

# Coccolithophore flux in a sediment trap off Cape Blanc (NW Africa)

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Manuscript received 10th May, 2008; revised manuscript accepted 12th December, 2008

**Abstract** The flux of coccoliths from a one-year-moored sediment trap (March, 1988 to March, 1989) off Cape Blanc, NW Africa (20°45'N, 19°44'W) was studied. Coccolith flux was at a minimum during spring and fall. The minimum flux ( $51 \times 10^7$  coccoliths  $\text{m}^{-2}\text{d}^{-1}$ ) in fall (September) corresponds to a strong decrease in nutrient content of the surface-waters. In winter, coccolith flux reached maximum values ( $384 \times 10^7$  coccoliths  $\text{m}^{-2}\text{d}^{-1}$ ). At that time, insolation, wind velocity, and sea-surface temperature had average values, indicating average nutrient content and average light penetration into surface-waters.

Detailed morphometric measurements were the basis for more precise estimations of the coccolith-derived carbonate content of the settled particles. Numerically significant taxa (*Emiliania huxleyi*, *Florisphaera profunda*, *Gephyrocapsa oceanica*), as well as low flux of large taxa, such as *Helicosphaera carteri*, *Coccolithus pelagicus* and *Calcidiscus leptoporus*, mainly form the coccolith carbonate contribution, which adds up to  $13.32 \text{ mg m}^{-2}\text{d}^{-1}$  ( $3.9\text{--}22.8 \text{ mg m}^{-2}\text{d}^{-1}$ ), with a relative contribution of coccoliths to the total carbonate flux of 18% (7–35%). The morphometric measurements further revealed a bimodal distribution of *F. profunda* allowing separation of two morphotypes, *F. profunda* var. *profunda* and *F. profunda* var. *elongata*.

The modern sediment-trap assemblage revealed a good correspondence with respect to coccolith flux (accumulation), species composition and the coccolith-derived carbonate content with the underlying Holocene surface sediment.

**Keywords** Cape Blanc, NW Africa, sediment trap, coccolithophores, seasonality, succession, morphometry of species, carbonate flux

## 1. Introduction

The development of phytoplankton populations, including coccolithophores, is influenced by the interaction of nutrients and light. Off NW Africa, the speed and direction of the trade winds determine upwelling intensity, and consequently additional nutrient input, as well as the development and extension of water-mass filaments from the coast to the open ocean. Wind strength has also an impact on the vertical mixing/stratification of the surface-water. Deep mixing reduces the mean irradiance experienced by phytoplankton, since maintenance in a water-depth with sufficient light may be inhibited for a significant time due to turbulence (Huntsman & Barber, 1977; Blasco *et al.*, 1981; Dugdale & Wilkerson, 1985).

To examine the export production of living surface-water communities, sediment trapping is a successful method. The quantity and composition of the sinking material are functions of variable components within the overlying pelagic system (Peinert *et al.*, 1989; Legendre & Rassoulzadegan, 1996; Delesalle *et al.*, 2001). The settling of biogenic material is directly related to surface production, and reflects the seasonality of such production (Deuser *et al.*, 1990). The samples provide valuable information on the species composition and seasonal variations in abundance (Samtleben & Bickert, 1990; Ziveri *et al.*, 1995; Broerse, 2000).

Off Mauritania, flux of particles into the deep ocean is well documented (Wefer & Fischer, 1993; Fischer *et al.*, 1996; Neuer *et al.*, 1997; Ratmeyer *et al.*, 1999a, b, c).

Lithogenic particles, carbonate and organic carbon are the major components, with foraminifera identified as one main carbonate producer (Fischer *et al.*, 1996). The coastal upwelling also influences offshore waters, through the formation of giant water-mass filaments that are characterised by high pigment concentrations (Estrada, 1974; Gabric *et al.*, 1993; Kostianoy & Zatsepin, 1996; Lange *et al.*, 1998; Thomas *et al.*, 2004). Information on coccolith export of this highly productive region is still not available, however.

In this paper, we present new data concerning the seasonal pattern of coccolith flux in the upwelling area off Cape Blanc (NW Africa). The settled coccolithophore assemblages from a year-round (1988–1989) moored sediment trap, at 2000m depth, from 176km west of Cape Blanc, were investigated in order to obtain insight into the seasonal variation of coccolith export and the influence of abiotic factors on such flux. This study focuses on (1) determination of the seasonal variation of the coccolith flux and species composition, with an attempt to gain further insight into influencing factors, (2) the assessment of coccolith-carbonate flux using morphometry, and the relationship of coccolith-derived carbonate to the total carbonate flux, and (3) the relationship of present-day flux of coccoliths and coccolith-carbonate to long-term Holocene accumulation rates in the underlying sediment.

## 2. Study area

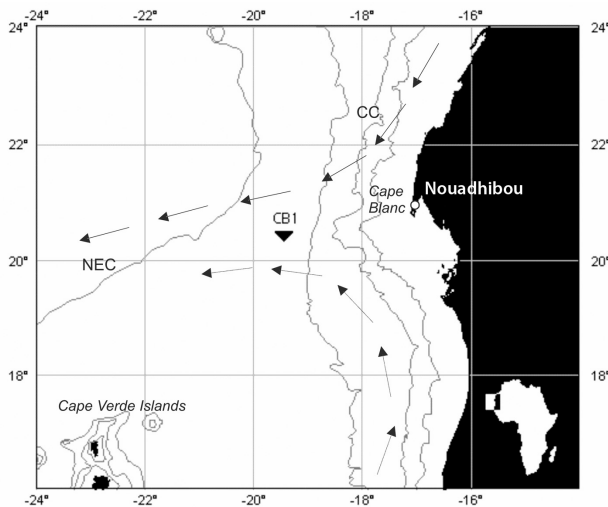
### 2.1 Oceanographic setting

The mooring station (20°45.3'N, 19°44.5'W) lies within

the eastern boundary current system of NW Africa, an upwelling region driven by the trade winds. Between 24°N and 20°N, intensity of the year-round upwelling varies interannually and seasonally as a result of the variability and seasonality of the trade winds (van Camp *et al.*, 1991).

The oceanography is dominated by the Canary Current (CC), which is a branch of the subtropical gyre that parallels, and then veers away from, the continental slope in a south-westerly direction (Figure 1). At the latitude of Cape Verde (15°N), all of the flow has turned westward to supply the North Equatorial Current (Barton, 1998). South of the area where the CC veers away from the continental slope, a cyclonic gyre exists that persists throughout the year (between 15° and 22°N). This mesoscale surface-water cyclonic gyre varies in position and lateral extent with the seasons, being furthest north in fall/winter and at its largest areal extent in summer (Barton, 1998).

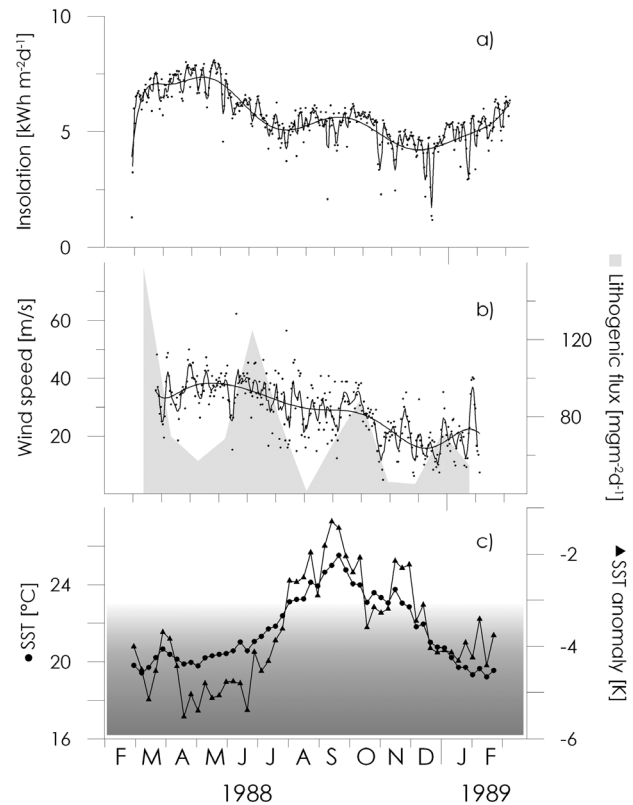
Besides the seasonal surface-water conditions, the deep water-masses also vary seasonally. In the vicinity of Cape Blanc, the frontal zone between North Atlantic Central Water and the more nutrient-rich, less saline South Atlantic Central Water is located, influencing the circulation through thermohaline mixing processes, and forming a complex mesoscale regime of (sub)surface currents (Gabric *et al.*, 1993).



