consists of warm and saline Indian Ocean water. At about 10˚E, the SAC deflects northward and merges into the BC. This southern end of the Benguela system, the retroflection of the Agulhas Current, is responsible for a substantial amount of warm and salty water being transported from the Indian Ocean to the South Atlantic.

The vertical distribution of temperature and nutrients (phosphate and nitrate) down to 200m water-depth are displayed along an E-W transect at 32.5˚S (Figure 2). Nutrient data were obtained using the World Ocean Atlas (Conkright *et al*., 1994). The data used in this study are monthly means, so that the limited number of data-points result only in a rather low resolution of nutrient and temperature in the presented transect. Monthly mean temperature data for February yields a rather consistent variation throughout the investigated transect. A slight increase in sea-surface temperatures, from 16-20˚C to 20-24˚C in the uppermost 100m of water-depth, is observed toward the west. Phosphate concentrations of up to 0.3μmol/l at the surface and >0.5μmol/l at a depth of >100m in the BC were slightly higher than in the SG, where surface values ranged from 0.1-0.2μmol/l. A similar distribution was observed for nitrate concentrations (Figure 2). In the BC, the nitrate content ranged from 2.0μmol/l at the surface to >7.0μmol/l at a depth of >150m, whereas the values in the SG extended from 0.5-1.5μmol/l at the surface (<50m water-depth) to 2.0-5.0μmol/l at a water-depth of >100m.

3. Material and methods

A total of 51 water-samples, from between the depths of 0m and 200m, were collected from 11 stations. The samples were taken during various R/V *Meteor* cruises in different years (see Table 1), forming an E-W transect between SW Africa and SE South America (Figure 1). Sample stations were located from about 29˚S to 37˚S and from 14˚E to 51˚W (Table 1). Although the gaps in sampling periods between the cruises may present difficulties in directly comparing the coccolithophore assemblages, the datasets were combined in order to gain a complete coverage of the various water-masses in the central South Atlantic.

Water-samples of generally 2l volume were taken by hydrocasts attached either to a multinet or to a rosette (Hydro-Bios, Kiel). Onboard, the sea-water was filtered immediately through cellulose nitrate filters (Sartorius™, 47mm or 25mm diameter, 0.45μm pore-size) and dried for 24 hours at 50˚C. The filters were then stored in plastic Petri dishes and were shrink-wrapped with silica gel in film to protect them from humidity.

In the laboratory at Bremen University, a piece of each filter was fixed, with double-sided adhesive tape, to an aluminium stub. These stubs were sputtered with gold and the filters were examined quantitatively for coccolithophores with a scanning electron microscope (SEM; Zeiss DSM 940A). During counting, each sample was examined at a magnification of 3000x in transects across the filter area. Whole coccospheres, as well as coccoliths, were counted. Identification and taxonomy of species follows that outlined by Kleijne (1993), Jordan & Kleijne (1994) and Winter & Siesser (1994). Thus, the taxonomy of the species *Emiliania huxleyi*, and especially *Calcidiscus leptoporus*, is the old, classical one – morphotypes and genotypes (*e.g*. Young & Westbroek, 1991; Hagino *et al*., 2005; Hagino & Okada, 2006) have not been distinguished, since part of the data stem from counts that were performed as part of a PhD project over 10 years ago (Čepek, 1996).

Coccolith numbers were converted to coccosphere units to obtain the number of individuals/l of sea-water. Therefore, numbers of coccoliths on a coccosphere of each of the different species were counted. For each species, a mean was then calculated. For species that were not observed as coccospheres in the studied samples, the data was taken from the literature (Table 2). Coccolithophore cells/l of sea-water were then calculated as follows:

$$\text{Cell numbers per litre} = \frac{C * A}{a * V}$$

where C is the number of coccospheres, A is the entire area of the filter, a is the counted area of the filter, and V is the volume of water filtered. The data presented in this paper are archived in the PANGAEA database (www.pangaea.de).

4. Results

4.1 Cell density and species diversity of total coccolithophores

Coccoliths were found in all of the studied samples, and intact coccospheres were also present in most of the samples. In the upper water-column of the oligotrophic gyre regime, the standing crop of coccolithophores was relatively low (<50*10^3 individuals/l), and the species diversity was at its lowest. In contrast, in the vicinity of the temperate BC, high coccolithophore cell densities of up to 396* 10^3 individuals/l were observed (Figure 3, Table 3), and the species diversity was relatively high in comparison to the SG. The highest species diversity was found at Stations GeoB 2008 (50m water-depth) and GeoB 2012 (20m water-depth), which each yielded 34 coccolithophore taxa. The highest diversities generally occurred at stations in the transition zone from the BC to the SG waters. In addition, the highest numbers of total holococcolithophores (up to 31*10^3 individuals/l) also occurred in the upper water-column of this area (Figure 3).

Cruise	Month/Year	GeoB Station	Position	Sampling depths (m)
M23-1	02/1993	2005	28˚53.7'S / 14˚09.4'E	0, 20, 40, 100
M23-1	02/1993	2006	29˚10.9'S / 13˚07.5'E	0, 20, 40, 60, 80, 100
M23-1	02/1993	2008	31˚06.1'S / 11˚42.9'E	25, 50, 100
M23-1	02/1993	2011	35˚36.6'S / 08˚15.8'E	20, 40, 60, 80, 100
M23-1	02/1993	2012	33˚02.7'S / 03˚20.3'E	0, 20, 40, 60, 80, 100
M23-1	02/1993	2017	32˚50.6'S / 02˚23.4'W	0, 20, 40, 60, 80, 100
M34-3	02/1996	3801	29˚30.0'S / 08˚17.6'W	20, 50, 150, 200
M34-3	02/1996	3808	30˚48.6'S / 14˚42.7'W	20, 50, 100, 150, 200
M46-4	03/2000	6430	31˚27.6'S / 24˚30.9'W	5, 20, 50, 100, 150
M46-4	03/2000	6435	31˚14.7'S / 39˚20.0'W	5, 10, 50, 100, 150
M46-2	12/1999	6229	37˚13.7'S / 51˚41.3'W	10, 20, 50

Table 1: Geographical positions and sampling depths of all GeoB stations

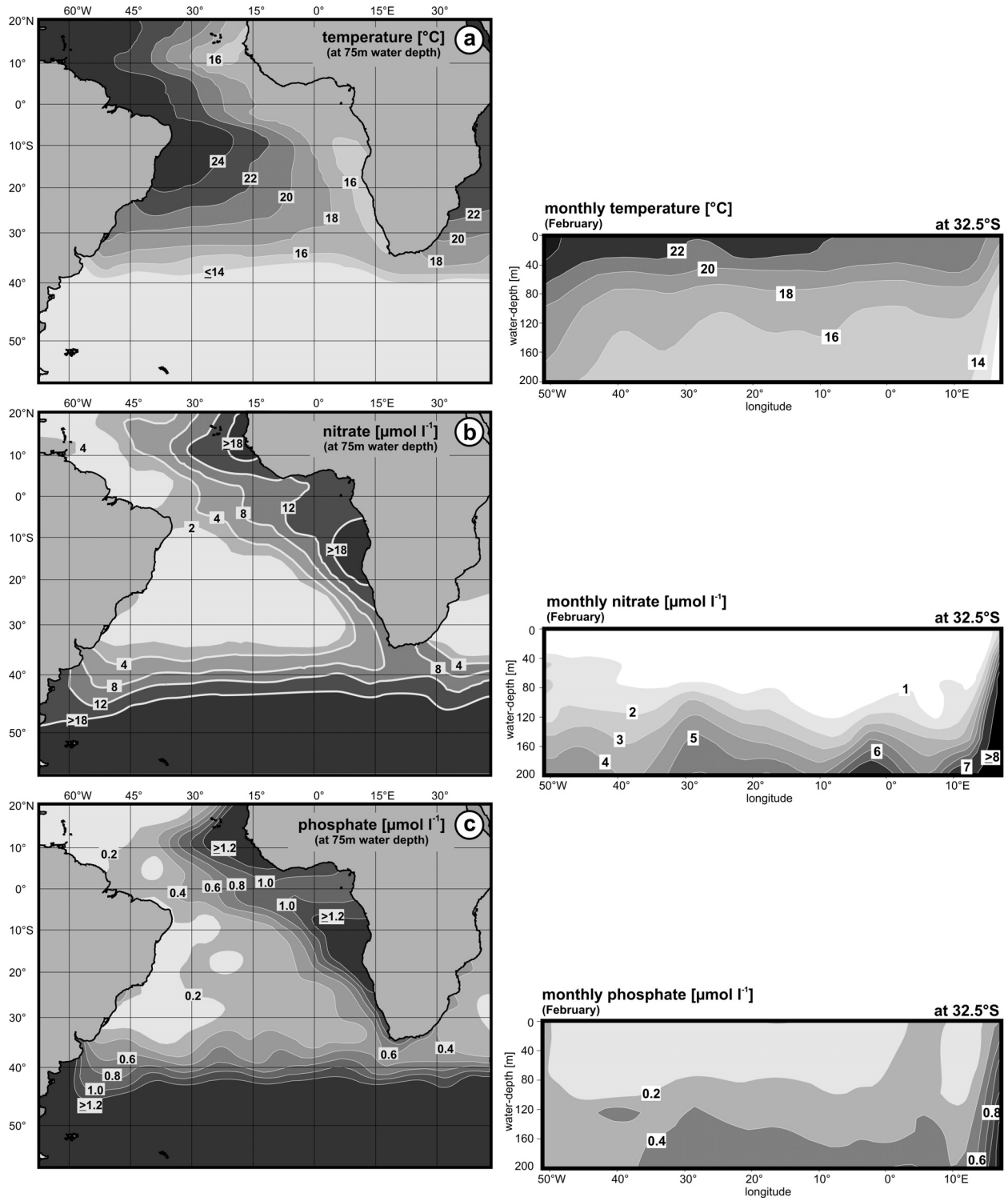

Figure 2: Maps of (**a**) temperature, (**b**) nitrate concentration and (**c**) phosphate concentration (all mean annual at 75m depth), as well as the corresponding transect at 32.5˚S (mean monthly data). Hydrographic data are available from the World Ocean Atlas (1994; see http://ingrid.ldgo.columbia.edu/SOURCES/.LEVITUS94/)

4.2 Distribution of coccolithophore assemblages and species

A total of 70 species was identified. The assemblages comprised 51 heterococcoliths and 19 holococcoliths. However, only 10 heterococcolithophore species, with the holococcolithophores, reached more than 10% of the nannoflora, in at least one of the studied samples. Of these, *Emiliania huxleyi* was the most abundant species in many of the samples (generally 10-65%). From the floral composition and the species cell densities, three broadly-defined coccolithophore assemblages were identified, which can be correlated to the BC, the oligotrophic SG, and the lower photic

Species	Coccoliths per coccosphere	Data source
Acanthoica acanthifera	42	Winter & Siesser (1994)
Calcidiscus leptoporus	24	this study
Calciosolenia brasiliensis	90	this study
Discosphaera tubifera	55	this study
Emiliania huxleyi	single-layered: 12	this study
Emiliania huxleyi	multi-layered: 44	this study
Florisphaera profunda	65	this study
Gephyrocapsa ericsonii	16	this study
Gephyrocapsa oceanica	16	this study
Oolithotus fragilis	37	this study
Rhabdosphaera clavigera	42	Kleijne (1993)
Rhabdosphaera xiphos	45	this study
Syracosphaera halldalii	44	this study
Syracosphaera pulchra	26	this study
Umbellosphaera irregularis	20	this study
Umbellosphaera tenuis	22	this study
Umbilicosphaera sibogae	80	this study

Table 2: Number of coccoliths per coccosphere of the most common species, as used in this study

zone. A more distinct differentiation of the assemblages is hampered by the relatively low depth-resolution, as well as the longitudinal resolution of the samples.

The predominant group in the BC (Figures 4, 5) consists of at least five species (*E. huxleyi*, *Gephyrocapsa ericsonii*, *Rhabdosphaera xiphos*, *Umbellosphaera irregularis*, *Syracosphaera halldalii*), all of which exhibit their highest cell numbers at the easternmost stations (2005, 2006, 2008). In this regime, the coccolithophore assemblage was dominated by *E. huxleyi* (29-62%), reaching its highest numbers in mid-depth waters (30-70m water-depth). In addition, *G. ericsonii* (up to 32%), *U. irregularis* (up to 16%) and *R. xiphos* (up to 12%) were particularly common components of the nannofloras.

The SG group consists of five species and species groups (*Discosphaera tubifera*, *Umbellosphaera tenuis*, *Calciosolenia brasiliensis*, *Syracosphaera pulchra*, *Acanthoica* spp.), together with the total holococcolithophores. Although all of these taxa reach their highest cell densities at stations in the transition zone from the BC to the SG waters, they all show high relative abundances in the upper water-column (<80m water-depth) of the oligotrophic SG (Figure 6). In particular, *U. tenuis* (up to 66%), *D. tubifera* (up to 18%), and *S. pulchra* (up to 10%) were common components of the nannoflora. In addition to the species mentioned above, *E. huxleyi* also occurred in relatively high abundances (up to 40%) in this regime.

The nannoflora in the lower photic zone (>80-100m water-depth) is characterised by abundant *Florisphaera profunda* (up to 52%) in the nutrient-depleted western part of the SG (Figure 7), whereas common to minor occurrences of *Calcidiscus leptoporus* (up to 20%), *Oolithotus fragilis* (up to 17%), and *Umbilicosphaera sibogae* (up to 10%) occurred in the boundary zone from the BC to the SG waters. Unfortunately, sampling at the easternmost stations never exceeded 100m water-depths, so that the depth-distribution in the BC region remains uncertain. *E. huxleyi* and *Gephyrocapsa oceanica*, although exhibiting their highest cell numbers in the middle photic BC region, were constrained to deeper waters in the warm, oligotrophic stations of the SG (Figure 4).

5. Discussion

5.1 Standing crop

Major changes in coccolithophore diversity, and especially in cell density, occur across the transition of the BC to the SG, which is associated with shifts in sea-surface temperature and nutrients. The coccolithophore cell numbers observed in the BC regime were significantly higher than

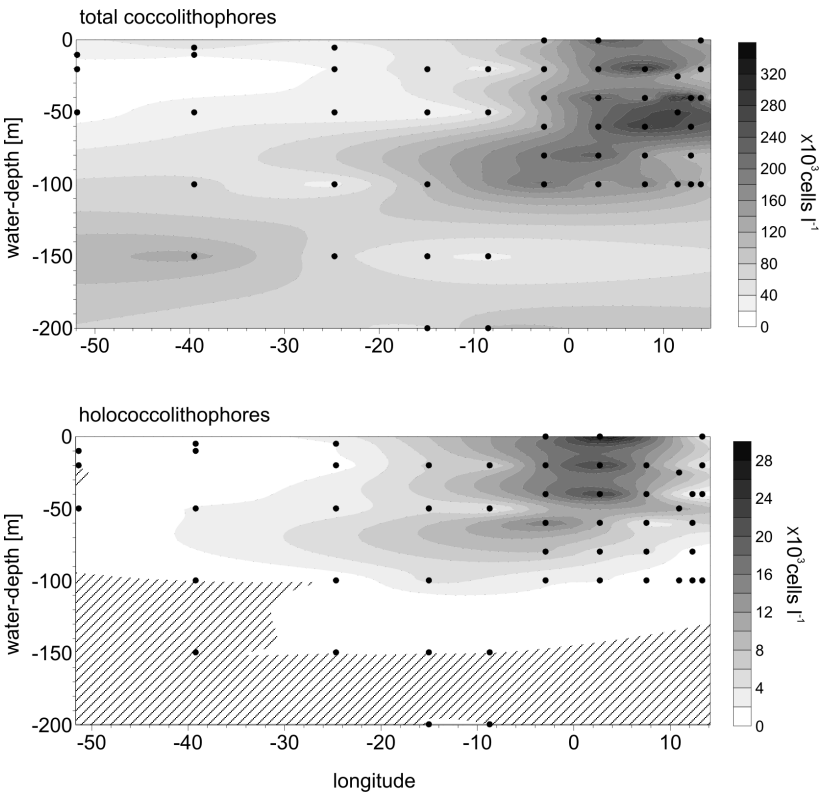

Figure 3: Vertical distribution of total standing crop of coccolithophores (**above**), and cell numbers of total holococcolithophores (**below**) along the studied transect. Hatched area represents absence of taxa