**Figure 1:** Mooring/sample location (CB1, GeoB 1121), bathymetry and schematic near-surface circulation at Cape Blanc off NW Africa (CC - Canary Current, NEC - North Equatorial Current)

## 2.2 Insolation, wind and sea-surface temperature anomaly

Stabilisation of the upwelled nutrient-rich water in the euphotic zone, by solar heating, is a fundamental mechanism supporting the high biological productivity of coastal upwelling ecosystems (Huntsman & Barber, 1977; Nykjær & van Camp, 1994). Insolation data (from <http://eosweb.larc.nasa.gov/sse/>) reveals a steady decrease in insolation from April to December, followed by a slight increase in spring; during fall and winter, the lowest insolation values



**Figure 2:** a) Insolation data with running average window width = 3, function of polynomial degree = 10. b) Wind speed (redrawn from Ratmeyer *et al.*, 1999b) with running average window width = 3, function of polynomial degree = 10 and lithogenic particle flux (Fischer *et al.*, 1996). c) SST and calculated SST anomaly. Grey shaded area indicates upwelling. All data were corrected for the settling time of 25 days (for more details, see Müller & Fischer, 2001)

were observed (Figure 2a).

During the study period, the average wind speed measured at Nouadhibou airport (Cape Blanc, Mauritania) showed a slight increase in spring, culminating in a June/July maximum (Figure 2b). Following this, the wind speed decreased steadily, reaching its minimum in December/January. In September/October, this decrease was interrupted by a short-lived, remarkable increase (Fischer *et al.*, 1996). In general, the wind direction was mostly from the east and north-east.

The mooring location was not located directly within the coastal upwelling region, but offshore, influenced by the coastal upwelling, as well as by the development and movement of the giant filaments. To determine the upwelling events and strength, the difference between the sea-surface temperature (SST) of the characteristically cold (upwelled) water of the mooring location and the SST of the open ocean (40°W) at the same latitude was calculated. This difference is defined as the SST anomaly (following Speth & Köhne, 1983; data from [http://ingrid.ldeo.columbia.edu/SOURCES/IGOSS/nmc/Reyn\\_SmithOIv2/](http://ingrid.ldeo.columbia.edu/SOURCES/IGOSS/nmc/Reyn_SmithOIv2/)). A difference of -3K or lower is interpreted as upwelling (Speth *et al.*, 1978). The SST anomaly for the sampling period displays strong upwelling from April to June, followed by a

steady decline in upwelling intensity, and with no upwelling signal in September (-1.2K). Between July and December, only a short period of weak upwelling in October/November was recorded. Upwelling was present again from December to February, but was not as intense as at the beginning of the study year (Figure 2c).

### 3. Material and methods

The sediment trap (CB1) was moored off Cape Blanc at a depth of 2195m (total water-depth 3646m). From March, 1988 to March, 1989, a total of 13 samples were collected, each sample with a collection time of 27 days. The deployment of the sediment trap, as well as the treatment of the collected samples, is described in detail by Fischer *et al.* (1996). The processing of the samples for scanning electron microscopy (SEM) followed the dilution/filtering method of Andrúleit (1996). Depending on the particle content of the samples, 1/3200, 1/4000 or 1/6400 split of the original were filtered. Qualitative and quantitative analyses of the coccolithophores were performed at x3000 magnification using a Zeiss DSM 940A at 10kV accelerating voltage. Each coccolith and coccosphere within an arbitrarily chosen transect was counted, until a total number of at least 500 coccoliths was reached. Species were identified to the lowest taxonomic level as possible, based on the taxonomical concepts of Cros & Fortuño (2002) and Young *et al.* (2003). To gain estimates of daily coccolith flux, each coccosphere was converted into number of coccoliths, based on species-specific values (Boeckel & Baumann, 2008).

The Holocene surface-sediment sample (GeoB 1121) was prepared for observation using a similar technique (Andrúleit, 1996). From the assumed accumulation rate of  $0.08 \text{ g m}^{-2} \text{ d}^{-1}$ , based on Winn *et al.* (1991), coccolith counts were converted into numbers per gram of dry sediment.

The coccolith-derived carbonate contribution was calculated using the mass equation of Young & Ziveri (2000) and the results of size measurements carried out in this study (see Table 1). Size measurements were made directly on the screen of the SEM at a magnification of x5000 or x10 000, using an internal Zeiss measuring system. The resolution was within  $0.1\text{--}0.2 \mu\text{m}$ . For all species, distal shield dimensions of at least 20, but often more than 30, randomly-selected specimens were measured for six of the 13 samples from the sediment trap. In total, more than 150 coccoliths were measured. The species measured were *Calcidiscus leptoporus*, *C. leptoporus* small morphotype, *C. quadriperforatus*, *Emiliania huxleyi*, *Florisphaera profunda*, *Gephyrocapsa* spp., *Umbilicosphaera sibogae* and *U. foliosa*.

## 4. Results

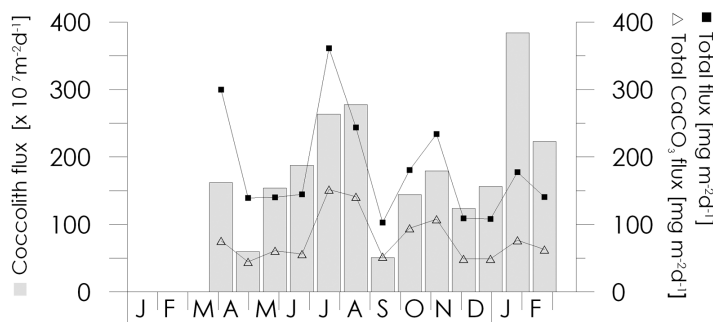
### 4.1 Seasonal species flux

Coccolith flux was high during summer (July to August) and winter (January to February), with low values during spring (March to April) and

Taxon	Coccolith-CaCO <sub>3</sub> [pg]	Mean length [ $\mu\text{m}$ ]
<i>Acanthoica</i> spp.	0.3	+
<i>Algirosphaera</i> spp.	0.9	2.38
<i>Alisphaera</i> spp.	2.6	+
<i>C. brasiliensis</i>	2.6	+
<i>C. quadriperforatus</i>	206.6	9.85
<i>C. leptoporus</i>	70.3	6.88
<i>C. leptoporus</i> (small)	18.5	4.41
<i>C. pelagicus</i>	336	12.75
<i>Calciopappus</i> spp.	2.6	+
<i>Calciosolenia</i> spp.	2.6	+
<i>Coronosphaera</i> spp.	12.1	+
<i>D. tubifera</i>	1.5	+
<i>E. huxleyi</i>	1.9	3.28
<i>F. profunda</i>	3.7	3.25
<i>G. ericsonii</i>	1	1.98
<i>G. flabellatus</i>	2.6	+
<i>G. muelleriae</i>	6.5	3.63
<i>G. oceanica</i>	14.6	4.77
<i>H. hyalina</i>	35.2	6.39
<i>H. carteri</i>	110	9.34
<i>M. elegans</i>	2.6	+
<i>Ophiaster</i> spp.	0.1	+
<i>P. discopora</i>	65.9	+
<i>Pontosphaera</i> spp.	70	+
<i>R. clavigera</i>	41	8.47
<i>R. stylifera</i>	40.5	+
<i>R. xiphos</i>	2.6	+
<i>Rhabdosphaera</i> spp.	8	+
<i>S. corona</i>	12.1	+
<i>S. pulchra</i>	16.6	5.9
<i>S. tumularis</i>	12.1	+
<i>Syracosphaera</i> spp.	0.1	+
<i>U. anulus</i>	8	+
<i>U. foliosa</i>	32	5.82
<i>U. irregularis</i>	5.8	+
<i>U. sibogae</i>	12.7	4.4
<i>U. tenuis</i>	8.7	+
Holococcoliths	2.6	+
Others	2.6	+

**Table 1:** Species-specific coccolith carbonate weights used and mean coccolith length of selected taxa, based on size measurements carried out for this study. (+ indicates no size measurements on CB trap samples available, in which case, data from Young & Ziveri (2000) was used)

fall (September to December) (Figure 3). The highest coccolith flux was recorded in January, 1989 ( $384 \times 10^7$  liths  $\text{m}^{-2} \text{d}^{-1}$ ), and the lowest in September, 1988 ( $51 \times 10^7$  liths  $\text{m}^{-2} \text{d}^{-1}$ ), coinciding with the maximum SST. In contrast, high coccolith flux was coincident with low SST. The mean coccolith flux was  $182 \times 10^7 \text{ m}^{-2} \text{d}^{-1}$ .