Water-column	Taxa	Subtropical Gyre Cell density * 10^3 cells/l min	max	mean	Benguela Current Cell density * 10^3 cells/l min	max	mean
entire	total coccolithophores	7.3	302.4	109.1	77.6	396.3	170.6
	E. huxleyi	0.6	129.9	31.8	34.4	199.7	76.7
	G. ericsonii	0.1	4.8	31.2	3.2	85.7	34.2
	G. oceanica	0.1	2.1	0.3	0.1	2.3	0.8
UPZ	*Acanthoica* spp.	0.1	6.4	1.1	4.2	4.2	0.6
(0-<80m)	*C. brasiliensis*	0.1	6.6	0.7	0.2	5.4	2.5
	D. tubifera	0.1	4.4	1.3	0.5	2.7	1.1
	R. xiphos	0.1	16.4	2.1	2.5	24.8	13.9
	S. halldalii	0.1	16.7	1.9	0.1	17.9	5.2
	S. pulchra	0.1	4.3	1.3	0.1	6.4	1.1
	U. irregularis	0.1	27.9	1.8	0.2	36.6	9.6
	U. tenuis	1.6	84.1	24.0	0.2	23.1	6.1
	holococcolithophores	0.8	30.6	8.6	1.4	10.7	4.5
LPZ	*C. leptoporus*	2.3	30.5	6.0	2.3	17.9	2.3
(80-100m)	*F. profunda*	0.5	34.6	7.3	2.2	12.7	5.4
	Oolithotus spp.	0.7	41.0	12.1	0.1	0.7	0.3
	U. sibogae	0.1	10.7	2.8	0.2	2.0	0.6

Table 3: Comparison of the most important nannofloral elements of the Subtropical Gyre and Benguela Current. Minimum, maximum and mean absolute cell numbers within the upper and lower photic zone are displayed

those in the oligotrophic gyre (Figure 3, Table 3). Although located far away from the actual upwelling, total cell densities are in the order of those previously reported from the Namibian upwelling system (Giraudeau *et al*., 1993). Coccolithophore standing crops reach up to 466*10^3 cells/l, the maximum cell density occurring at the shallow-water stations (Giraudeau *et al*., 1993). The presented data is also in good agreement with the results of Giraudeau & Bailey (1995), who examined coccolithophores in an upwelling cell off Hondeclip Bay and calculated total cell densities of up to 278*10^3 cells/l. However, water-samples from a nearby region, investigated by Mitchell-Innes & Winter (1987), revealed greater differences, compared to our data. The authors observed assemblages of up to 2340*10^3 cells/l in mature, upwelled water, adjacent to an upwelling cell off the Cape Peninsula. The influence of the coastal upwelling cells on the offshore waters, through offshore migration of chlorophyll filaments, is strongest during austral summer (Romero *et al*., 2002). During this time of the year, the coccolith flux, as observed in a mooring site close to the Namibian Upwelling (at about 29˚S, 13˚E), shows bimodal seasonality, with major peaks in austral winter and summer. Therefore, it can be inferred that the good correspondence of the present cell densities at the sites within the BC with those previously reported from the Namibian and South African shelves reflects the influence of filaments which supply nutrients to the surface-waters, resulting in higher numbers of mainly placolith-bearing species.

Placolith-bearing species occur in much higher cell densities than umbelliform species, which typically inhabit oligotrophic regimes (*e.g*. Young, 1994; Haidar & Thierstein, 2001; Hagino & Okada, 2006). Thus, a generally low standing stock was observed, especially in the upper photic zone (<80m water-depth) of the SG. Here, the coccolithophore flora was rather similar to previously-published assemblages from comparable oceanic settings (*e.g*. Hagino *et al*., 2000; Kinkel *et al*., 2000), in terms of cell density and the dominance of typically non-placolith-bearing species. The extremely low coccolithophore cell densities in the upper photic zone (<50m water-depth) may be explained by the extremely low nitrate concentrations during the sampling period in

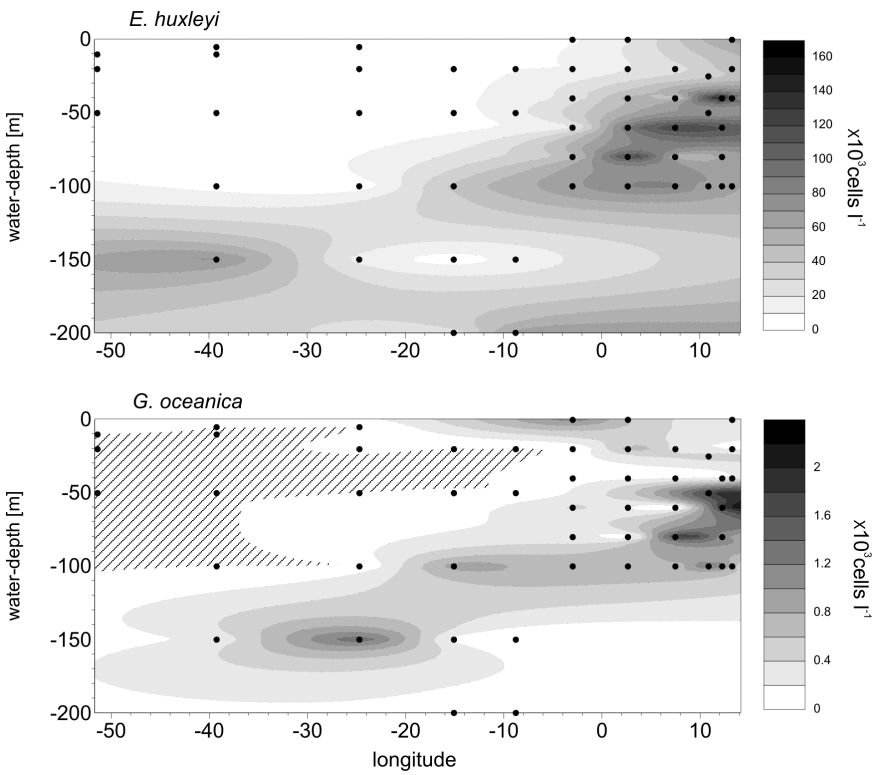

Figure 4: Vertical distribution of *Emiliania huxleyi* and *Gephyrocapsa oceanica* (absolute cell numbers) along the studied transect. Hatched area represents absence of taxa

austral summer.

Cell densities in the SG increased below 80-100m water-depth. *Florisphaera profunda* dominated the coccolithophore assemblage of the lower photic zone and was largely responsible for this increase in cell density. This species is known to occur in relatively high abundances, even under relatively low-nutrient conditions (Haidar & Thierstein, 2001). In addition, the highest concentrations of coccolithophores were observed at the thermocline in well-stratified waters (*e.g.* Hagino *et al.*, 2000). The upper or lower vertical distribution limits of many coccolithophore taxa coincided with the top of the thermocline. However, species such as *Emiliania huxleyi* and *Gephyrocapsa oceanica*, which exhibit their highest cell numbers in the middle photic zone of the BC region, also contributed to the lower-photic assemblage in the warm, oligotrophic stations of the SG (Figure 4).

5.2 Environmental controls on coccolithophore species distribution

The present study reveals hydrographic controls on the distribution of some of the major taxa. The nannofloras in the nutrient-enriched stations of the BC are characterised by high cell numbers of *Emiliania huxleyi* and *Gephyrocapsa ericsonii*, while the other species occur in much lower absolute cell numbers. Whereas *E. huxleyi* was often found to dominate assemblages in temperate to arctic waters (*e.g.* Mitchell-Innes & Winter, 1987; Kleijne, 1993; Giraudeau & Bailey, 1995), another *Gephyrocapsa* species, *G. oceanica*, is well known to also prefer eutrophic waters (Kleijne, 1993; Andruleit *et al.*, 2000). However, *G. oceanica* only occurs in extremely low cell numbers in the studied samples, whereas *G. ericsonii* is numerically much more abundant and exhibits a distribution pattern rather similar to that of *E. huxleyi*. Nevertheless, not much is known about the ecology of *G. ericsonii*. Winter *et al.* (1979) reported *G. ericsonii* as a predominant nannoplankton species, along with *E. huxleyi*, in the Gulf of Elat, with a preference for near-coastal currents with high nutrient-contents. Work on sediment cores by Takahashi & Okada (2000) and Okada & Wells (1997) from off western Australia also suggest that *G. ericsonii* prefers eutrophic conditions. This is also supported by the correlation of cell numbers and nutrient concentrations in the present study (Figure 8). In addition, a clear correlation of higher cell numbers with decreasing temperatures can be seen, indicating a preference for eutrophic, upwelling conditions.

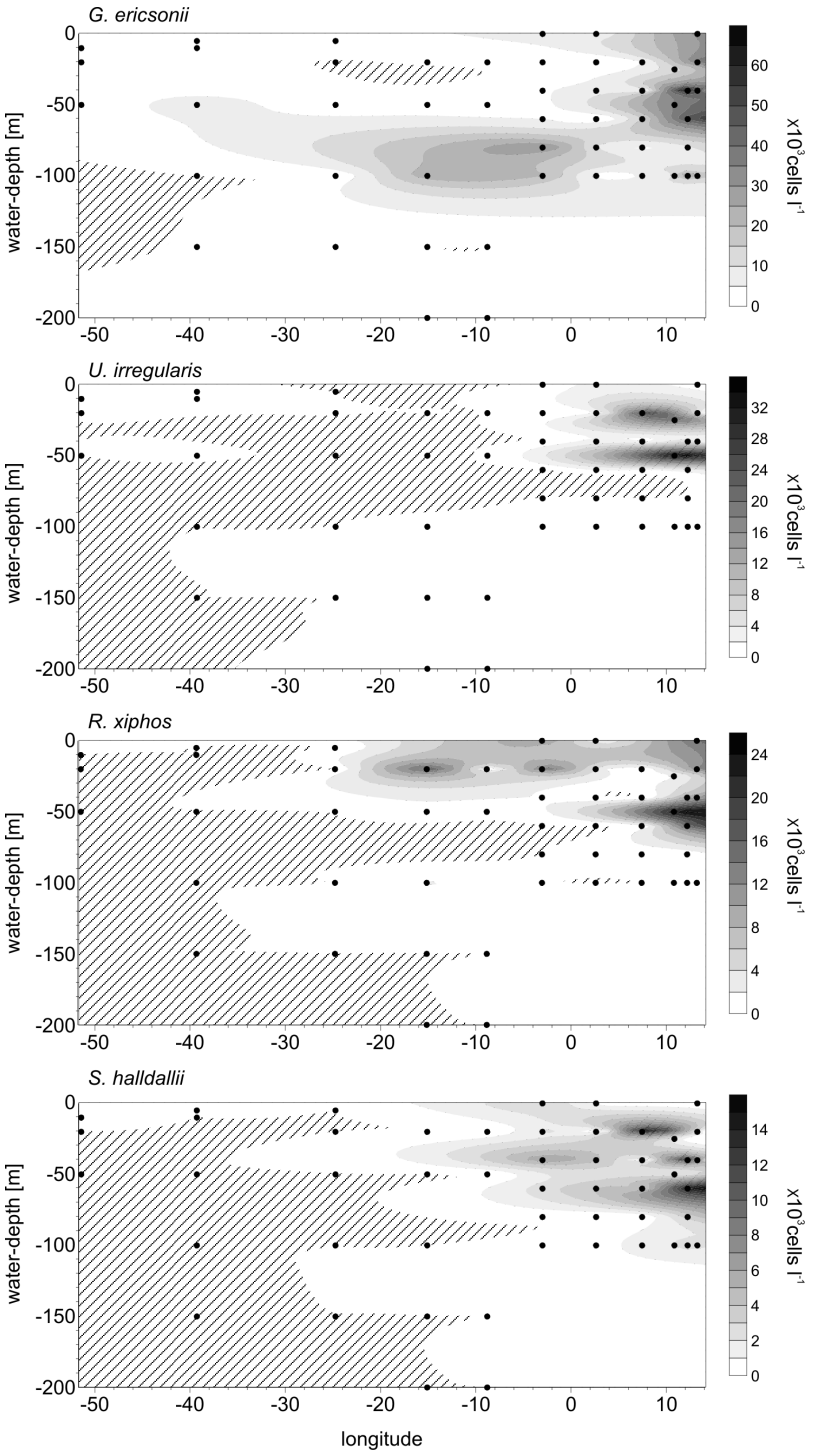

Figure 5: Vertical distribution of cell numbers of the species of the Benguela Current assemblage (*Gephyrocapsa ericsonii, Umbellosphaera irregularis, Rhabdosphaera xiphos, Syracosphaera halldalii*) along the studied transect. Hatched area represents absence of taxa

E. huxleyi is known to be the most ubiquitous of all living coccolithophore species (*e.g.* McIntyre & Bé, 1967;

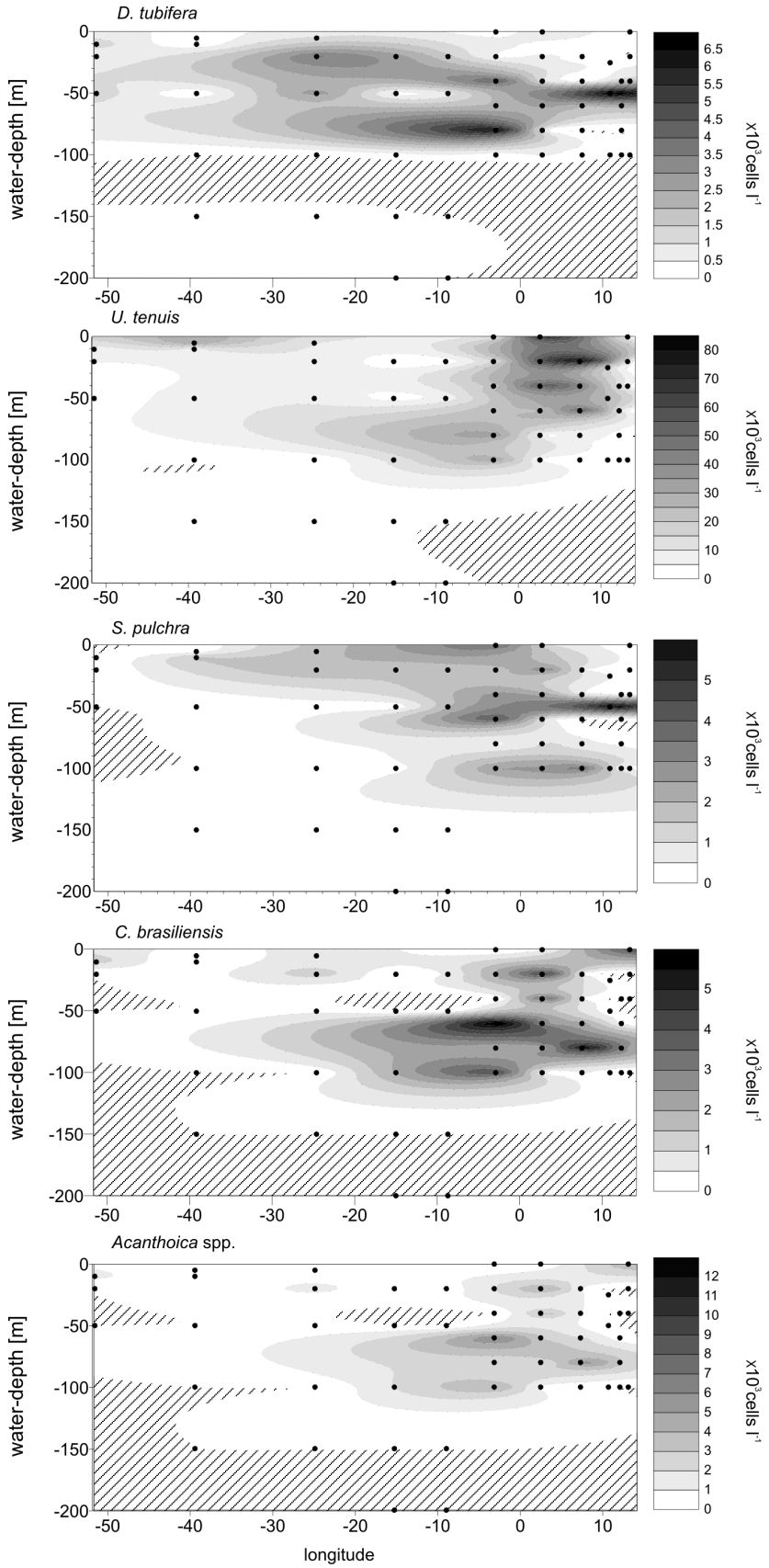

Figure 6: Vertical distribution of cell numbers of the upper-photic-zone species of the Subtropical Gyre (*Discosphaera tubifera, Umbellosphaera tenuis, Syracosphaera pulchra, Calciosolenia brasiliensis, Acanthoica* spp.) along the studied transect. Hatched area represents absence of taxa