**Figure 3:** Flux of coccoliths, total carbonate and total mass

The samples revealed a diverse coccolithophore assemblage. In total, 63 heterococcolith-bearing species, one species in its hetero-/holococcolith-bearing state (*Syracosphaera pulchra* – *Calyptrorphaera oblonga*), and one species bearing holococcoliths (*Syracolithus dalmaticus*) were identified. Coccoliths were excellently preserved, with no signs of dissolution. The most abundant species are listed in Table 2. For the following interpretation and discussion, only species exceeding 5% relative abundance at least once during the study period are considered.

<i>Acanthoica</i> spp.	<i>Ophiaster</i> spp.
<i>Algirosphaera</i> spp.	<i>Palusphaera</i> spp.*
<i>Calcidiscus quadriperforatus</i> *	<i>Rhabdosphaera</i> spp.
<i>Calcidiscus leptoporus</i>	<i>Syracosphaera</i> spp.
<i>Calciosolenia brasiliensis</i>	<i>Syracosphaera anthos</i>
<i>Discosphaera tubifera</i>	<i>Syracosphaera pulchra</i> *
<i>Emiliania huxleyi</i>	<i>Syracosphaera tumularis</i>
<i>Florisphaera profunda</i>	<i>Umbellosphaera irregularis</i>
<i>Gephyrocapsa ericsonii</i>	<i>Umbellosphaera tenuis</i>
<i>Gephyrocapsa muelleriae</i> *	<i>Umbilicosphaera annulus</i> *
<i>Gephyrocapsa oceanica</i>	<i>Umbilicosphaera hultburtiana</i>
<i>Gladiolithus flabellatus</i>	<i>Umbilicosphaera foliosa</i>
<i>Helicosphaera carteri</i>	<i>Umbilicosphaera sibogae</i>
<i>Helicosphaera hyalina</i> *	Holococcoliths

**Table 2:** Identified coccolithophore taxa found during sampling period in sediment trap samples off Cape Blanc (CB1). \*At maximum, absent from two samples

In general, *Emiliania huxleyi*, *Gladiolithus flabellatus*, *Algirosphaera* spp., *Umbilicosphaera* spp., *Helicosphaera* spp. and *Rhabdosphaera* spp. reached their flux maxima in January (1989) and exhibited additional high flux in August (1988). *Gephyrocapsa ericsonii* also showed maximum flux in winter, but without a pronounced summer peak. *Gephyrocapsa oceanica*, *Calcidiscus leptoporus*, *Umbellosphaera* spp. and *Discosphaera tubifera* reached their flux maxima between May and August and had an additional high flux period in winter (January or February; Figure 4). The flux of *Coccolithus pelagicus*, *Syracosphaera* spp., *Ophiaster* spp., *Acanthoica* spp., *Calciosolenia brasiliensis* and of the holococcolith-bearing species varied throughout the year (Figure 4).

The coccolithophore assemblages were dominated by *E. huxleyi* (30–45%), *Florisphaera profunda* (6–19%) and *G. oceanica* (3–13%; Figure 5). *Algirosphaera* spp., *G. flabellatus*, *F. profunda* and *Umbellosphaera* spp. made a constant contribution to the assemblage, with two distinct maxima (May/June and December/January). *G. oceanica* steadily decreased in abundance from summer onward, with an increase during October/November 1988.

## 4.2 Morphometric measurements

In general, *Emiliania huxleyi* is the most abundant living coccolithophore and dominates the coccolith flux in this study. The morphology of 194 coccoliths of *E. huxleyi* shows a unimodal distribution (Figure 6a). Length ranges

from 2.5–4.9  $\mu\text{m}$ , with a mean of 3.3  $\mu\text{m}$ . Varieties, as given by Westbroek & Young (1991), were not distinguished during the counting. However, the majority of the measured specimens are assigned to *E. huxleyi* type A. A few specimens with more delicate rays indicate that *E. huxleyi* type C is also present.

*Florisphaera profunda* is the main contributor to the lower-photoc-zone flora of low to mid latitudes (Okada & Honjo, 1973; Okada & McIntyre, 1977). Overall, lith lengths in the studied sediment trap samples are 1.4 to 6.4  $\mu\text{m}$  (Figure 6b). However, the scatter plot and frequency distributions clearly document a bimodal pattern, indicating that two varieties of *F. profunda* are present in the investigated samples, with var. *elongata* forming larger liths (Reid, 1980). The larger liths are between 4.3  $\mu\text{m}$  and 6.5  $\mu\text{m}$  in length, whereas liths of 1.4  $\mu\text{m}$  to 3.9  $\mu\text{m}$  may correspond to *F. profunda* var. *profunda*. Varieties, as indicated by the size data, were not distinguished in the counts, and lith-carbonate flux calculations were made using total mean size (3.4  $\mu\text{m}$ ).

Placoliths of the heterococcolith-bearing stage of the *Calcidiscus leptoporus* group into three indistinct clusters, consistent with *C. leptoporus* small type, intermediate *C. leptoporus* and the large *C. quadriperforatus*, as introduced by Geisen *et al.* (2002), with overall lengths of 3.4–5.5  $\mu\text{m}$ , 5.1–8.4  $\mu\text{m}$  and 6.9–11.4  $\mu\text{m}$ , respectively (Figure 7).

The coccoliths of *Umbilicosphaera sibogae* and *U. foliosa* show distinct variation in diameter, element numbers, and diameter of the central area. The distal shield diameter of *U. sibogae* is 3.1  $\mu\text{m}$  to 5.1  $\mu\text{m}$ , with a mean of 4.4  $\mu\text{m}$ , with the larger proximal shields having a mean of 4.9  $\mu\text{m}$ . The distal shield of *U. foliosa* is 5.0–6.8  $\mu\text{m}$  in diameter, with a mean of 5.8  $\mu\text{m}$ .

In the present study, *Gephyrocapsa* coccoliths were distinguished by morphological differences (length, width, structure). Overall, length and width of the placoliths are extremely well correlated ( $r^2 = 0.97$ ). *G. ericsonii* coccoliths are 1.6–2.7  $\mu\text{m}$  long. Small *G. oceanica* coccoliths are medium-sized, 3.1–4.4  $\mu\text{m}$  long, whereas the length of large-sized *G. oceanica* generally ranges from 4.2  $\mu\text{m}$  to 5.9  $\mu\text{m}$  (Figure 8).

## 4.3 Coccolith-carbonate flux

Calculated coccolith-carbonate flux, based on morphometric measurements and literature data (Table 1) varied significantly between 3.9 and 22.8  $\text{mg m}^{-2}\text{d}^{-1}$  in the studied sediment trap. The mean calculated coccolith-carbonate flux was 13.32  $\text{mg m}^{-2}\text{d}^{-1}$ . On average, coccoliths contributed 18% to the measured total carbonate flux. Variation in the relative fraction of coccolith-carbonate to the total carbonate was high (7%–35%; Figure 9).

Only a few species contributed significantly to the coccolith-carbonate flux, either due to their high specific carbonate mass or due to their high numbers. Thus, the rare and subordinate species *Helicosphaera carteri*, *Calcidiscus leptoporus* and *Coccolithus pelagicus* were significant contributors due to their coccolith weight (Young & Ziveri,

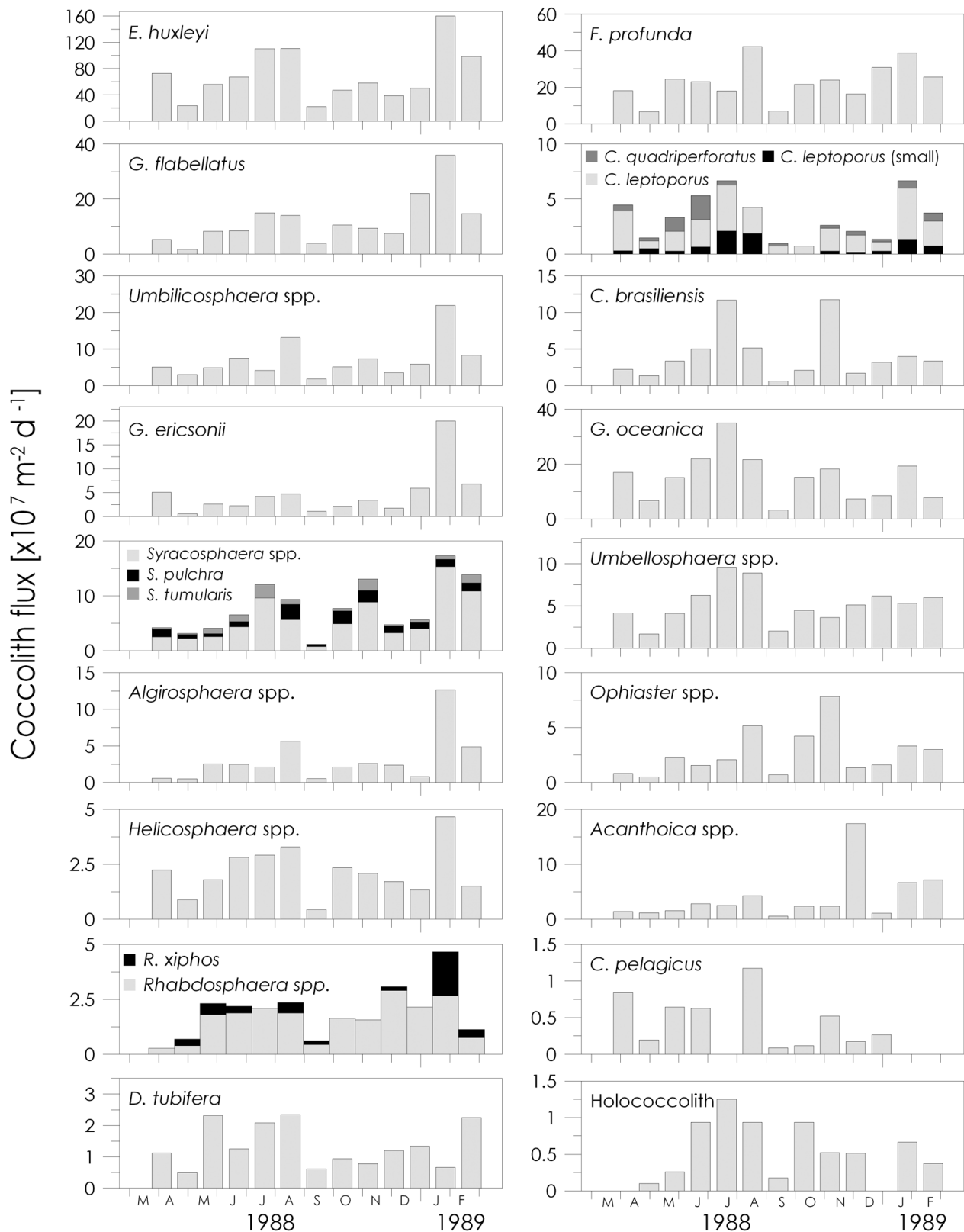
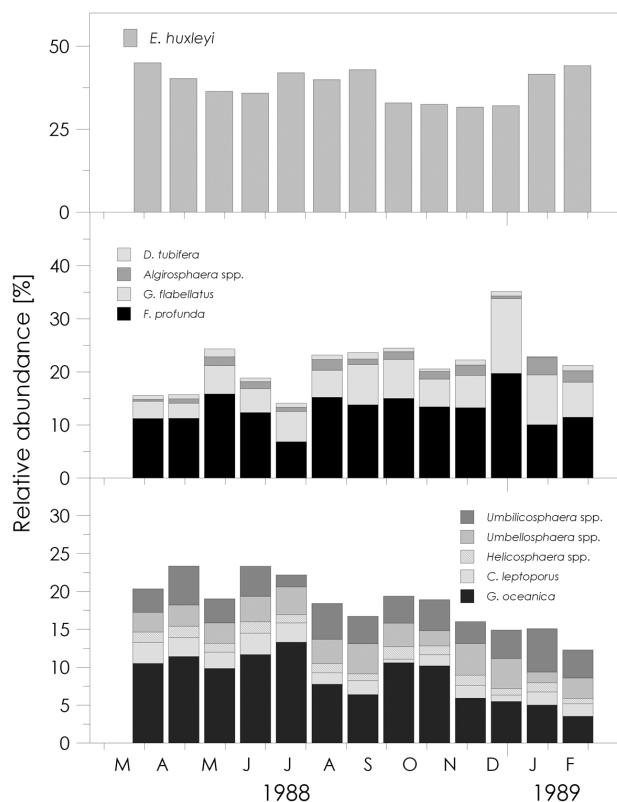


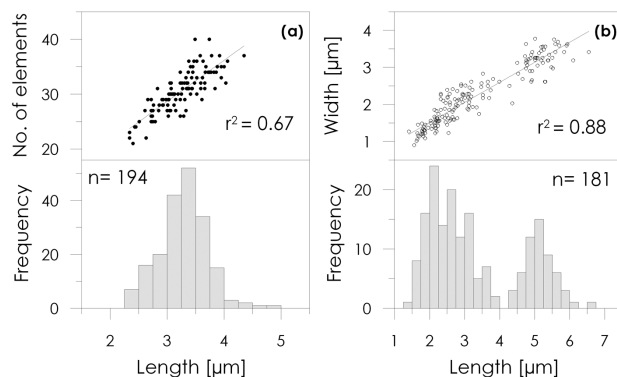
Figure 4: Seasonal flux of the most common coccolithophore species of the settling assemblage of CB1

2000). These relatively massive species contributed 35-40% to the coccolith-carbonate flux. Due to their high abundance, *Emiliania huxleyi*, *Gephyrocapsa oceanica* and

*Florissphaera profunda* contributed 35-40% to the coccolith-derived carbonate.



**Figure 5:** Relative abundance of coccolithophores off Cape Blanc during 1988-89

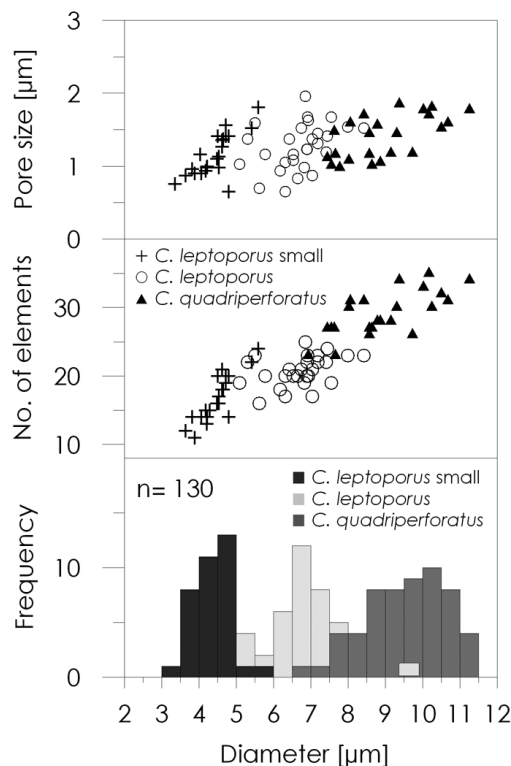


**Figure 6:** a) Size variation and frequency distribution ( $0.25\mu\text{m}$  intervals) of *E. huxleyi*. b) Length and width variation, and frequency distribution ( $0.25\mu\text{m}$  intervals), of *F. profunda*