Winter & Siesser 1994; Ziveri *et al*., 1995a; Hagino *et al*., 2000). It tolerates a temperature range from 1˚C to 30˚C, although its highest abundances occur at water-temperatures of <23˚C (Haidar & Thierstein, 2001), and it is common in eutrophic as well as oligotrophic conditions. In the present study, the highest abundance of *E. huxleyi* appeared in the BC at temperatures comparable to those of previous investigations (*e.g*. Haidar & Thierstein, 2001; Hagino & Okada, 2006). Nevertheless, the abundances at the other stations were high as well, so this species could be characterised as a euryoecious species, having a wide range of habitat tolerance. In addition, *G. oceanica* exhibits a rather similar distribution to *E. huxleyi*. Although cell numbers are extremely low, the species appeared with elevated cell numbers in the upper photic layer in the BC, whereas in the SG, *G. oceanica* was mainly observed below the thermocline. The species is also regarded as a eutrophic species (Kleijne *et al*., 1989; Kleijne, 1993), but it is also adapted to higher sea-surface temperatures (Hagino *et al*., 2000; Hagino & Okada, 2006). As shown by Brand (1994), coccolithophores such as *E. huxleyi* and *G. oceanica* tend to live at greater depths in the central gyres because of the higher nutrient availability at these depths. This finding is supported by the observations of Hagino *et al*. (2000), who found similar distribution patterns of these species in the Pacific. The authors explained the distribution by invoking different morphotypes, some occurring in the photic zone of the dynamic, eutrophic, mixed-water regimes, whereas other morphotypes occurred below the thermocline in the well-stratified stations.

The coccolithophore flora in the surface layer of the well-stratified SG could be distinguished from the BC nannoflora by the higher abundances of *Discosphaera tubifera*. This species generally occurred outside the upwelling areas, and has been referred to as part of the sub-

tropical zone flora (Jordan & Chamberlain, 1997), which is consistent with our observations. *D. tubifera* is reported to live at water-depths down to 40-80m in oligotrophic environments (*e.g.* Honjo & Okada, 1974; Reid, 1980; Hagino *et al.*, 2000; Malinverno *et al.*, 2003), also rather consistent with our observations (Figure 9). The same pattern is displayed by *Syracosphaera pulchra*, *Calciosolenia brasiliensis* and *Umbellosphaera tenuis*, all of which are non-placoliths known to prefer stable, stratified waters (Okada & McIntyre, 1977; Hagino *et al.*, 2000).

Umbilicosphaera irregularis has also been reported as a typical oligotrophic species (*e.g.* Young, 1994; Baumann *et al.*, 1999; Haidar & Thierstein, 2001). Its occurrence in the BC stations is surprising, and contradicts the usual notion. However, *U. irregularis* has been found in the Pacific Ocean, both at stations with extremely high temperatures (>30˚C) and high nutrient levels (Hagino *et al.*, 2000), as well as in the usual warm, oligotrophic environments. Hagino & Okada (2006) also showed that the concentration of this species generally had no relation to nutrient concentrations, except that it is absent when the phosphate concentration is relatively high. And therefore, the threshold of >0.7μmol/l was probably not reached in the studied BC stations. It is notable that the highest numbers of *U. tenuis* occurred in the transition zone from the BC to the SG. The correlation of its cell numbers with nitrate concentration clearly demonstrates that this species is adapted to low nutrient levels. Nevertheless, the tolerance of some morphotypes of *U. tenuis* (Kleijne, 1993; Hagino & Okada, 2006) for slightly nutrient-enriched, and possibly relatively stratified, waters cannot be excluded. So far, it is known that the SG assemblage within the upper 50m of the photic zone is mainly composed of *U. tenuis* Types III and IV (Boeckel & Baumann, 2008).

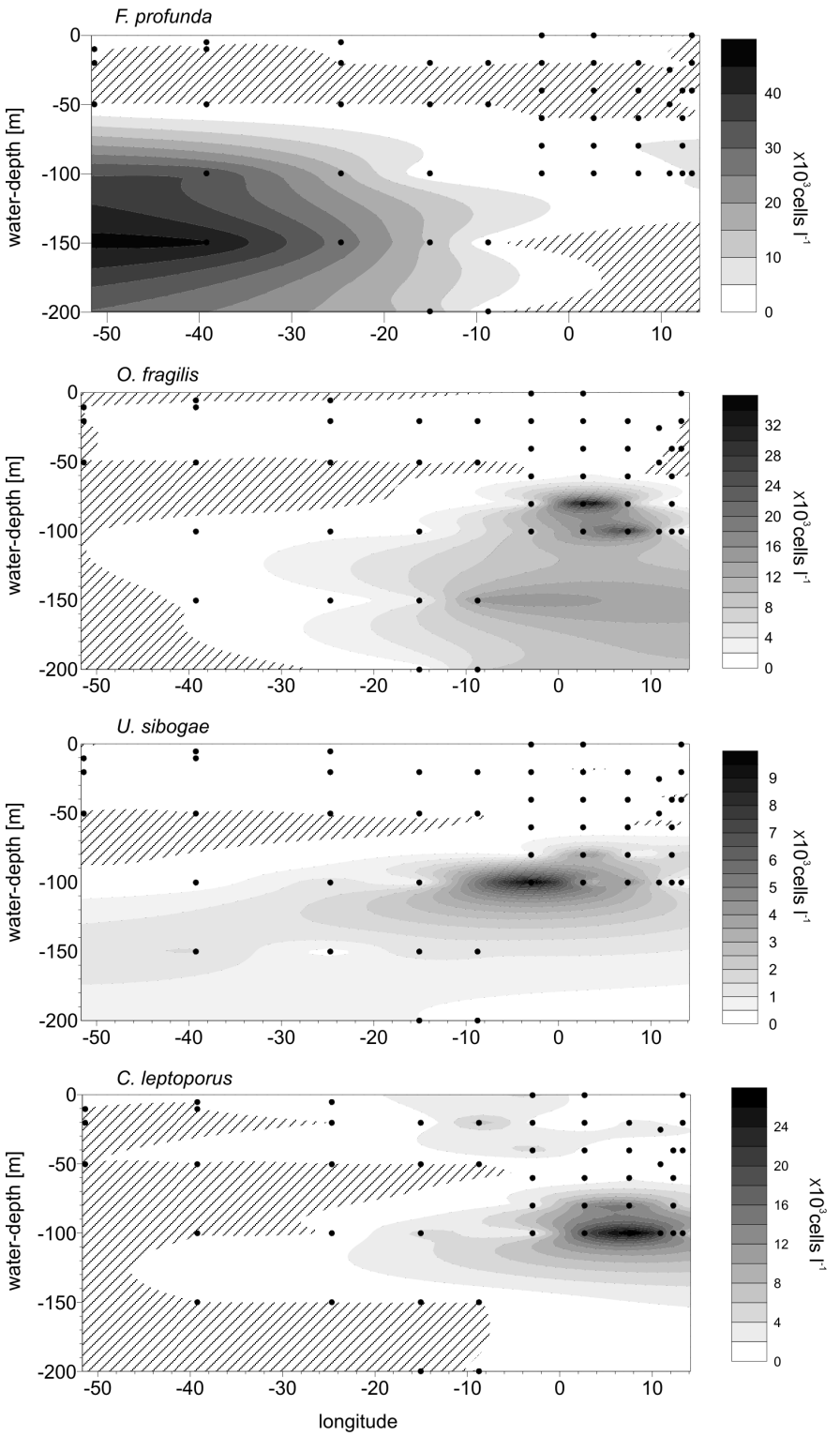

Figure 7: Vertical distribution of cell numbers of the deep-dwelling species (*Florisphaera profunda*, *Oolithotus fragilis*, *Umbilicosphaera sibogae*, *Calcidiscus leptoporus*) along the studied transect. Hatched area represents absence of taxa

Calcidiscus leptoporus, *Oolithotus fragilis* and *Umbilicosphaera sibogae* have been regarded as rather oligotrophic species in previous investigations (Okada & Honjo, 1975; Okada & McIntyre, 1979; Mitchell-Innes &

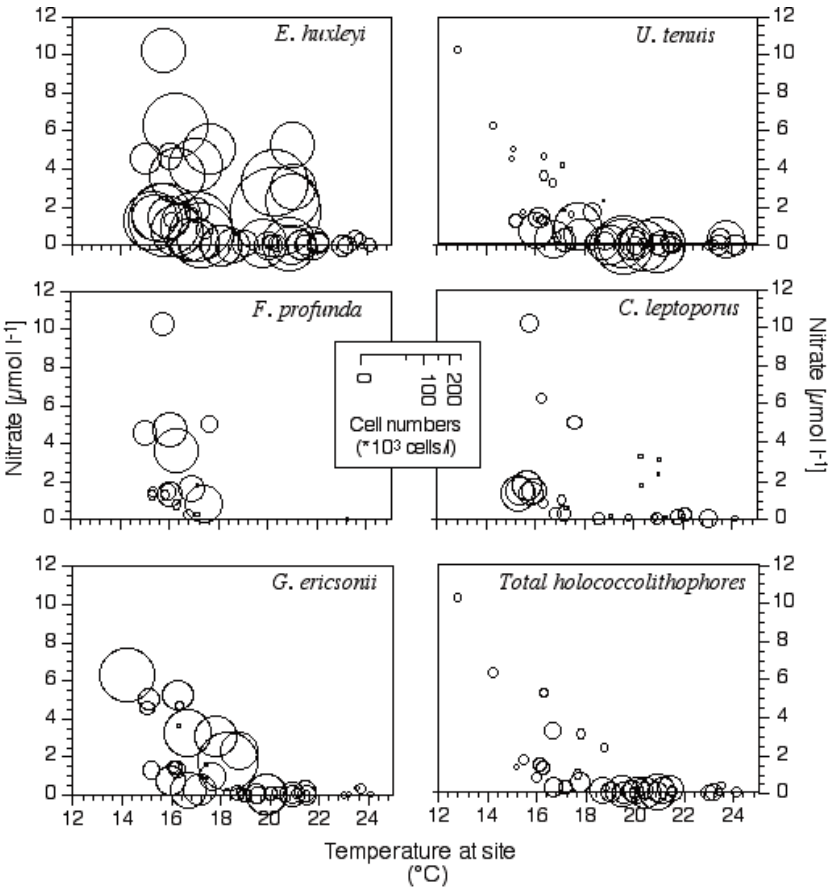

Figure 8: Correlation of nitrate concentration, water temperature (from conductivity-temperature-depth [CTD] casts) and absolute cell numbers of the most common species. Monthly mean values of nitrate at each station were obtained from the World Ocean Atlas (Conkright *et al*., 1994). The scale in the middle refers to the size of the bubbles (= absolute cell numbers)

Winter, 1987; Giraudeau, 1992), which is supported by our study. All of them showed their highest abundances below the thermocline (80m-100m), in the transition zone between the BC and SG regimes. High abundances of *U. sibogae* in the upper photic zone have previously been observed in the Gulf of Elat (Winter *et al*., 1979). Nevertheless, these species are regarded as deep-living taxa, basically influenced by water-mass stratification and nutrient level.

Modern holococcolithophores have been intensively investigated with respect to their geographical distribution (Kleijne, 1991). Their highest absolute abundances occur in the Mediterranean Sea and in the NE Atlantic Ocean, and are associated with lower nutrient levels. This generally corresponds well with the results of the present study, with holococcolithophores reaching their highest abundances at low nutrient concentrations.

5.3 Coccolithophore depth-distribution

Typical depth-related assemblages can be identified from the depth-distribution of the species, although the entire photic zone was not studied at high resolution. However, it is in fact possible to identify two main assemblages in the photic zone, an upper photic zone assemblage (UPZ) as well as the typical lower photic zone (LPZ) assemblage (Figure 9). The UPZ assemblage can generally be recognised until about 80m, to a maximum 100m, of water-depth, and is characterised by the highest coccolithophore cell numbers. Typical members of this group are species of the Syracosphaerales, the Rhabdosphaeraceae (*Discosphaera tubifera*, *Rhabdosphaera xiphos*, *Acanthoica* spp.), Syracosphaeraceae (*Syracosphaera halldalii*, *S. pulchra* shown as examples), Umbellosphaeroideae (*Umbellosphaera tenuis*, *U. irregularis*), as well as all of the holococcolithophore species observed in this study. Thus, the composition is rather similar to those previously published as UPZ assemblages (*e.g.* Winter *et al*., 1994; Jordan & Chamberlain, 1997; Hagino *et al*., 2000; Malinverno *et al*., 2003).

Some of the species, particularly *Calciosolenia brasiliensis*, *D. tubifera*, *Acanthoica* spp. and *Gephyrocapsa ericsonii*, do exhibit their highest cell numbers in the lowermost part of this UPZ. Some of them are already known to occupy intermediate water-depths, and have been termed middle photic zone (MPZ) assemblages, which are usually found between 80-120m of water-depth (Okada & Honjo, 1973; Jordan & Chamberlain, 1997). However, since all of these species are also present in the upper photic layer, a further differentiation has not been made in this study. Unlike the LPZ nannoflora, there is no hydrographic restriction for the MPZ nannoflora to move (or be moved) into shallower waters. In addition, the optimal depth-range of the species may vary due to changing environmental conditions during different seasons of a year, when, for example, surface-water stratification may be more pronounced (Reid, 1980). For this area of coccolithophore distribution, more study and detailed sampling across the thermocline is needed.

In addition, most of the lower-photic dwellers are abundant in tropical to subtropical regions, regardless of water stratification, as has been commonly observed in previous studies (*e.g.* Hagino *et al*., 2000). In particular, *Florisphaera profunda* is well known to occupy this niche in the LPZ regime (Jordan & Chamberlain, 1997) and also dominates the samples studied in the SG. Its cell density drastically decreased eastwards, and is low in the area of the BC. As reported previously (*e.g.* Okada & Honjo, 1973; Jordan & Chamberlain, 1997; Hagino *et al*., 2000; Malinverno *et al*., 2003), other species, such as *Oolithotus fragilis*, are mainly restricted to the LPZ. In addition,

Calcidiscus leptoporus and, especially, *Umbilicosphaera sibogae* were observed as deep-living species (Figure 9). *Emiliania huxleyi*, present in cell numbers similar to those of *F. profunda*, as well as *G. ericsonii* and *G. oceanica*, also occurred in the LPZ of the SG.

Thus, the vertical distribution of all coccolithophore taxa, except the three placolith-bearing species *G. ericsonii*, *G. oceanica* and *E. huxleyi*, was probably controlled by UPZ water-temperature and stratification of the water-column. The latter certainly has an influence on the presence of nutrients in the study area.

6. Summary and conclusions

A total of 70 species (19 holococcolithophores, 51 heterococcolithophores) was observed in this study. *Emiliania huxleyi* was numerically the most abundant species in the majority of samples, but high cell numbers (>50*10^3 cells/l) of *Gephyrocapsa ericsonii* and *Umbellosphaera irregularis* were also observed.

1) Coccolithophores showed a difference in lateral distribution. This distribution was controlled by the relatively cool, nutrient-enriched waters of the BC, as well as by the warm, nutrient-depleted waters of the SG. Assemblages in the BC were characterised by at least five species (*E. huxleyi*, *G. ericsonii*, *Rhabdosphaera xiphos*, *U. irregularis*, *Syracosphaera halldalii*), which exhibit their highest cell numbers at the easternmost stations, reflecting higher nutrient levels. The SG generally contained the holococcolithophores and the species *Discosphaera tubifera*, *Umbellosphaera tenuis*, *Calciosolenia brasiliensis* and *Syracosphaera pulchra*, which exhibit an affinity for lower nutrient levels.