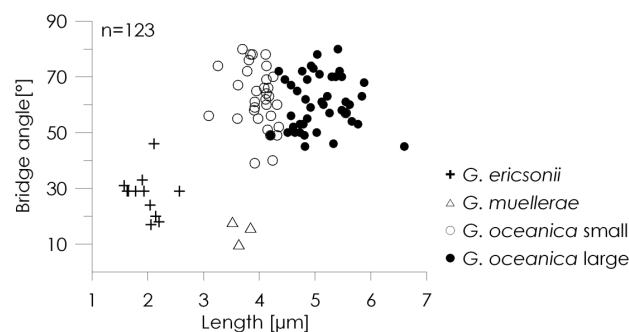
#### 4.4 Coccolith and coccolith-carbonate accumulation rates

The total coccolith accumulation rate of the Holocene sediment sample (GeoB 1121) was  $59 \times 10^7$  liths  $\text{m}^{-2}\text{d}^{-1}$ . In total, 20 heterococcolith-bearing species were identified. *Emiliania huxleyi*, *Florisphaera profunda* and *Gephyrocapsa oceanica* were the most abundant species, with relative abundances of 48.5%, 17% and 14.3%, respectively. *Umbilicosphaera* spp., *Calcidiscus leptoporus* and *Helicosphaera* spp. were common (3.6%, 4.0% and 2.6%, respectively).

The calculated coccolith-carbonate content accounts for



**Figure 7:** Scatter plots of diameter vs. pore size and number of elements in the distal shield of *Calcidiscus*, and frequency size distribution ( $0.5\mu\text{m}$  intervals)



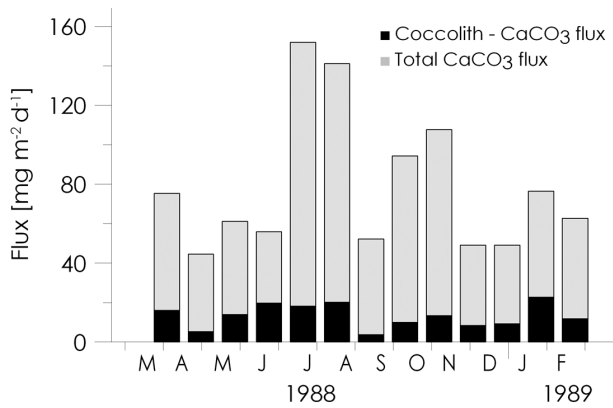
**Figure 8:** Length vs. bridge-angle measured in *Gephyrocapsa* spp.

$85.7\text{mg g}^{-1}$  sediment ( $8.57\text{wt}\%$ ) and an accumulation rate of  $6.52\text{mg m}^{-2}\text{d}^{-1}$  ( $17.86\text{g m}^{-2}\text{y}^{-1}$ ), which is 14.9% of the total carbonate accumulation rate (measured carbonate content of the sediment is 57.40wt%).

## 5. Discussion

### 5.1 Seasonality of the coccolith assemblages

To explain the seasonal flux pattern of coccoliths and their species composition during 1988-1989, we focused on the interaction of wind, nutrients and light for the study period and area, since the dynamics of phytoplankton populations in upwelling regions are very much controlled by such forcing factors (Margalef, 1978a). The export of phytoplankton is based, to a great extent, on the productivity in



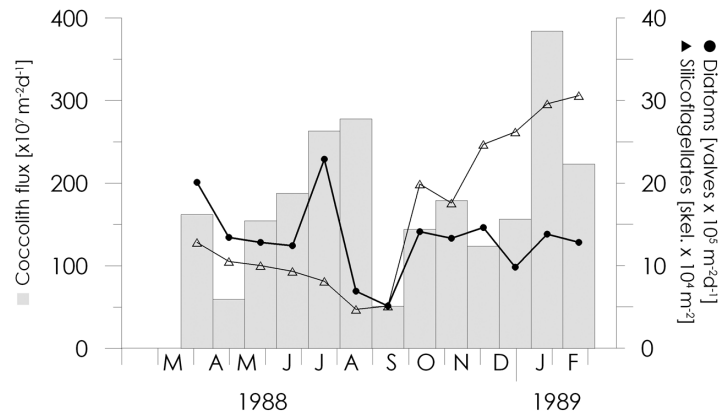
**Figure 9:** Comparison of total carbonate flux with calculated coccolith-derived carbonate flux at the sample site

the surface-waters. Comparison of the coccolith flux to the flux of siliceous phytoplankton (Romero *et al.*, 2002b) is here used to explain the seasonal flux patterns exhibited by the coccoliths (Table 3).

The mean irradiance experienced by phytoplankton is influenced by the intensity of insolation, upwelling and wind speed, thus by the strength of turbulence and mixing of the water-column. As Margalef (1978a) described, in Margalef's Mandala, the ecological preferences of living coccolithophores are characterised by medium turbulence and mesotrophic waters, whereas diatoms dominate in nutrient-rich and turbulent environments. Balch (2004) extended this profile to include light. Taking this into consideration, the low flux of coccoliths in spring, 1988 (Figure 10) can be explained as follows. Upwelling determined by SST anomaly is strongest, as was the wind strength (Figure 2). The strong influence of the (coastal) upwelling is also indicated by the dominance of neritic diatoms over oceanic ones at that time (Romero *et al.*, 2002b). High wind-speed and strong upwelling, causing

turbulence and vertical mixing, induced a decrease in light conditions in the surface-waters (Fischer *et al.*, 1996; Rost & Riebesell, 2004). Nelson & Conway (1979) concluded that the light regime is more important than nutrient concentration in controlling the use of inorganic nutrients in the NW African upwelling system by phytoplankton. Strong winds limit the effective time period for light-driven primary production (Dugdale & Wilkerson, 1985). The wind strength off Cape Blanc often causes the mixed layer to be deeper than the euphotic zone, thus light limitation of the primary productivity is likely to occur (Blasco *et al.*, 1981). In general, the maximum production rates are achieved only during periods of wind relaxation when vertical mixing is reduced (Gabric *et al.*, 1993).

From April to July, coccolith flux increased up to the first seasonal maximum in August, 1988. Diatom flux increased as well, up to their maximum in July (Romero *et al.*, 2002b; Figure 10). Simultaneously, upwelling and wind speed decreased. We deduce that the water movement and



**Figure 10:** Total coccolith flux vs. siliceous phytoplankton flux (redrawn from Romero *et al.*, 2002b)

turbulence ebbed allowing light availability in the surface-water to increase, thus positively influencing primary production, as shown by the peaks in diatom and high coccolith fluxes (Figure 10). Phytoplankton differ in their ability to cope with variable irradiance. Coccolithophores seem to have a slightly higher light saturation for optimum growth compared to diatoms (Rost & Riebesell, 2004). As a consequence, diatoms are commonly the first to bloom when the water-column begins to stabilize early in the seasonal cycle (Rost & Riebesell, 2004). The coccolith and diatom flux patterns at CB1 seem to agree with these general concepts.

In September, 1988, the overall flux, and consequently also the coccolithophore flux, reached a minimum. Upwelling ceased, and no additional input of nutrients occurred. After the high flux of diatoms in March and

	Spring (Mar-May)	Summer (Jun-Aug)	Fall (Sep-Nov)	Winter (Dec-Feb)
<b>Flux of coccoliths</b>	average	high	minimum	maximum
<b>Upwelling</b>	strong	weakening	no	average
<b>Nutrients</b>	high	low	low	average
<b>Irradiance (in water column)</b>	low	high	low	average

**Table 3:** Summary of the interaction of light, nutrient availability and wind that determine coccolith flux at CB1. The upwelling intensity can be described based on the SST anomaly and, consequently, the nutrient input

July, and the first peak coccolith flux in June/July, the water was probably depleted in nutrients. Dugdale & Wilkerson (1985) showed that the euphotic zone in that area *can* temporarily be depleted in nutrients.

Later on in fall, the increase in coccolith flux corresponded to the onset of increasing upwelling, most likely resupplying the surface-water with nutrients. An intense aeolian input (Romero *et al.*, 2003) represents a further nutrient source for that interval. The light regime for the sampling period seems favourable as well, since upwelling was not strong and wind speed was at its lowest (Ratmeyer *et al.*, 1999b; Romero *et al.*, 2003).

In January and February, maximum coccolith export corresponded to average values of the influencing forces, such as light availability, nutrients, upwelling intensity and SST. Thus, Margalef's Mandala is depicted by the seasonal flux pattern of coccoliths and diatoms in this highly variable environment.

The upwelling region off NW Africa is known to reveal its highest chlorophyll pigment concentration during spring and winter (Thomas *et al.*, 2004), and even far offshore, high pigment concentrations have regularly been found (Estrada, 1974; Gabric *et al.*, 1993; Kostianoy & Zatsepin, 1996; Thomas *et al.*, 2004). The seasonal fluxes of coccoliths and diatoms in this region, in 1988-1989 (Figure 10), imply a change in the dominating phytoplankton group to cause these elevated pigment concentrations. The spring/summer peak seems to be dominated by diatoms, whereas the winter peak is dominated by coccolithophores (Figure 10). The change in dominance is supported by the model calculation of Giraud (2006).

## 5.2 Coccolithophore assemblages

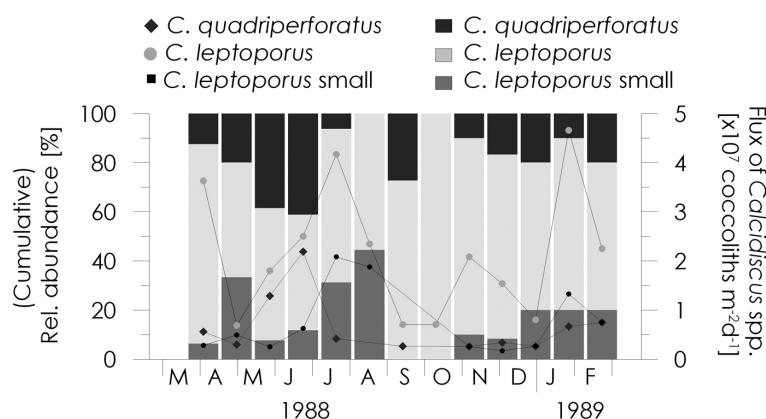
*Emiliania huxleyi*, *Florisphaera profunda*, *Gladiololithus flabellatus*, *Algirosphaera* spp., *Umbilicosphaera* spp. and *Syracosphaera* spp. reflect the described general pattern of coccolith flux by revealing two seasonal maxima, high flux in summer and maximum flux in winter. These species do not generally occupy the same ecological niches, *E. huxleyi* being a bloom-forming, placolith-bearing cosmopolitan species (Westbroek *et al.*, 1993), *F. profunda* and *G. flabellatus* living in the lower photic zone, with *F. profunda* indicating the vicinity of the nutricline (Winter & Siesser, 1994), and *Umbilicosphaera* spp. being weakly associated with warm, saline, rather oligotrophic water (Okada & McIntyre, 1979; Ziveri *et al.*, 1995, 2004). However, the sediment trap material is somewhat averaged, with respect to time and space, thus the entire ecological structure is represented in one sample. The phytoplankton community may have had a patchy distribution. Margalef (1978b) described the plankton community off NW Africa as having small-scale fluctuations developed around a trend that showed larger-scale fluctuations. This dynamic pattern is

linked to processes of decaying movement associated with the giant water-mass filaments mentioned above (Margalef, 1978b; Gabric *et al.*, 1993). Thus, finding coccolithophore species together in one sample, which are associated with differing ecological preferences, can be explained by small-scale spatial diversity above the sediment trap.

As described by Young & Westbroek (1991), separation of the different *E. huxleyi* types, based on biometric analysis, is difficult, since a great overlap of size exists, hence the unimodal distribution does not distinguish between type A and type C in our samples (Figure 6a). Type A was the common morphotype in our study, as documented for the world ocean. The presence of *E. huxleyi* type C may indicate the influence of (coastal) upwelled, cold water, since type C is generally associated with cold-water conditions (McIntyre & Bé, 1967; Hagino *et al.*, 2005).

Species of the lower photic zone, such as *F. profunda* and *G. flabellatus*, increased in relative abundance in winter (December to January), when insolation was at its lowest and wind turbulence was low. They may have benefited from low irradiance associated with these environmental factors, due to their apparent adaptation to low light conditions (Quinn *et al.*, 2005). Furthermore, their habitat close to the nutricline would provide the requisite nutrients during this time of lower nutrient input (fall to early winter). The simultaneous occurrence of *F. profunda* var. *profunda* and *F. profunda* var. *elongata* is well documented (Quinn *et al.*, 2005). However, it is not yet clear whether the distinct size morphotypes correspond to typological varieties, since further morphological differentiation is missing.

The (morpho)types of *Calcidiscus* revealed discrete flux patterns, with maximum flux of *C. quadriperforatus* and *C. leptoporus* low in summer, but with the small type increasing later on. The intermediate-sized *C. leptoporus* has a fluctuating seasonal pattern (Figure 11). To assign the distribution of the different morphotypes of *Calcidiscus* to specific environmental parameters during the study period would be highly speculative. The continuous dominance of *C. leptoporus* intermediate morphotype, during signifi-

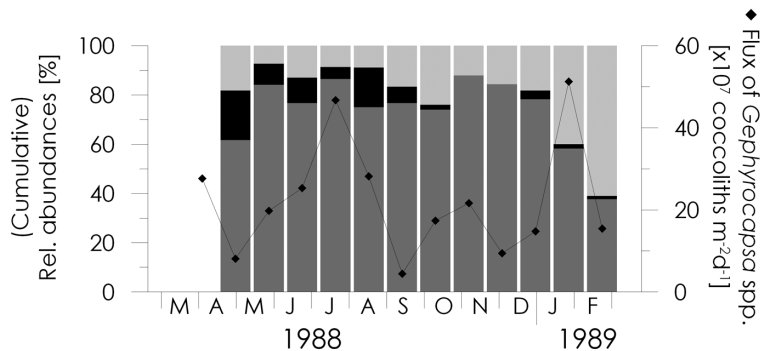


**Figure 11:** Flux of *Calcidiscus* spp. from CB1 plotted against their relative abundances (100% = flux of *Calcidiscus* spp. only)



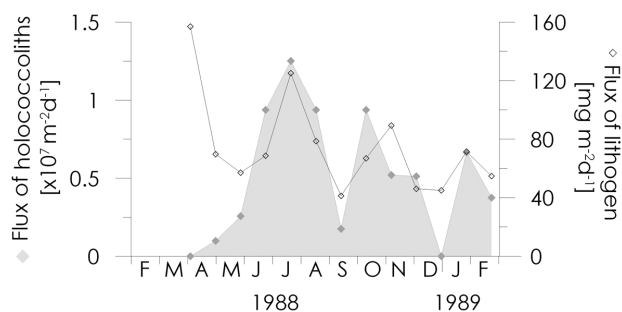
cantly changing environmental conditions may indicate its broad tolerance, as documented by Boeckel *et al.* (2006).

During spring and summer, *Gephyrocapsa muelleriae* was present, indicating cold and nutrient-enriched waters, based on the interpreted strong upwelling (Figure 2). Its steady decrease in relative abundance (Figure 12) corresponds to the decreasing influence of the cold, upwelled coastal water. The decline in *G. oceanica* relative abundance (Figures 4, 12), supports the interpretation of reduced influence of turbulent and nutrient-enriched waters, induced by the steady decrease in wind speed; Boeckel *et al.* (2006) showed that *G. oceanica* abundance seemed to be correlated to turbulence, and it has also been shown to have a relationship with the nutrient content of surface-waters (Andruleit *et al.*, 2003; De Bernardi *et al.*, 2005).