2) A distinct vertical stratification in the coccolithophorid assemblages was observed. Typical members of the UPZ assemblage are *D. tubifera*, *R. xiphos*, *Acanthoica* spp., *S. halldalii*, *S. pulchra* and, especially, *U. tenuis* and *U. irregularis*. The flora in the LPZ (>80-100m water-depth) was characterised by abundant *Florisphaera profunda* in the nutrient-depleted SG, whereas *Calcidiscus leptoporus*, *Oolithotus fragilis* and *Umbilicosphaera sibogae* occurred in the lower-photic boundary zone, from the BC to the SG waters.

3) Some species, such as *E. huxleyi*, *G. ericsonii* and *G. oceanica*, lived in a wide range of water-depths. In the BC, they appeared with higher abundances in the mixed layer, whereas they were more common at greater depths in the SG.

4) In the study area, the vertical distribution of all coccolithophore taxa, except the three placolith-bearing species mentioned above, was controlled by upper photic zone temperature and water stratification.

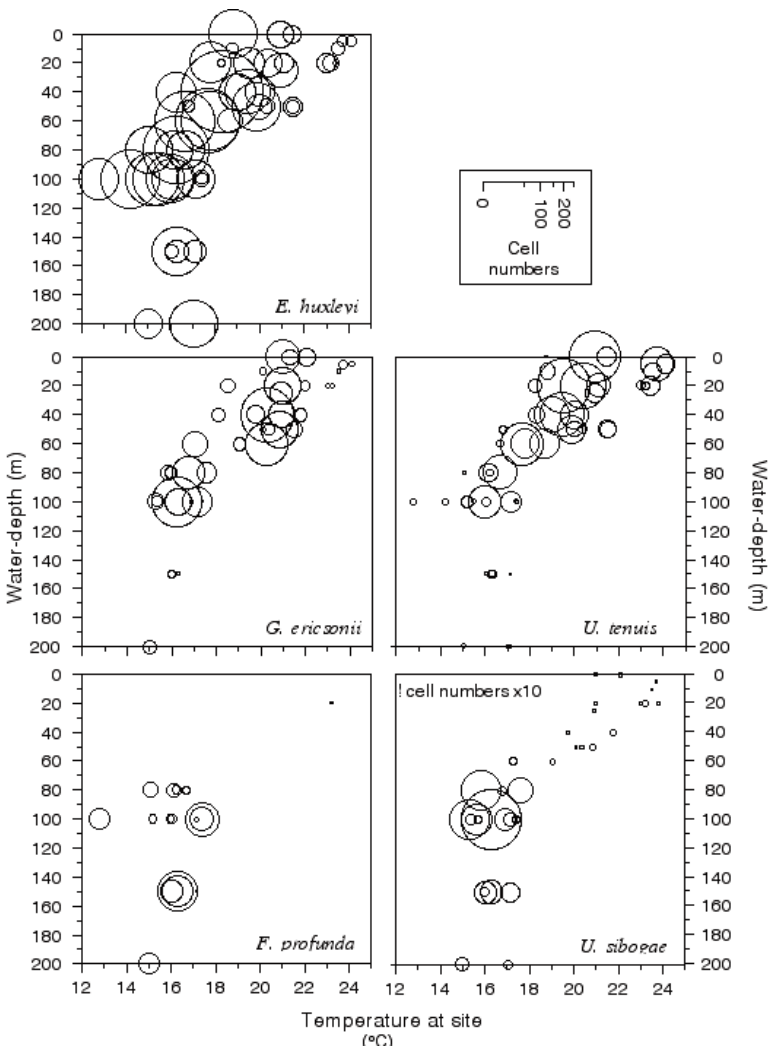

Figure 9: Correlation of absolute cell numbers of the most common species with water-depth and *in situ* water-temperature (from CTD casts). The scale in the middle refers to the size of the bubbles (= absolute cell numbers)

Acknowledgements

The authors would like to thank the officers and crew of the R/V *Meteor* and the scientific crews of the various *Meteor* cruises for their assistance. We are grateful to the reviewers, Drs Maria Triantaphyllou and Ric Jordan, and the Editor, Jackie Lees, for their constructive comments and suggestions on the manuscript. This research was funded by the Deutsche Forschungsgemeinschaft (Research grant BA 1648/11).

References

Andruleit, H., Stäger, S., Rogalla, U. & Čepek, P. 2000. Living coccolithophores in the northern Arabian Sea: ecological tolerance and environmental control. *Mar. Micropaleontol.*, **49**: 157-181.

Baumann, K.-H., Andruleit, H. & Samtleben, H. 2000. Coccolithophores in the Nordic Seas: Comparison of living communities with surface sediment assemblages. *Deep-Sea Res. II*, **47**: 1743-1772.

Baumann, K.-H., Čepek, M. & Kinkel, H. 1999. Coccolithophores as indicators of ocean water masses, surface-water temperature, and paleoproductivity – Examples from the South Atlantic. *In*: G. Fischer & G. Wefer (Eds). *Use of proxies in paleoceanography: Examples from the South Atlantic*. Springer, Berlin: 117-144.

Boeckel, B. & Baumann, K.-H. 2004. Distribution of coccoliths in surface sediments of the south-east South Atlantic Ocean: ecology, preservation and carbonate sedimentation. *Mar. Micropaleontol*., **51**: 301-320.

Boeckel, B. & Baumann, K.-H. 2008. Vertical and lateral variations in coccolithophore community structure across the subtropical frontal zone in the South Atlantic Ocean. *Mar. Micropaleontol*, **67**: 255-273.

Boeckel, B., Baumann, K.-H., Henrich, R. & Kinkel, K. 2006. Coccolith distribution patterns in South Atlantic and Southern Ocean surface sediments in relation to environmental gradients. *Deep-Sea Res. I*, **53**: 1073-1099.

Brand, L.E. 1994. Physiological ecology of marine coccolithophores. *In*: A. Winter & W.G. Siesser (Eds). *Coccolithophores*. Cambridge University Press, Cambridge: 39-49.

Čepek, M. 1996. Zeitliche und raeumliche Variationen von Coccolithophoriden-Gemeinschaften im subtropischen Ost-Atlantik: Untersuchungen an Plankton, Sinkstoffen und Sedimenten. *Ber. FB Geowissensch* (Univ. Bremen), **86**: 160pp.

Conkright, M.E., Levitus, S. & Boyer, T.P. 1994. World Ocean Atlas 1994 Volume 1: Nutrients. *NOAA Atlas NESDIS*, **vol.1**. US Depatment of Commerce, Washington DC: 150pp.

Cros, L., Kleijne, A., Zeltner, A., Billard, C. & Young, J.R. 2000. New examples of holococcolith-heterococcolith combination coccospheres and their implications for coccolithophorid biology. *Mar. Micropaleontol*., **39**: 1-34.

Friedinger, P.J.J. & Winter, A. 1987. Distribution of modern coccolithophore assemblages in the southwest Indian Ocean off southern Africa. *J. Micropaleontol*., **6**(1): 49-56.

Giraudeau, J. 1992. Distribution of recent nannofossils beneath the Benguela system: southwest African continental margin. *Mar. Geology*, **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**(14): 1825-1852.

Giraudeau, J., Bailey, G.W. & Pujol, C. 2000. A high-resolution time-series analysis of particle fluxes in the Northern Benguela coastal upwelling system: carbonate record of changes in biogenic production and particle transfer processes. *Deep-Sea Res. II*, **47**: 1999-2028.

Giraudeau, J., Monteiro, P.M.S. & Nikodemus, K. 1993. Distribution and malformation of living coccolithophores in the northern Benguela upwelling system off Namibia. *Mar. Micropaleontol*., **22**: 93-110.

Hagino, K. & Okada, H. 2006. Intra- and infra-specific morphological variation in selected coccolithophore species in the equatorial and subequatorial Pacific Ocean. *Mar. Micropaleontol*., **58**: 184-206.

Hagino, K., Okada, H. & Matsuoka, H. 2000. Spatial dynamics of coccolithophore assemblages in the equatorial western-central Pacific Ocean. *Mar. Micropaleontol*., **39**: 53-57.

Hagino, K., Okada, H. & Matsuoka, H. 2005. Coccolithophore assemblages and morphotypes of *Emiliania huxleyi* in the boundary zone between the cold Oyashio and warm Kuroshio currents off the coast of Japan. *Mar. Micropaleontol*., **55**: 19-47.