**Figure 12:** Relative abundances of *G. oceanica*, *G. muelleriae* and *G. ericsonii* (100% = flux of *Gephyrocapsa* spp. only) plotted against absolute flux of *Gephyrocapsa* spp. at CB1

The holococcolith flux corresponded very well to the flux of lithogenic particles (Figure 13). As holococcoliths are composed of numerous minute crystallites, which do not tightly interlock, their morphology is rather fragile and easily disintegrated (Young *et al.*, 2003). In the arid area of the Sahara, strong wind carries great quantities of dust far out to sea. These dust loads can be released into the ocean during times of wind relaxation. From 1988-89, high sinking velocities of particles in the water-column, thus a short settling time, were observed (Ratmeyer *et al.*, 1999b). The high lithogenic flux during that period may have acted as a carrier system for the fragile holococcoliths. The lithogenic constituents off Cape Blanc appear to be coupled with the organic carbon flux documented by Ratmeyer *et*



**Figure 13:** Flux of holococcoliths vs. lithogenic material at CB1

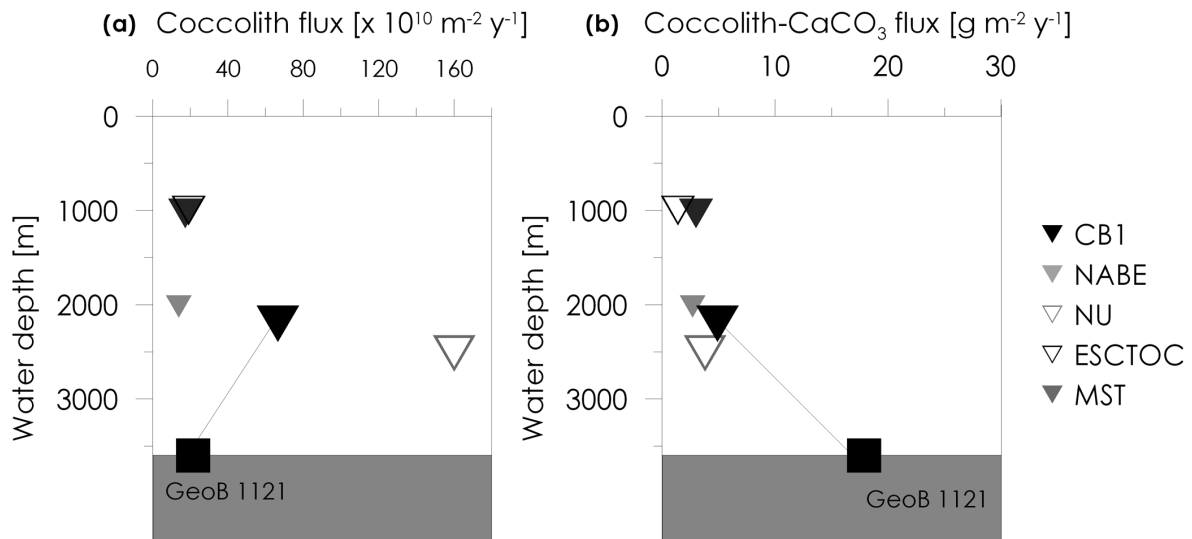
*al.* (1999b). Thus, high sinking speeds, as a consequence of the high organic matrix loading, may have slowed/stopped the degradation and disintegration of holococcospheres. In spring, the time of strong mixing and upwelling, environmental factors may be unfavourable for the settling (and/or production) of the holococcoliths.

### 5.3 Upwelling regions – a comparison

For different upwelling regions, the comparison of yearly mean coccolithophore flux shows similar values. The mean flux off Cape Blanc (CB1 -  $65 \times 10^{10}$  liths  $\text{m}^{-2} \text{y}^{-1}$ ) lies between the range of the Somalian upwelling flux ( $17 \times 10^{10}$  liths  $\text{m}^{-2} \text{y}^{-1}$  - sediment trap MST-9: Broerse *et al.*, 2000) and that of the Namibian upwelling ( $160 \times 10^{10}$  liths  $\text{m}^{-2} \text{y}^{-1}$  - sediment trap NU: Romero *et al.*, 2002a). The mooring stations of CB and MST-9 lay in comparable oceanographic regions. They were influenced by upwelling and/or filaments that developed between the coastal upwelling and the open ocean, but were not moored in the coastal upwelling itself. The NU sediment trap was moored closer to the coastal upwelling cell. In oligotrophic sites, a flux of  $14 \times 10^{10}$  liths  $\text{m}^{-2} \text{y}^{-1}$  (sediment trap NABE-48: Ziveri *et al.*, 2000) and  $19 \times 10^{10}$  liths  $\text{m}^{-2} \text{y}^{-1}$  (sediment trap ESTOC: Sprengel *et al.*, 2000) were reported (Figure 14a).

Milliman (1993) estimated the carbonate export production to range between  $2\text{--}5 \text{ g m}^{-2} \text{y}^{-1}$  in the central ocean gyres and  $30\text{--}40 \text{ g m}^{-2} \text{y}^{-1}$  in the eastern upwelling zones. The mooring stations off Somalia (MST-9), Namibia (NU) and Mauritania (CB) have a yearly carbonate export production of  $22$ ,  $21$  and  $22 \text{ g m}^{-2} \text{y}^{-1}$ , respectively. All mooring stations lay close to the upwelling, revealing high carbonate export, due to the influence of the upwelling. The mooring station of NABE 48 (North Atlantic), with a yearly carbonate flux of  $11 \text{ g m}^{-2}$ , resembles an oligotrophic site, as do sediment traps off the Canary Islands (ESTOC), with  $8.7 \text{ g m}^{-2}$ .

Comparing the yearly mean carbonate flux derived from coccoliths, these trap sites show values in the same range:  $4.9 \text{ g m}^{-2} \text{y}^{-1}$  for CB1,  $3.8 \text{ g m}^{-2} \text{y}^{-1}$  for the upwelling off Namibia (NU),  $3.6 \text{ g m}^{-2} \text{y}^{-1}$  for the Canary Islands (Sprengel *et al.*, 2000),  $3 \text{ g m}^{-2} \text{y}^{-1}$  for the upwelling off Somalia (MST 9: Broerse *et al.*, 2000), and  $2.7 \text{ g m}^{-2} \text{y}^{-1}$  for the oligotrophic site (NABE-48: Ziveri *et al.*, 2000). However, the proportion of coccolith-carbonate to the total carbonate export differs significantly. In the upwelling region off NW and SW Africa, the contribution of coccolith-carbonate to the total carbonate is the same, at 18%, whereas off Somalia, it accounts for 13%, and around the Canary Islands, 41%. With 24% of the total carbonate contribution from coccoliths, the mooring location of the North Atlantic (NABE-48) lies between these.



**Figure 14:** Comparison of average coccolith flux/accumulation (a) and average coccolith-carbonate flux/accumulation (b) recorded in sediment traps and surface-sediments in the region

### 5.3 Export production versus surface-sediment accumulation

A good correlation between coccolith flux and accumulation in the sediment can be seen (Figure 14), despite a slight discrepancy in numbers and species composition (Figure 15). In general, coccolith flux recorded in the trap is slightly higher than coccolith accumulation in the underlying sediment. The annual coccolith flux at 2200m water-depth was about three-fold the coccolith accumulation rate in the sediment (Figure 14). The higher coccolith flux in the sediment trap samples is accounted for by higher abundances of more fragile and small-sized taxa, such as *Syracosphaera* spp. (Figure 15). Absence of these more delicate coccoliths from the sediment might be due to enhanced dissolution at the sediment-water interface, and to destruction due to mechanical impact. Nevertheless, coccolith and coccolith-carbonate flux and accumulation rates (Figure 14), as well as the relative contributions of single species (Figure 16), are of the same order of magnitude. The slight discrepancies may be a combination of transport and dissolution processes. Furthermore, the flux derived from the sediment trap displays one seasonal cycle, with distinct hydrographic and climatic conditions, whereas the sediment sample reveals an integrated picture of several hundred years, thus seasonal characteristics are likely overprinted by interannual variability. The higher coccolith-derived carbonate accumulation of the sediment compared to the sediment trap resulted from the enrichment of the sediment by large, massive and carbonate-rich taxa, such as *Helicosphaera* spp. and *Calcidiscus*

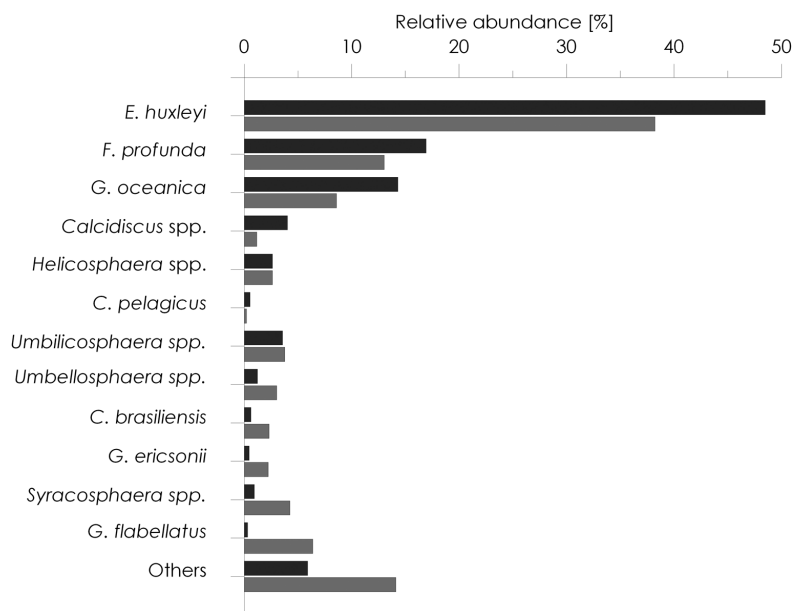
*leptoporus* (Figure 16).