Haidar, A.T. & Thierstein, H.R. 2001. Coccolithophore dynamics off Bermuda (N. Atlantic). *Deep-Sea Res. II*, **48**: 1925-1956.

Honjo, S. & Okada, H. 1974. Community structure of coccolithophores in the photic layer of the mid-Pacific. *Micropaleontology*, **29**: 209-230.

Jordan, R.W. & Chamberlain, A.H.L. 1997. Biodiversity among haptophyte algae. *Biodiversity Conserv*., **6**: 131-152.

Jordan, R.W. & Green, J.C. 1994. A check-list of the extant haptophyta of the world. *J. Mar. Assoc., UK*, **74**: 149-174.

Jordan, R.W. & Kleijne, A. 1994. A classification system for living coccolithophores. *In*: A. Winter & W.G. Siesser (Eds). *Coccolithophores*. Cambridge University Press, Cambridge: 83-105.

Kinkel, H., Baumann, K.-H. & Čepek, M. 2000. Coccolithophores in the equatorial Atlantic Ocean: response to seasonal and Late Quaternary surface water variability. *Mar. Micropaleontol*., **39**: 87-112.

Kleijne, A. 1991. Holococcolithophorids from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. *Mar. Micropaleontol*., **17**: 1-76.

Kleijne, A. 1992. Extant Rhabdosphaeraceae (coccolithophorids, Class Prymnesiophyceae) from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean. *Scripta Geologica*, **100**: 1-63.

Kleijne, A. 1993. *Morphology, taxonomy and distribution of extant coccolithophorids (calcareous nannoplankton)*. Unpubl. PhD thesis, Vrije Universiteit Amsterdam: 321pp.

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.

Lutjeharms, J.R.E & Meeuwis, J.M. 1987. The extent and variability of South-East Atlantic upwelling. *South African J. Mar. Sci*., **5**: 51-62.

Malinverno, E., Ziveri, P. & Corselli, C. 2003. Coccolithophorid distribution in the Ionian Sea and its relationship to eastern Mediterranean circulation during late fall to early winter 1997. *J. Geophys. Res*., **108**(C9), 8115, doi:10.1029/2002JC001346.

McIntyre, A. & Bé, A.W.H. 1967. Modern coccolithophoridae of the Atlantic Ocean. I. Placoliths and Cyrtoliths. *Deep-Sea Res*., **14**: 561-597.

Mitchell-Innes, B.A. & 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.

Mostajo, E.L. 1984. Nanoplancton calcareo del Oceano Atlantico Sur. *Rev. Españ. Micropaleontol*., **17**(2): 261-280.

Okada, H. & Honjo, S. 1973. The distribution of oceanic coccolithophorids in the Pacific. *Deep-Sea Res*., **20**: 355-374.

Okada, H. & Honjo, S. 1975. Distribution of coccolithophores in marginal seas along the western Pacific Ocean and in the Red Sea. *Mar. Biol*., **31**: 271-285.

Okada, H. & McIntyre, A. 1977. Modern coccolithophores of the Pacific and North Atlantic Oceans. *Micropaleontology*, **23**: 1-55.

Okada, H. & McIntyre, A. 1979. Seasonal distribution of modern coccolithophores in the western North Atlantic Ocean. *Mar. Biol*., **54**: 319-328.

Okada, H. & Wells, P. 1997. Late Quaternary nannofossil indicators of climate change in two deep-sea cores associated with the Leeuwin Current off Western Australia. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, **131**: 413-432.

Peterson, R.G. & Stramma, L. 1991. Upper-level circulation in the South Atlantic Ocean. *Prog. Oceanog.*, **26**: 1-73.

Reid, F.M.H. 1980. Coccolithophorids from the North Pacific central gyre with notes on their vertical and seasonal distribution. *Micropaleontology*, **26**: 151-176.

Reid, J.R. 1996. On the circulation of the South Atlantic. *In*: G. Wefer, W.H. Berger, G. Siedler & D.J. Webb (Eds). *The South Atlantic*. Springer, Berlin, Heidelberg: 13-49.

Romero, O., Boeckel, B., Donner, B., Lavik, G., Fischer G. & Wefer, G. 2002. Seasonal productivity dynamics in the pelagic central Benguela System inferred from the flux of carbonate and silicate organisms. *J. Mar. Systems*, **37**: 259-278.

Samtleben, C., Schaefer, P., Andruleit, H., Baumann, A., Baumann, K.-H., Kohly, A., Matthiessen, J. & Schröder-Ritzrau, A. 1995. Plankton in the Norwegian-Greenland Sea: from living communities to sediment assemblages – an actualistic approach. *Geol. Rundschau*, **84**: 108-136.

Samtleben, C. & Schröder, A. 1992. Living coccolithophore communities in the Norwegian-Greenland Sea and their record in sediments. *Mar. Micropaleontol.*, **19**: 333-354.

Shannon, L.V. & Nelson, G. 1996. The Benguela: large scale features and processes and system variability. *In*: G. Wefer, W.H. Berger, G. Siedler & D.J. Webb (Eds). *The South Atlantic*. Springer, Berlin, Heidelberg: 163-210.

Smythe-Wright, D., Chapman, P., Duncombe Rae, C., Shannon, L.V. & Boswell, S.M. 1998. Characteristics of the South Atlantic subtropical frontal zone between 15˚W and 5˚E. *Deep-Sea Res. I*, **45**: 167-192.

Takahashi, K. & Okada, H. 2000. The paleoceanography for the last 30, 000 years in the southeastern Indian Ocean by means of calcareous nannofossils. *Mar. Micropaleontol.*, **40**: 83-103.

Triantaphyllou, M.V., Dermitzakis, M.D. & Dimiza, M.D. 2002. Hetero- and holococcolithophorids (calcareous nannoplankton) in the Gulf of Korthi (Andros Island, Aegean Sea, Greece) during late summer 2001. *Rev. Paleobiol.*, **21**(1): 353-369.

Triantaphyllou, M.V., Dimiza, M.D. & Dermitzakis, M.D. 2004. *Syracosphaera halldalii* and *Calyptrolithina divergens* var. *tuberosa* life-cycle association and relevant taxonomic remarks. *In*: M.V. Triantaphyllou (Ed.). Advances in the biology, ecology and taphonomy of extant calcareous nannoplankton. *Micropaleontology*, **50**(1): 121-126.

Venrick, E.L. 1982. Phytoplankton in an oligotrophic ocean: Observations and questions. *Ecol. Monogr.*, **52**: 129-154.

Verbeek, J.W. 1989. Recent calcareous nannoplankton in the southernmost Atlantic. *Polarforschung*, **59**(1/2): 45-60.

Winter, A. 1985. Distribution of living coccolithophores in the California Current System, southern California borderland. *Mar. Micropaleontol.*, **9**: 385-393.

Winter, A., Jordan, R.W. & Roth, P.H. 1994. Biogeography of living coccolithophores. *In*: A. Winter & W.G. Siesser (Eds). *Coccolithophores*. Cambridge University Press, Cambridge: 161-178.

Winter, A., Reiss, Z. & Boaz, L. 1979. Distribution of living coccolithophore assemblages in the Gulf of Elat (Aqaba). *Mar. Micropaleontol.*, **4**: 197-223.

Winter, A. & Siesser, W.G. 1994. *Coccolithophores*. Cambridge University Press, Cambridge: 321pp.

Young, J.R. 1994. Function of coccoliths. *In*: A. Winter & W.G. Siesser (Eds). *Coccolithophores*. Cambridge University Press, Cambridge: 63-82.

Young, J.R., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I. & Østergaard, J.B. 2003. A guide to extant coccolithophore taxonomy. *J. Nannoplankton Res., Spec. Issue*, **1**: 125pp.

Young, J.R. & Westbroek, P. 1991. Genotypic variation within the coccolithophorid species *Emiliania huxleyi*. *Mar. Micropaleontol.*, **18**: 5-23.

Ziveri, P., Thunell, R.C. & Rio, D. 1995a. Export production of coccolithophores in an upwelling region: Results from San Pedro Basin, Southern California Borderlands. *Mar. Micropaleontol.*, **24**: 335-358.

Ziveri, P., Thunell, R.C. & Rio, D. 1995b. Seasonal changes in coccolithophore densities in the Southern California Bight during 1991-1992. *Deep-Sea Res.*, **42**: 1881-1903.