Compared to other upwelling regions (off SW Africa, generally, the contribution of coccoliths is 23% (Boeckel, 2002) and in the Canary Islands region 26% (Sprengel *et al.*, 2002)), the contribution of coccoliths to the total carbonate content of the sediment (15%) is relatively low off Cape Blanc.

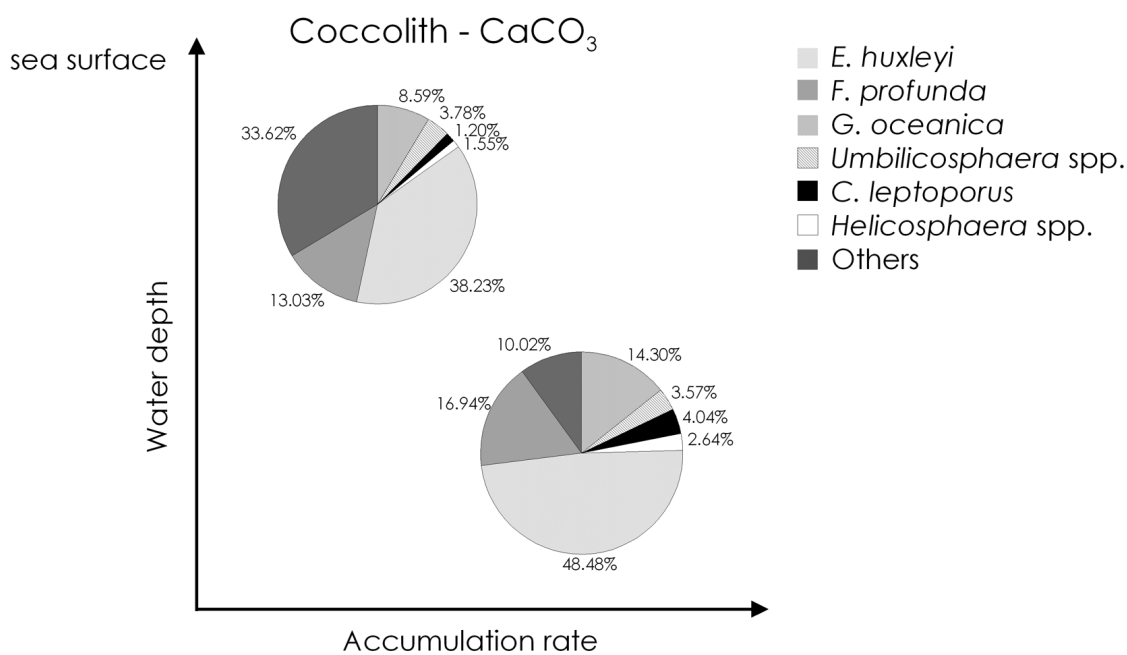
### 6. Conclusions

Our study of settled coccolithophore assemblages from a year-round (1988-89) moored sediment trap (CB1) off NW Africa revealed the following main facts:

The coccolith flux shows seasonal changes, with high values in summer, a peak in winter and minima in fall and



**Figure 15:** Comparison of coccolith relative abundance between sediment trap samples (light grey) and underlying Holocene surface-sediment samples (dark grey)



**Figure 16:** Main species contributing to the coccolith-derived carbonate flux, presented as relative abundances. The mean coccolith-derived carbonate flux is slightly smaller in the trap

spring. The relatively diverse assemblage consisted of 63 heterococcolith-bearing species, one species in its hetero-/holococcolith-bearing state, and one species bearing holococcoliths only.

Minimum coccolith flux corresponds to maximum SST, and high flux occurs with low SST. Maximum coccolith export reflects an oceanic setting, in which influencing factors, such as wind strength, upwelling intensity, nutrient content and light availability in the surface-waters were at their respective medium values.

Respective maximum fluxes of diatoms, coccolithophores and silicoflagellates occurred in different seasons, starting with diatoms in fall, followed by coccolithophores in winter, and finally silicoflagellates in later winter. It is concluded that diatoms reacted first to additional nutrients, whereas coccolithophores dominated after some depletion of these, when neither high nor low hydrographical and climatic conditions prevailed. The complex setting of the NW African upwelling, nevertheless, represents an example of Margalef's (1978a) Mandala and its extension by Balch (2004).

*Emiliana huxleyi* was the dominant species. Morphometric measurements revealed a unimodal distribution of *E. huxleyi* coccoliths. The majority of the specimens belong to *E. huxleyi* type A and only a few specimens to type C.

Species of the lower photic zone, *Florisphaera profunda* and *Gladiolithus flabellatus*, increased in winter and were most abundant during conditions of minimum insolation and minimum water turbulence. The sizes of the nanoliths of *F. profunda* have a bimodal distribution pattern, indicating two varieties of *F. profunda*, with var. *elongata* forming larger coccoliths.

*Calcidiscus leptoporus*, *C. leptoporus* small morphotype and *C. quadriperforatus* reveal different seasonal abundance patterns, with *C. leptoporus* dominating and strongly fluctuating in abundance during the year, indicating a broader tolerance to the changing environmental conditions. *C. quadriperforatus* and *C. leptoporus* small morphotype show similar seasonal patterns, with high flux in summer and low in fall/winter. However, *C. quadriperforatus* reaches its maximum flux earlier in summer. The assumed addition of nutrients seems to favour their occurrence.

Decreased relative abundances of *Gephyrocapsa oceanica* and *G. muelleriae* indicate the reduced influence of cold, nutrient-enriched and turbulent waters. The documented decrease in wind strength supports this assumption. The flux of holococcoliths parallels the measured lithogenic flux. Off Cape Blanc, the lithogenic material appears to be coupled with the organic carbon flux. The high sinking speeds, as a consequence of the high organic matrix loading, may slow or stop the degradation and disintegration of holococcoliths.

The mean coccolith-derived carbonate, based on broad morphometric measurements, adds up to  $4.9 \text{ g m}^{-2} \text{ y}^{-1}$ . Compared to other oceanic regions, the mooring location represents a meso-eutrophic environment. The proportion of coccolith carbonate to the total carbonate production accounts for 18% in the upwelling region of NW Africa. This is within the range of the upwelling region of SW Africa, but is less than that of the Canary Island region (41%).

A good correlation between the coccolith flux and the accumulation in the underlying Holocene surface-sediment can be seen. Nevertheless, with respect to species composition, relative and absolute abundances, small discrepan-

cies were observed, with a slightly higher abundance of more fragile and small-sized coccoliths in the sediment-trap samples. In the underlying surface-sediment, coccolith-derived carbonate accounts for 15% of the total carbonate flux. This is less than that of the upwelling region off SW Africa (23%) and of the Canary Island region (26%).

## Acknowledgements

We are grateful to Dr. B. Boeckel for the intensive discussions and valuable suggestions on the manuscript. The comments of Drs M. Geisen, B. De Bernardi, J. Lees, and a further anonymous reviewer of an early version of the manuscript, were thankfully considered. M. Krysta is thanked for technical support in preparation of the samples. This research was funded by the Deutsche Forschungsgesellschaft as part of the European Graduate College 'Proxies in Earth History' EUROPROX, Bremen Universität.

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